Understanding growth of East Africa highland banana: experiments and simulation

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This research was conducted under the auspices of the C.T. de Wit Graduate School of Production Ecology and Resource Conservation.

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Thesis

submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus
Prof. Dr. M.J. Kropff,
in presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Tuesday 2 March 2010
at 4 p.m. in the Aula.

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Understanding growth of East Africa highland banana: experiments and simulation, 198 pages.

Thesis, Wageningen University, Wageningen, NL (2010)
With references, with summaries in English and Dutch

ISBN: 978-90-8585-550-7

Dedication

To my dear family, living and deceased, with deep gratitude for their support. Most especially to my mother, wife and sons for their love, encouragement, patience and sacrifices during the study period.

Prayer

Glory to him who is able to give you the strength to live according to the Good news which I preach, and in which I proclaim Jesus Christ, the revelation of a mystery, kept secret for endless ages, but now so clear that it must be broadcast to the peoples everywhere, bringing them to the obedience of faith. This is what scripture predicted and it is all part of the way the eternal God wants things to be. ***He alone is wisdom.*** *Give glory therefore to him through Jesus Christ for ever and ever. Amen*

Romans 16:25−27.

Abstract

East Africa Highland banana yields on smallholder farms in the Great Lakes region are small (11−26 Mg ha^{-1} $cycle^{-1}$ in Uganda, 21−43 Mg ha^{-1} $cycle^{-1}$ in Burundi and 25−53 Mg ha^{-1} $cycle^{-1}$ in Rwanda). The major causes of poor yields are declining soil fertility and soil moisture stress. In order to improve production, knowledge on highland banana physiology, growth patterns and response to fertilization is important, to establish the potential yield of the crop, to quantify the yield gaps between potential and actual yield, and to explore options for closing the yield gaps.

Measurements of plant morphological characteristics, radiation interception and biomass (by destructive harvesting) were taken in experimental fields in central and southwest Uganda. Results showed that total leaf area can be estimated by using height and girth (used to estimate middle leaf area) and number of functional leaves. The light extinction coefficient, *k* determined from photosynthetically active radiation (PAR) measurements over the entire day was 0.7. Banana plants partitioned more dry matter (DM) to the leaves during first phase of vegetative growth, with the pseudostem becoming the dominant sink later with 58% of total DM at flowering, and the bunch at harvest with 53% of the total DM. Changes in dry matter partitioning influenced the allometric relationships between above-ground biomass (AGB in kg DM) and girth (cm), the relationship following a power function during the vegetative phase ($AGB = 0.0001\ (girth)^{2.35}$), and exponential functions at flowering ($AGB = 0.325\ e^{0.036\ (girth)}$) and at harvest ($AGB = 0.069\ e^{0.068\ (girth)}$). This thesis shows that allometric relationships can be derived and used to estimate biomass and bunch weights.

In fertilizer trials, yield increases above the control (13.0 Mg ha^{-1} yr^{-1}) ranged from 2.2−11.2 Mg ha^{-1} yr^{-1} at Kawanda, to more than double at Ntungamo, 7.0−29.5 Mg ha^{-1} yr^{-1} (control 7.9 Mg ha^{-1} yr^{-1}). The limiting nutrients at both sites were in the order K>P>N. Differences in soil moisture availability and texture resulted in higher yields and total nutrient uptakes (K>N>P) at Ntungamo, compared with Kawanda. Per unit dry matter yield, highland bananas take up a similar amount of N (49.2 kg finger DM kg^{-1} N), half the amount of P (587 kg finger DM kg^{-1} P), and five times the amount of K (10.8 kg finger DM kg^{-1} K), when compared with cereal grain. Calibration results of the static nutrient response model QUEFTS using data from Ntungamo were fair (R^2 = 0.57, RMSE = 648 kg ha^{-1}). The calibrated QUEFTS model predicted yields well using data from Mbarara southwest Uganda (R^2 = 0.68, RMSE = 562 kg ha^{-1}).

A new dynamic radiation and temperature-driven growth model, LINTUL BANANA 1 was developed to the compute potential yields of East Africa highland banana. The model considers (i) the physiology of the highland banana crop; (ii) the plant dynamics (i.e. three plant generations, Plant 1, 2 and 3 at different stages of growth constituting a mat); and (iii) three canopy levels formed by the leaves of the three plants. Average computed potential bunch dry and fresh matter were slightly higher at Ntungamo (20 Mg ha^{-1} DW; 111 Mg ha^{-1} FW), compared with Kawanda (18.25 Mg ha^{-1} DW; 100 Mg ha^{-1} FW), and values compared well with banana yields under optimal situations at comparable leaf area index values (20.3 Mg ha^{-1} DW; 113 Mg ha^{-1} FW). Sensitivity analysis was done to assess the effects of changes in parameters (light use efficiency, *LUE*; the light extinction coefficient, *k*; specific leaf area, *SLA*; the relative death rate of leaves, r_d; relative growth rate of leaf area, *RGRL*; and the initial dry matter values) on bunch dry matter, leaf dry matter and leaf area index (*L*) at flowering. Sensitivity results for Kawanda and Ntungamo showed that changes in LUE1 resulted in more than proportional increase in bunch DM (1.30 and 1.36), a higher leaf DM (0.60 and 0.67) and *L* at flowering (0.60 and 0.67). Changes in r_d1 values reduced bunch dry matter, leaf dry matter and *L* at flowering. Changes in SLA1 reduced only leaf DM, whereas both leaf DM and *L* at flowering were reduced by changes in *k*1 at both sites. Initial dry matter values had a small effect (sensitivity < 0.0263) for bunch DM, leaf DM and *L* at flowering. Based on the model results, it is clear that the potential yield of East Africa highland bananas is more than 18 Mg ha^{-1} DW. Management options that increase LUE and reduce the relative death rate of leaves, and improvements in parameters related to light interception (SLA and *k*) are important to increase yield.

Key words: leaf area; radiation interception; QUEFTS model; fertilizer recovery fractions; nutrient mass fractions; crop growth; calibration; validation; radiation use efficiency; sensitivity analysis

Contents

CHAPTER 1

General introduction

1.1. Background

Bananas and Plantains (family *Musaceae*) are rhizomatous, monocotyledonous herbs grown in the tropics and sub-tropics, where they are adapted to a wide range of temperature and water supply regimes (Stover and Simmonds, 1987). Their fruits are important staple and cash crops for about 100 million people in the Great Lakes region (i.e. Uganda, Tanzania, Rwanda, Burundi, parts of eastern Democratic Republic of Congo, and Bukoba and Kilimanjaro areas of Tanzania). Globally, bananas are the fourth most important food commodity after rice, wheat and maize in terms of gross value of production. In Uganda, the East Africa highland cooking bananas (*Musa* spp., AAA-EAHB) locally known as 'Matooke' is the most abundantly cultivated crop and rank highest among the food crops (NARO, 2000). The Ganda and Soga people to the north of Lake Victoria, the Konjo and Bamba in the Rwenzori region and the Gishu people around Mount Elgon have traditionally exclusively relied on bananas (Allan, 1965). Amongst the Ganda, it is often stated that a meal without bananas is no meal.

Per capita banana consumption is estimated at about 0.7 kg per person per day. Cooking banana fingers are peeled to obtain the pulp, which is steamed in banana leaves, and then smashed to form a mash that is consumed with a sauce (e.g. vegetable, fish or beef). The nutritional value of cooking highland banana is 4.04 g crude protein, 0.64 g crude fat and 367.62 kcal per 100 g of dry weight (Muranga et al., 2007). It is estimated that Uganda produces over 10% of the world's bananas and plantains, with only 0.02% exported. Cultivation is mainly on plots less than 0.5 ha around the homestead, characterized by high cultivar diversity (4-22 per farm), but medium scale plantations (> 1 ha) are common in western Uganda (Gold et al., 1998; Gold et al., 1999; Bagamba, 2007).

Bananas are believed to have originated in Indochina and South East Asia, where the earliest domestication is considered to have occurred, and the greatest diversity of wild Musa species (*Musa acuminata* – AA and *Musa balbisiana* - BB) is found today (Simmonds, 1962). Hybridizations between the various sub-species of the polymorphic species of *Musa acuminata* gave rise to a variety of AA diploid cultivars. Through chromosome restitution during meosis, diploid AA gave rise to triploid AAA types. First introductions of bananas to sub-Saharan Africa are thought to have occurred after the birth of Jesus Christ, through North and Eastern Africa by Arab traders (Stover and Simmonds, 1987; Vansina, 1990; Price, 1995). East Africa highland bananas are diverse, unique to this region and are thought to have arisen as a result of somatic mutations (Simmonds, 1966). Using plant morphological characteristics, Karamura (1998)

characterized and classified over 130 highland banana cultivars into five major clone sets; Musakala, Nakabululu, Nakitembe, Nfuuka and Mbidde (brewing type). The Musakala clone set includes cultivars like Kisansa, Musakala, Mudwale and Mpologoma which are popular due to their large bunches with loosely packed clusters. World wide, the vast majority of bananas grown today are triploids – AAAs, with the AABs and ABB being starchy and tetraploids (e.g. AAAA) for dessert purposes.

1.2. Morphology and growth requirements

A banana plant consists of the corm (true stem) from which fibrous roots (primary, secondary and tertiary), the pseudostem and the leaves grow. Plant height varies with the cultivar, ranging from 2 m for dwarf cultivars to 6 m for tall cultivars. The corm is differentiated into the central cylinder (vascular bundles) from which roots develop and an outer cortex (parenchyma cells). The terminal growing point of the corm is a flattened dome, with leaves formed around it in spiral succession (Purseglove, 1988). The enveloping leaf sheaths form the pseudostem that supports the leaves. The midribs and petioles support the lamina, which intercepts photosynthetically active radiation (PAR). The centre of the meristem (flattened dome) is transformed into the inflorescence (bunch) after production of 25−40 leaves. During leaf production, a vegetative bud is produced 180° opposite each leaf, on the outer surface of the cortex, a few of which later develop into suckers. Sword suckers have a strong attachment to the mother plant and develop a thick rhizome of their own, which can be used for propagation. In the early stage of development, their leaves are small, thin and bract like structures, later developing into broad sword leaves and eventually large functional leaves (Robinson, 1996). The mother plant and the suckers form a *'mat'*. The mat thus consists of plants at different stages of growth developing at their own rate. At bunch maturity, the shoot is cut away and the selected lateral buds or suckers form the next crop cycle.

Bananas require a deep, well drained retentive loam soil with high humus content and good water holding capacity for satisfactory growth (Purseglove, 1988). However, bananas also grow well on lighter sandy soils with good soil organic matter content (Delvaux, 1995; Stover and Simmonds, 1987). In Uganda, bananas are grown on diverse soil types from the relatively heavy Ferralsols, Nitisols and Acrisols mainly in the Lake Victoria basin (Zake et al., 2000) to Fluvisols and Plinthosols in mainly Tororo and Pallisa (Bekunda et al., 2002). Generally, bananas require an abundant supply of nutrients, compared with other crops (Turner, 1985; Robinson, 1996; Purseglove, 1988),

particularly potassium and nitrogen. Simmonds (1962) reported that most banana species grow best in open sun provided moisture is not a limiting factor. As a rule of thumb, soil water should not be allowed to fall below 20−30% of the total available water (TAW) if optimum growth is to be maintained (Robinson and Bower, 1987). Uniformly warm (optimum air temperature of about 25−27 °C) conditions are important for optimal growth (Turner and Lahav, 1983).

1.3. Production problems in banana based farming systems of Uganda

Reduced productivity and loss of sustainability (i.e. low yields and reduced mat life) have been widely reported among highland banana farmers especially in the central part of Uganda (Bekunda and Woomer, 1996; Bekunda, 1999). For example, banana yields are reported to have declined from 8.4 Mg ha^{-1} yr^{-1} in 1970 to 5.6 Mg ha^{-1} yr^{-1} in the late 1980s (Gold et al., 1999). Irrespective of the accuracy of the yield estimations and the extent of yield decline, it is clear that the widely reported actual banana yields on smallholder farms (5−30 Mg ha^{-1} yr^{-1}) are far below the estimated potential yields (> 70 Mg ha^{-1} yr^{-1}). Low yields are attributed to poor soil fertility, moisture stress, pest pressure (banana weevil - *Cosmopolites sordidus*; nematodes - *Radopholus similis*, *Helicocotylenchus multicinctus* and *Pratylechus goodeyi*), diseases (black sigatoka - *Mycosphaerella fijiensis*, banana wilt, banana streak virus, banana bacterial wilt) and poor crop husbandry (Gold et al., 1999; NARO, 2000).

Soils under bananas are generally old and highly weathered (Zake et al., 2000). Nutrient availability largely depends on mineralization of soil organic matter (Sanchez et al., 1989). Although the application of residues (i.e. dead leaves, leaf sheaths, pseudostems and banana peels), grasses (swamp, spear and napier) and crop residues (maize stover, soybean residue, bean residue) is a traditional practice in the banana based farming systems of Uganda (Wortmann and Kaizzi, 1998), the quantities applied are usually not adequate to sustain soil fertility (Nyombi et al., 2006). Nutrient resource utilization often results into large gradients in crop performance from backyard gardens to distant plots (Wortmann and Kaizzi, 1998). Bananuka and Rubaihayo (1994) reported 66% yield increase when moving from distant to homestead plots. The use of inorganic fertilizers in banana plantations is not a common practice in Uganda due to lack of awareness and high prices. Bekunda and Woomer (1996) and Sseguya et al. (1999) noted that 1−5% of the banana farmers in the Lake Victoria basin use mineral fertilizers. Despite the limited inputs of nutrients, increasing urbanization continues to put pressure

on the traditional banana based farming systems. Banana bunches and leaves are increasingly exported from rural areas to urban centres. The banana bunches, especially the peels, are particularly rich in potassium and exportation of this element, which is crucial in banana production, is a major concern (Baijukya and Steenhuijsen-Piters, 1998).

Bananas are known to have a high moisture demand, which is attributed to both the large plant fresh biomass and the broad leaves (Robinson, 1996), although Turner et al., (2008) argue that this belief has no strong physiological basis. In addition, they possess a shallow rooting system (90% of the root biomass is found in the top 30 cm of the soil) and banana roots have low efficiency to extract water from drying soils (Kashaija et al., 2004; Landon, 1991). Thus, they are sensitive to drought. Estimates of annual evapotranspiration (ET) of banana plantations range from 1200−2690 mm yr^{-1} (Robinson and Alberts, 1989). Most of the banana growing regions in Uganda recieve between 1000 and 1300 mm of rainfall per annum, with dry spells from June to July and from December to February. Okech et al. (2004) reported that low annual rainfall (678 mm) reduced yields by about 50% in southwest Uganda. Nonetheless, moisture stress has received relatively little attention in banana research in Uganda.

1.4. Banana growth modelling

Banana systems can be studied in two ways; experimentally and theoretically. The theoretical way involves the development of banana growth models based on the underlying process. The model and its components can be evaluated using especially designed experiments. Turner (1981) highlighted the importance of dynamic simulation models in integrating the complex systems of the banana plant, development, environment and soil. Kooman and Jones (1995) modified a relatively simple general crop growth model developed by Spitters and Schapendonk (1990) and used it to simulate banana growth for a single crop cycle in Honduras. The standard crop growth simulator model (STICS) which simulates crop growth as well as soil water and nitrogen balances driven by daily climate data, was adapted and used to simulate banana growth in the French West Indies (Brisson et al., 1998). STICS can not be used to estimate potential production and does not capture banana plantation dynamics. The SIMBA-POP model based on the cohort population concept was built and used to predict phenological patterns of the population and harvest dynamics for Cavendish Grand Nain in the West Indies (Tixier et al., 2004). The CENTURY model (plant-soil environmental) developed by Parton et al. (1987) to simulate plant growth and organic matter dynamics in temperate regions was

adapted and used to simulate East Africa highland banana growth and carbon dynamics, giving not very good results (Woomer et al., 1998). It is necessary to develop a new physiological banana model that captures plantation dynamics (i.e. 2 or 3 plants at different stages of growth), which can be used to estimate potential production. Such a model should allow modifications to be made in order to simulate water, potassium and nitrogen-limited production.

1.5. Approach to modelling East Africa highland banana growth

As a first step to improve banana growth and yields, the potential yield as determined by radiation, temperature, crop physiology and canopy characteristics, with water and nutrients not limiting, and in absence of diseases, pests and weeds have to be determined (c.f. Lövenstein et al., 1995) – (Figure 1).

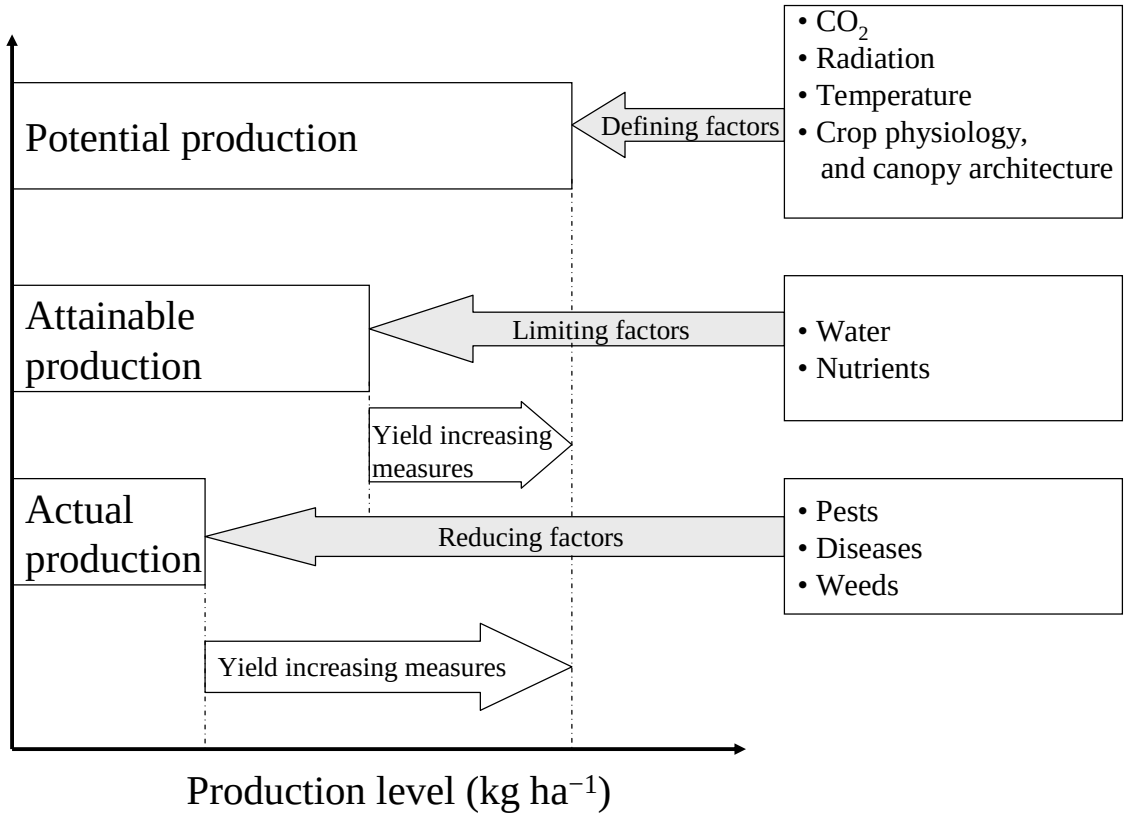

Figure 1. Production situations with corresponding yields. Source: Lövenstein et al., 1995.

This will enable quantification of the loss in banana yield that can be attributed to yield limiting factors (nitrogen, potassium phosphorus and water) and yield reducing factors (pests, diseases and weeds). The difference between potential and actual yields can be used to quantify the yield for a particular location.

1.6. Goal and Objectives of the study

This study employs a systems approach to understanding banana production in Uganda. It aims to identify opportunities to increase actual yields on smallholder farms through improved crop management and to assist banana breeders with optimum phenotype recommendations.

The specific objectives were:

1. to develop methodologies for total plant leaf area estimation using simple morphological attributes like girth and height and for PAR interception measurement; generate allometric relationships for bunch yield and biomass estimation; estimate the light extinction coefficient, k for highland banana and to study dry matter partitioning in highland bananas during growth.
2. to study the effects of K, N and P fertilization on growth, biomass production and economic yield of highland bananas, calibrate and test the model QUEFTS for highland banana.
3. to develop a simulation model to better understand and estimate how potential banana yield is attained in highland banana.
4. to suggest improvements on the model to allow the simulation of water, potassium and nitrogen-limited situations.

1.7. Outline of the thesis

Chapter 2 details methodology for estimating area of a single leaf and total plant leaf area using simple morphological attributes like girth and height. A simple method for PAR interception measurement in highland bananas was developed and evaluated. Allometric relationships for biomass estimation and between proportions partitioned to different parts and simple attributes e.g. girth are generated.

Highland banana response (biomass production and yield) to mineral fertilizers is described in Chapter 3. The major nutrients limiting production are identified and the possibilities of using mineral fertilizers to improve yields on smallholder farms explored.

The results from the trial at Ntungamo are summarised in the model QUEFTS. A new dynamic simulation model, LINTUL BANANA 1 with basic processes such as radiation interception, conversion of radiation into dry matter, distribution of dry matter within the plant and dry matter transfers between the plants was developed for potential production situations and is presented in Chapter 4.

In Chapter 5, the steps that need to be taken to improve the capabilities of the growth model LINTUL BANANA 1 and its utility as a tool are given. The main focus is improving the tool to simulate water and nutrient-limited production. This should lead to increased understanding of banana growth, and the realization of crop's potential. A synthesis of the results presented in the previous chapters is made in Chapter 6. Emphasis is placed on increasing banana yields, which would help close the gaps between potential, and water and nutrient-limited yields. The response to fertilizers and the need to increase fertilizer recovery fractions in order to reduce the amount of fertilizer required for a target yield (Chapter 3) are discussed. The knowledge gained from the crop growth modelling exercise (i.e. LINTUL BANANA 1) and the contribution of the model to breeding and crop management are discussed. Finally, recommendations for future research are made.

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CHAPTER 2

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

This chapter has been published as:

K. Nyombi, P.J.A. van Asten, P.A. Leffelaar, M. Corbeels, C.K. Kaizzi, K.E. Giller, 2009. Allometric growth relationships of East Africa highland bananas (*Musa* spp., AAA-EAHB) cv. Kisansa and Mbwazirume. Annals of Applied Biology 155, 403−418.

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

2.1. 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 parameterising 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.

2.2. Materials and methods

2.2.1. 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.

2.2.2. 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:

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

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.

2.2.3. 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:

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

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.

2.2.4. 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.

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).

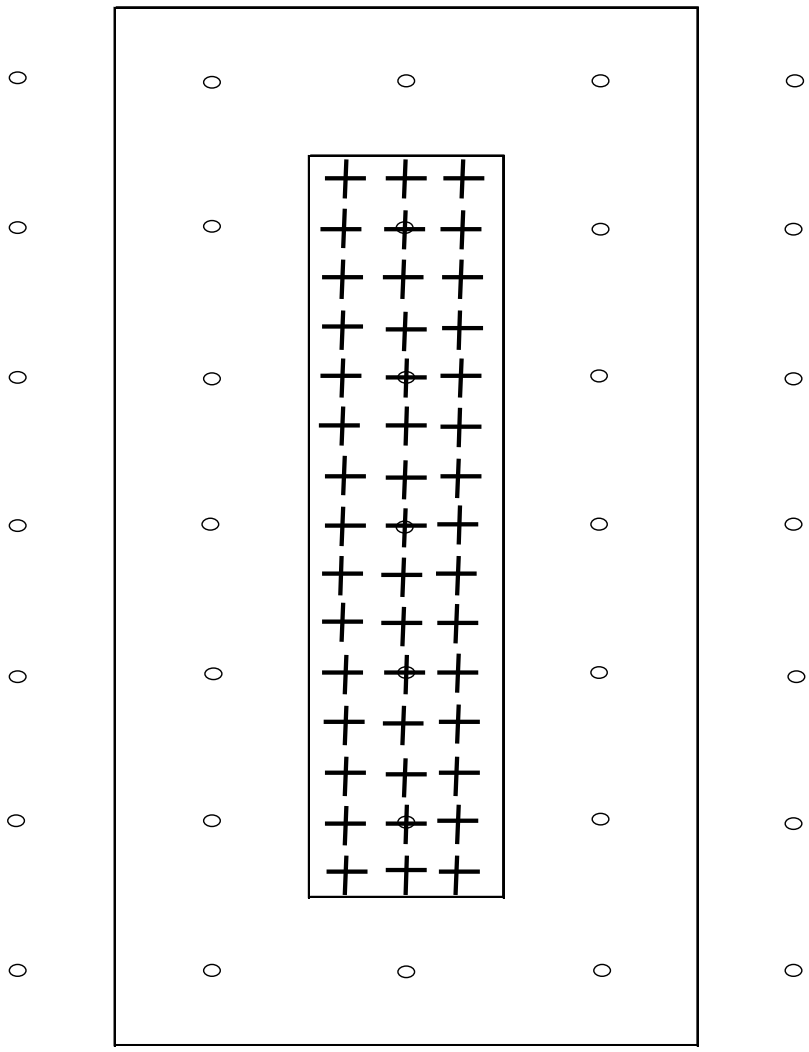

Figure 1. Scheme used to measure PAR in experimental plots of 35 plants (315 m^2) at Kawanda, central Uganda and Ntungamo southwest Uganda. Five plants in the inner rectangle were used for PAR measurements, whereas leaf area data were collected from the 21 plants in the outer rectangle.

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.

2.3. Results

2.3.1. 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 at flowering was 68 cm with a reduction of 12% in girth from flowering to harvest.

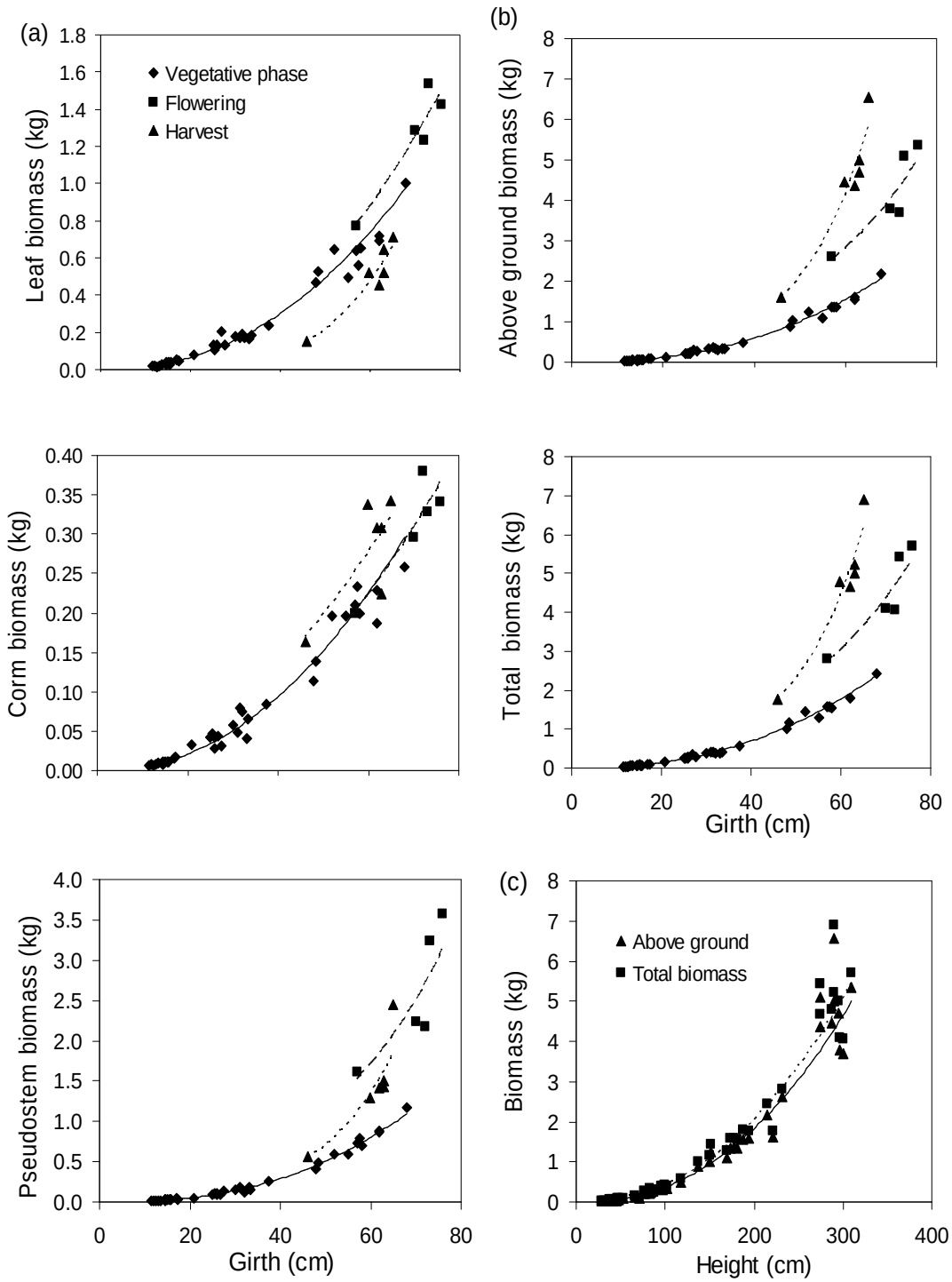

Figure 2. Relationships during the vegetative phase, at flowering and at harvest between leaf, corm and pseudostem biomass with girth – left top to bottom (a), above ground biomass, total biomass and girth (b) and biomass (total and above ground) and height (c) – right top to bottom, for banana plants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

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:

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

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).

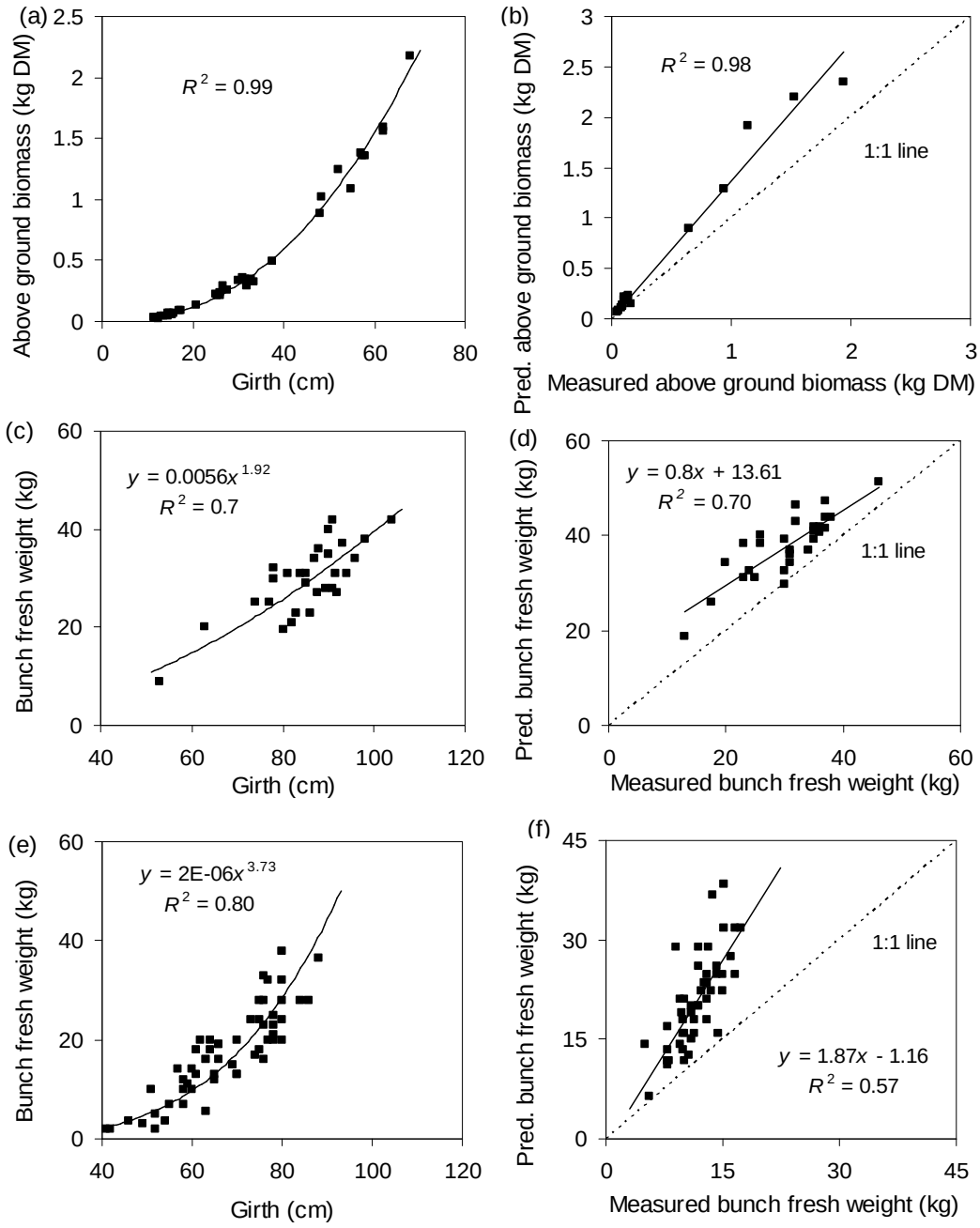

Figure 3. (a) The allometric relationships for above ground biomass estimation during the vegetative phase for banana plants (cv. Kisansa) sampled at Kawanda, central Uganda. (b) the relationship between measured and predicted above ground biomass using the relationship in (a). (c) the allometric equation 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.

2.3.2. 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.

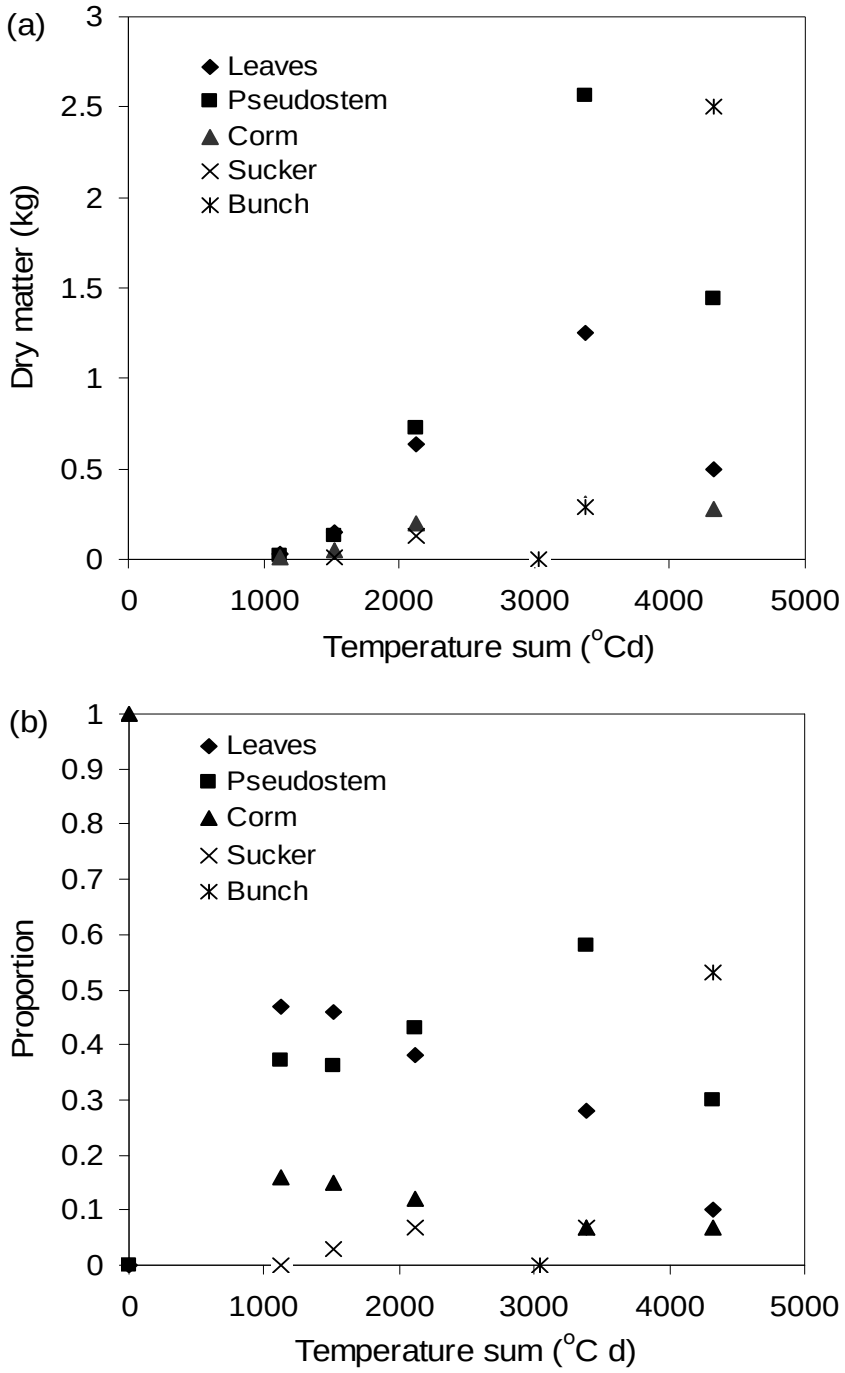

Figure 4. Plant component dry weights (a) and proportions (b) for corm-derived banana plants (cv. Kisansa) sampled at Kawanda, central Uganda, as a function of physiological age, expressed as temperature sum (TSUM). The vegetative phase occurs 0−3034 °C d and floral phase 3034−4326 °C d. At 3383 °C d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

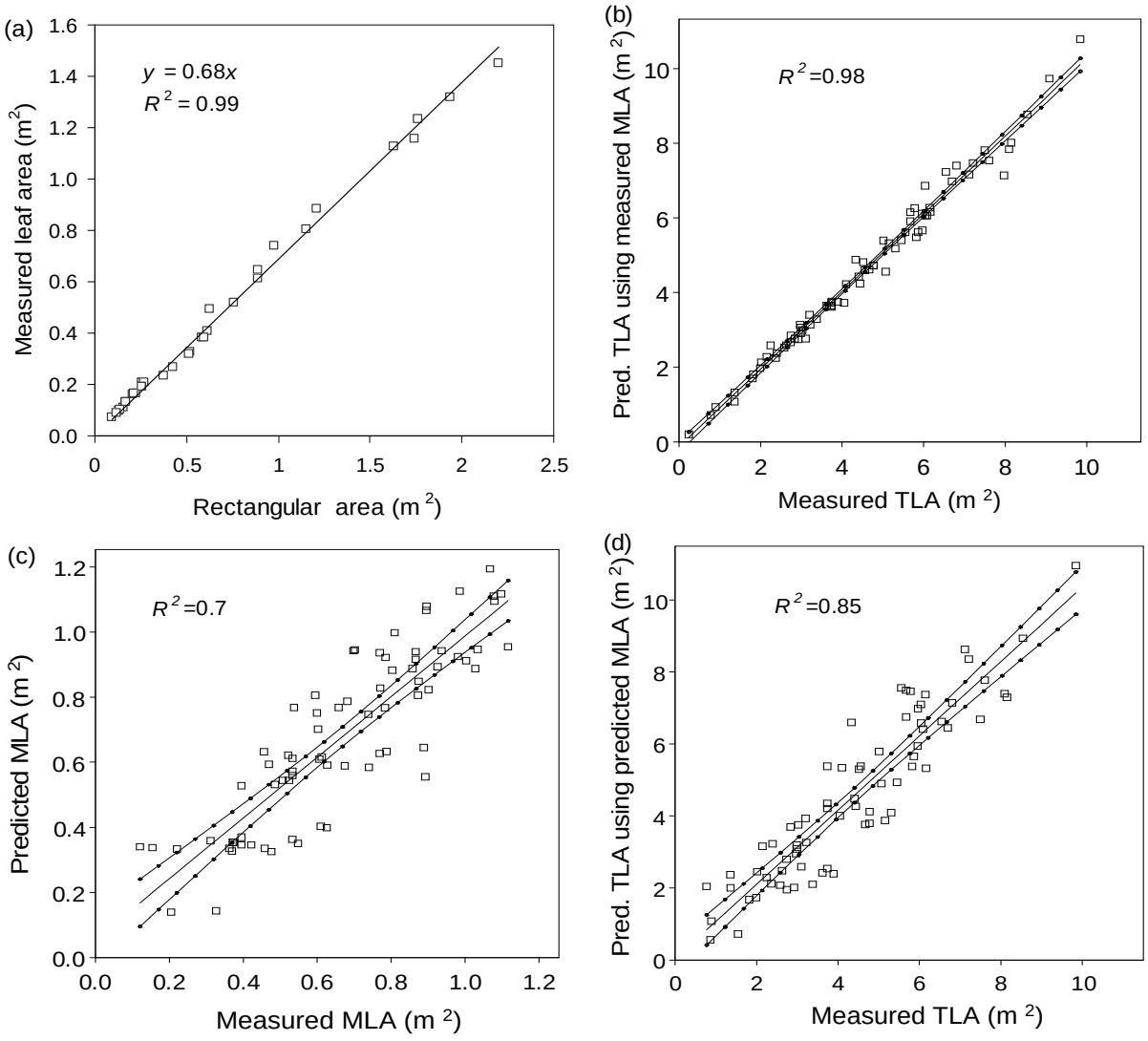

Figure 5. Relationship between measured leaf area and rectangular area (a). Fitted and observed relationships with 95% confidence limits for relationships between measured and predicted total leaf area (measured MLA (middle leaf area) x number of functional leaves) (b), measured and predicted middle 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).

2.3.3. 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).

2.3.4. 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.

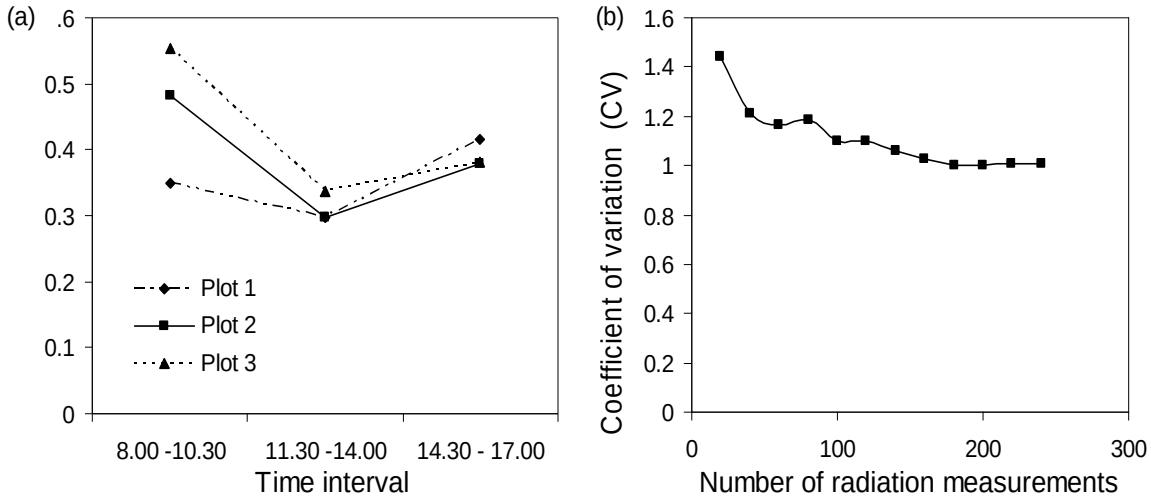

Figure 6. Relationships between the fraction of radiation intercepted and time interval of measurement (a) and between the coefficient of variation and the number of radiation measurements for LAI = 2.67 (b) for measurements at Kawanda, central and Ntungamo, southwest Uganda.

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).

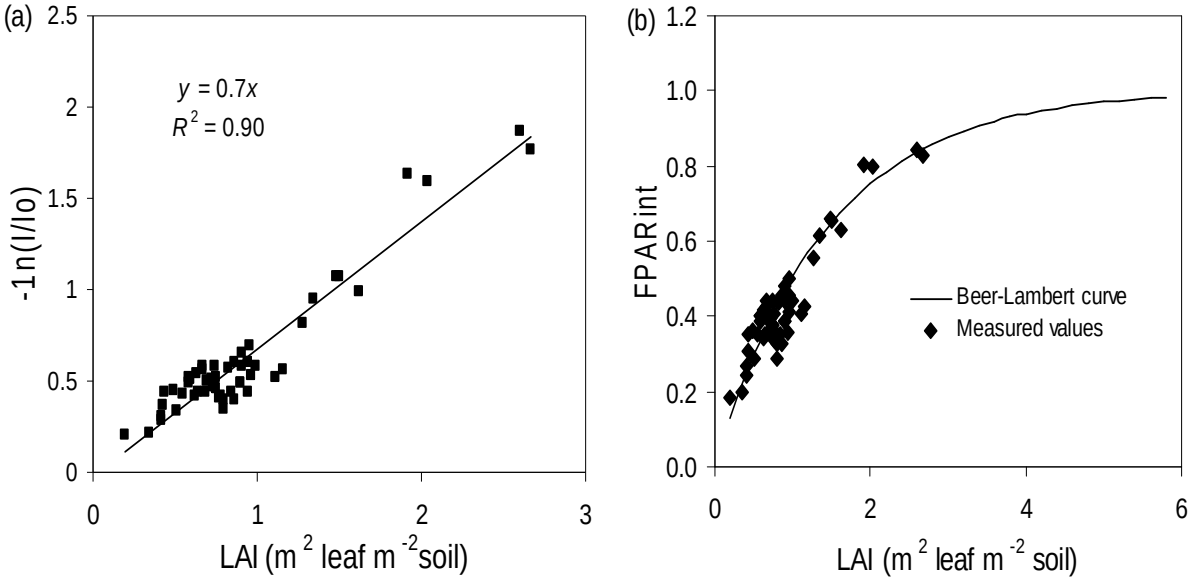

Figure 7. Relationships between the leaf area index and –ln (I/I_0) from which k was found by fitting as 0.7 (a) and the fraction of PAR intercepted – *FPARint* using the k from (a) - (b) from measurements at Kawanda, central and Ntungamo, southwest Uganda and Beer-Lambert curve. I is PAR below the canopy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

2.4. Discussion

2.4.1. 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.

2.4.2. 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.

2.4.3. 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.

2.4.4. 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.

2.5. 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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CHAPTER 3

Mineral fertilizer response and nutrient use efficiencies of East African highland banana (*Musa* spp., AAA-EAHB, cv. Kisansa)

This chapter has been accepted for publication as:

K. Nyombi, P.J.A. van Asten, M. Corbeels, G. Taulya, P.A. Leffelaar and K.E. Giller, 2009. Mineral fertilizer response and nutrient use efficiencies of East African highland banana (*Musa* spp., AAA-EAHB, cv. Kisansa). Field Crops Research.

Abstract

Poor yields of East African highland bananas (*Musa* spp., AAA-EAHB) on smallholder farms have often been attributed to problems of poor soil fertility. The effects of mineral fertilizers on crop performance were measured at two sites over two to three crop cycles; Kawanda in central Uganda and Ntungamo in southwest Uganda. Fertilizers were applied at rates of 0N−50P−600K, 150N−50P−600K, 400N−0P−600K, 400N−50P−0K, 400N−50P−250K and 400N−50P−600K kg ha^{-1} yr^{-1}. In addition 60Mg−6Zn−0.5Mo−1B kg ha^{-1} yr^{-1} was applied to all treatments, with the exception of the control plots which received no fertilizer. Fresh bunch mass and yield increased with successive cycles. Yield increases above the control ranged from 3.1−6.2 kg $bunch^{-1}$ (average bunch weight for all treatments 11.5 kg $bunch^{-1}$) and 2.2−11.2 Mg ha^{-1} yr^{-1} (average yield for all treatments 15.8 Mg ha^{-1} yr^{-1}) at Kawanda, compared with 12.4−16.0 kg $bunch^{-1}$ (average bunch weight for all treatments 14.7 kg $bunch^{-1}$) and 7.0−29.5 Mg ha^{-1} yr^{-1} (average yield for all treatments 17.9 Mg ha^{-1} yr^{-1}) at Ntungamo. The limiting nutrients at both sites were in the order K>P>N. Foliar nutrient mass fractions were below previously established Diagnosis and Recommendation Integrated System (DRIS) norms, with the smallest K mass fractions observed in the best yielding plots at Ntungamo. Total nutrient uptakes (K>N>P) were higher at Ntungamo as compared with Kawanda, probably due to better soil moisture availability and root exploration of the soil. Average N, P and K conversion efficiencies for two crop cycles at both sites amounted to 49.2 kg finger DM kg^{-1} N, 587 kg finger DM kg^{-1} P and 10.8 kg finger DM kg^{-1} K. Calibration results of the model QUEFTS using data from Ntungamo were reasonable (R^2 = 0.57, RMSE = 648 kg ha^{-1}). Using the measured soil chemical properties and yield data from an experiment at Mbarara in southwest Uganda, the calibrated QUEFTS model predicted yields well (R^2 = 0.68, RMSE = 562 kg ha^{-1}). We conclude that banana yields can be increased by use of mineral fertilizers, but fertilizer recovery efficiencies need to improve substantially before promoting wide-scale adoption.

Key words: QUEFTS model, recovery fractions, nutrient mass fractions, fertilizer recommendations

3.1. Introduction

East African highland cooking banana (*Musa* spp., AAA-EAHB) locally known as 'matooke' is a primary staple crop grown for food and sale by smallholder farmers in Uganda, Rwanda, Burundi, East DR Congo, and parts of Tanzania and Kenya. Uganda is the largest producer of highland bananas in the region, but its yields are reported to have declined (NARO, 2000), from 8.4 Mg ha^{-1} yr^{-1} in 1970 to 5.6 Mg ha^{-1} yr^{-1} fresh weight (FW) in the late 1980's (Ministry of Agriculture, Animal Industries and Fisheries, 1992; Gold et al., 1999). A recent study by Wairegi et al. (2008) reported average farm yields in Uganda of 15.6 Mg ha^{-1} yr^{-1} (range 9.7−25.5 Mg ha^{-1} yr^{-1} FW), but these yields remain small compared with yields of 60−70 Mg ha^{-1} yr^{-1} FW achieved at a research station (Tushemereirwe et al., 2001), and in good farmer fields in the far south-west of Uganda (Rubale) when fertilizer (100N−25P−100K kg ha^{-1} yr^{-1}) was applied (Smithson et al., 2001).

Smallholder farmers in Uganda attribute low banana yields to poor soil fertility, increasing pest pressure (especially the banana weevil - *Cosmopolites sordidus*) and moisture stress (NARO, 2000). Most farmers cultivate bananas continuously on Ferralsols or Acrisols that are highly weathered, with limited capacity to supply nutrients (Zake et al., 1994). Bekunda and Woomer (1996) and Sseguya et al. (1999) noted that very few (<5%) banana farmers in Uganda use chemical fertilizers due to perceived high cost, poor availability, and lack of knowledge related to their use. The use of organic nutrient resources in banana-based farming systems is constrained by their availability, with farmers applying the available resources preferentially on plots near the homestead (Bekunda and Woomer, 1996; Wortmann and Kaizzi, 1998). However, nutrient flows from outfields and grazing areas to the homestead banana fields, as observed in traditional banana-based systems, have largely collapsed due to increased land pressure and a shift from free to zero-grazing livestock (Baijukya et al., 2005). Banana crop residues are the major mulching materials used, but these neither prevent nutrient losses, nor provide a full mulch cover to conserve soil moisture (Stover and Simmonds, 1987). Lack of nutrients thus often limits banana yields (Zake et al., 1999).

Although concerted research efforts have highlighted the extent of soil fertility decline, they have contributed little to reduce the problem. In the 1960s, soils from 62 sites distributed over the whole of Uganda were sampled to determine soil nutrient concentrations (Foster, 1981), and were re-sampled during the Land Management Study (1999−2002). Results showed that soil pH, extractable phosphorus (P), calcium (Ca), and

potassium (K) were often below critical concentrations for most crops, although the amount of soil organic matter (SOM) had not changed significantly (Ssali, 2002). In some cases, concentrations of available P, Ca and K in the top soil had declined by 20−70% compared with the 1960s. In general, soil fertility seems poor to sustain good yields, so nutrients need to be added to improve yields. Increased agricultural productivity is envisaged as key to alleviating poverty and ensuring food security in rural parts of Uganda (GOU, 2000). The African Green Revolution efforts supported by large donors are also calling for agricultural intensification through the use of fertilizer inputs.

In Uganda, the official mineral fertilizer recommendation for highland bananas is a single blanket rate of 100N–30P–100K–25Mg kg ha^{-1} yr^{-1} (Ssali et al., 2003), irrespective of the inherent soil fertility status. The blanket fertilizer recommendation fails to address variability in soil quality (chemical and physical properties) on banana farms. Van Asten et al. (2008) reported a range of nutrient deficiencies after application of 71N–8P–32K kg ha^{-1} yr^{-1} in banana demonstration plots in districts in south-west, south Uganda and around Mount Elgon. There is a need to develop site-specific fertilizer recommendations that take into account the variability in soil chemical properties. The QUEFTS (QUantitative Evaluation of the Fertility of Tropical Soils) model (Janssen et al., 1990) can be used to derive such site-specific fertilizer recommendations tailored to the target yield (Mingqiang et al., 2006; Tittonell et al., 2008). In order to understand banana systems and apply the QUEFTS model, nutrient omission trials (NOTs) were established at two locations to: (i) identify limiting nutrients and nutrient interactions for banana growth; (ii) quantify banana yield responses to mineral fertilizers; and (iii) increase our knowledge of nutrient use in banana plantations through the calculation of conversion efficiencies of N, P and K.

3.2. Materials and Methods

3.2.1. Trial design and management

Nutrient omission trials were located at Kawanda, central Uganda (00°25’N, 32°31’E, 1156 m.a.s.l), and at Ntungamo in southwest Uganda towards the Albertine rift (00°54.53’S, 30°14.86’E, 1405 m.a.s.l). Soils at Kawanda are Haplic Ferralsols (FAO/ISRIC/ISSS, 1998) on a gentle slope (5%), while soils at Ntungamo are Lixic Ferralsols with a slope 15%. Soil pH was 5.5 at Kawanda and 4.8 at Ntungamo, indicating

some acidity (Table 1). Average SOM and total N values were higher at Kawanda (2.6% and 0.1%), compared with Ntungamo (0.7% and 0.07%). Average Mehlich-3 extractable P was higher at Ntungamo, but exchangeable K and Mg were lower (Table 1). The ratio of exchangeable K to Mg at Kawanda and Ntungamo (0.27:1) was close to the optimal relationship of 0.3:1 (Delvaux, 1995). Rainfall at both sites showed a strong bimodal pattern with dry periods from June to July and December or January to March (Figure 1a and 1b). Reference evapotranspiration at Kawanda for the period 1997−1999 averaged 3410 mm yr^{-1} as compared with the rainfall total of 2930 mm during this period (Ssali et al., 2003). Average minimum and maximum temperatures during the experimental period at Kawanda were 17.0 and 27.4 ^{o}C and at Ntungamo 13.0 and 27.2 ^{o}C, respectively.

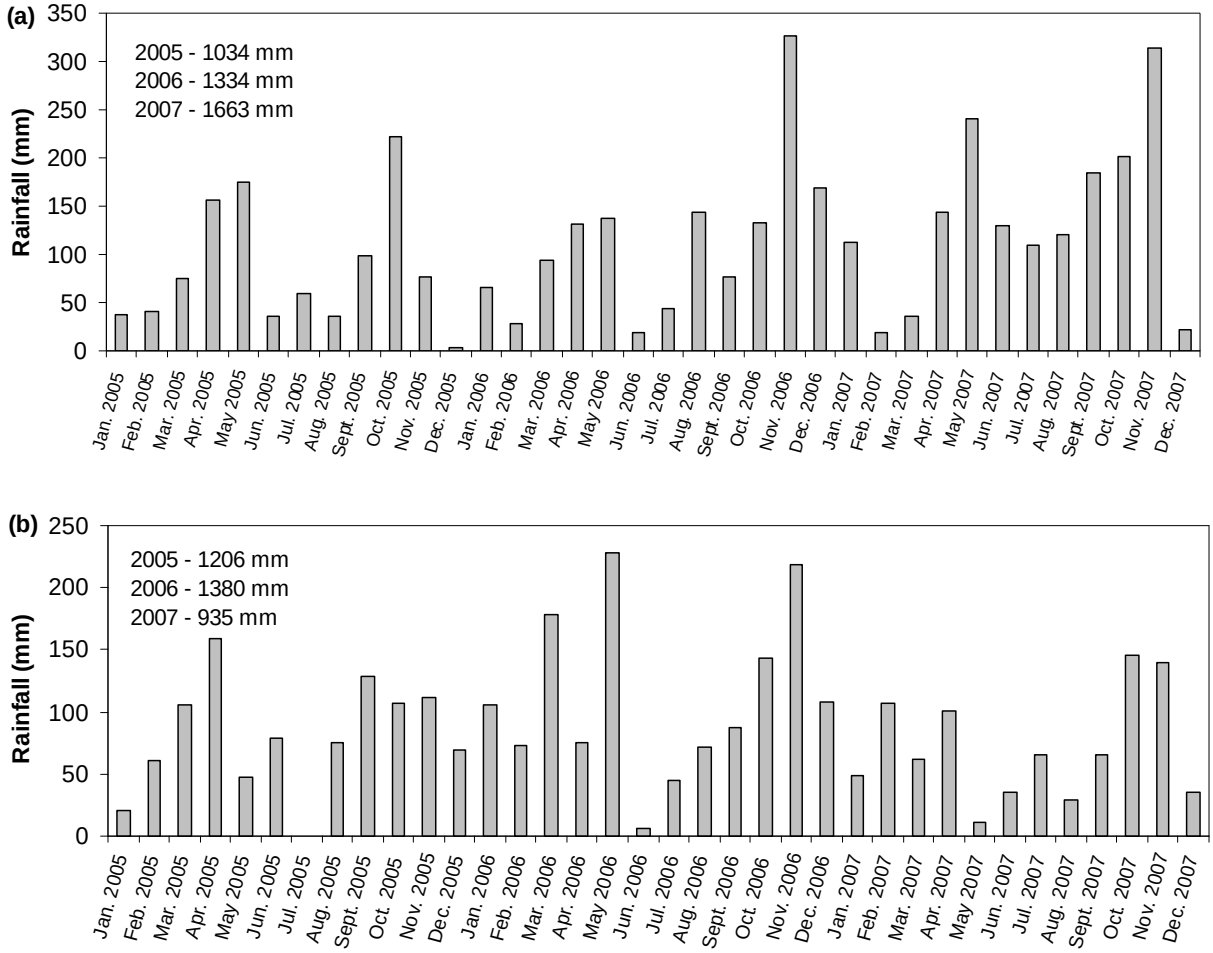

Figure 1. Monthly rainfall amounts at Kawanda (a) and Ntungamo (b) during the trial period and annual total rainfall for each of the years at each site.

Table 1. Mean initial soil indicators and their range (in parentheses) measured on the highland banana (cv. Kisansa) trial plots with soil depth 0−32 cm at Kawanda, central Uganda and Ntungamo, southwest Uganda.

Locality	pH water (1:2.5)	Organic matter (%)	Total soil N (%)	Extractable P (mg kg^{-1})	Exchangeable K ($cmol_c$ kg^{-1})	Exchangeable Ca ($cmol_c$ kg^{-1})	Exchangeable Mg ($cmol_c$ kg^{-1})	Clay (%)	Silt (%)
Kawanda	5.5	2.6	0.1	1.8	0.4	4.5	1.48	40.2	7.9
	(4.9– 6.2)	(1 – 4.6)	(0.05 – 0.2)	(0.7 – 8.6)	(0.04 – 1.0)	(2.2 – 8.6)	(0.9 – 2.9)	(26– 64)	(0.9– 21)
Ntungamo	4.8	0.7	0.07	3.52	0.12	1.67	0.45	23.8	5.6
	(4.6 – 5.6)	(0.14– 1.9)	(0.04 – 0.14)	(0.61 – 38)	(0.02 – 0.36)	(0.47 – 7.4)	(0.001 – 1.6)	(18 – 32)	(1.3– 13)

3.2.2. Trial establishment and design

The trials were established during the period October to December 2004 on fields with no recent history of banana cultivation. The field at Kawanda was previously used for annual crop experiments (beans, maize), and the field at Ntungamo had been fallow for at least 10 years. Fields were cleared and ploughed. The trials were laid out in a completely randomised block design and the four replicate blocks were perpendicular to the slope as much as possible. Treatments consisted of the following nutrient applications (kg ha^{-1} yr^{-1}): (1) 0N–0P–0K; (2) 0N–50P–600K; (3) 150N–50P–600K; (4) 400N–0P–600K; (5) 400N–50P–0K; (6) 400N–50P–250K, and (7) 400N–50P–600K. Nitrogen was applied as urea (46% N), K as muriate of potash (52% K), and P as triple super phosphate (20% P). With the exception of the control treatment (0N–0P–0K), all plots received 60 Mg, 6 Zn, 0.5 Mo, 1B (kg ha^{-1} yr^{-1}) using magnesium sulphate, zinc sulphate, sodium molybdate and borax. Nitrogen and K were applied manually in 8 splits each year (4 times during each rain season), while P, Mg, Zn, Mo, and B were applied in two splits at the start of each rain season (twice per year). Triple super phosphate was applied in granular form and other fertilizers were dissolved in water to facilitate accurate rates of application and to minimise urea volatilization losses (Chan, 1986). All fertilizers were applied in a circle at 0.4–0.5 m from the base of the plant. Each plot was 315 m^2 with 35 mats at a spacing of 3 x 3 m, resulting in a density of 1,111 plants ha^{-1}. Planting holes were 0.6 x 0.6 x 0.45 m deep. Pest-free highland banana tissue-cultured plants (*Musa* spp., AAA-EAHB cv. Kisansa) were used. Kisansa is a popular cultivar due to its large bunch size and large fingers. Some irrigation was done after planting for 3−4 months during the dry season to facilitate plant establishment. Gap filling was done for plants that did not establish properly (<10%).

Two trenches were constructed across the upper and lower sides of each plot to control soil erosion. Blocks and plots were separated with grass strips to reduce fertilizer run-on or run-off effects. Pesticide (Dursban – active ingredient chlorpyrifos) was applied to control banana weevils. De-suckering was carried out to maintain mat densities, whereby each mat consists of a maximum of three connected plants; i.e., cycle 1 (mother plant), cycle 2 (first ratoon) and cycle 3 (second ratoon). Weeding was done by hand and by application of herbicide (glyphosate). Dead leaves were pruned at monthly intervals and spread out as mulch. At harvest, bunches were cut off at the point where the peduncle intersected with the two upper leaf sheaths. Bunches were removed from the field, but the remaining above-ground biomass (i.e. leaves, corm and pseudostem) were chopped and spread as surface mulch.

3.2.3. Soil sampling and analysis

Composite soil samples (of 5 sub-samples per plot) were taken at 0–8 cm, 8–16 cm and 16–32 cm soil depth at planting. Samples were oven-dried at 40–50 ^{o}C for two consecutive days and ground to pass a 2 mm sieve. The soils were analysed at Kawanda soil and plant analytical laboratory in Uganda. Soil pH was determined using deionised water with a soil to water ratio of 1:2.5 and soil texture using the hydrometer method (Bouyoucos, 1936). Soil organic matter was determined by the Walkley-Black method. Total N was determined 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, K using a flame photometer and the other bases by atomic absorption spectrometry (Okalebo et al., 2002).

3.2.4. Plant measurements

Fifteen mats in each net plot (i.e. excluding 20 border plants) were marked and monitored individually. In this study, data from cycle 1, cycle 2 and cycle 3 plants at Kawanda, and from cycle 1 and 2 plants at Ntungamo was used. Height, girth at base, number of functional (> 50% of leaf surface area green) and dead leaves were recorded at monthly intervals. Phenological stages i.e. sucker emergence, flowering and harvest were recorded. Foliar samples were collected at flowering from the third fully expanded leaf for determination of foliar nutrient mass fractions (Hewitt, 1955). Plant shoots were completely removed at harvest, and the fresh weights of the bunch (fingers plus peduncle), fingers, corm, pseudostem and leaves were recorded in the field. Roots were not excavated. Samples for each plant part were taken for dry matter (DM) determinations. The samples consisted of composites from sub-samples taken across the plant organ at equal distances along the organ (corm, pseudostem, finger, peduncle, and leaves). Samples were oven-dried, ground to < 1 mm and digested using modified Kjeldahl oxidation. Mass fractions of N, P, K, Ca and Mg in the extract were determined as described above.

3.2.5. Data analysis and calculations

Total uptakes of N, P and K were calculated at harvest stage of plant 1, thus crop cycle 1 (at harvest), and cycle 2 and 3 plants were sampled. Allometric relationships were used to estimate total plant dry matter, and partitioning fractions were used to calculate biomass in plant parts of the cycles 2 and 3 plants (Nyombi et al., 2009). Total plant biomass for crop cycle 1 plants was defined as the sum of dry weights of the fingers, peduncle, pseudostem, leaves and corm (roots excluded). Total nutrient uptake for cycle 1 plants was calculated from measurements of N, P and K mass fractions in the fingers, peduncle, leaves, pseudostem and corm biomass and the dry weights of the plant parts at harvest.

Cycle 2 and 3, plants were categorized into: (i) sword sucker (corm and shoot), (ii) small sucker (produced up to 10 broad leaves) and (iii) large suckers (> 10 broad leaves). In order to determine nutrient uptake in the suckers at the time of harvest of cycle 1 plant, N, P and K mass fractions from a study on AAA bananas by Twyford and Walmsley (1973) were used, assuming (i) the same nutrient mass fractions across all treatments for each sucker category, with plant weight determining the total uptake, and (ii) nutrient mass fractions in Robusta banana suckers (*Musa* AAA; Cavendish subgroup) are comparable with highland banana. N, P and K mass fractions in the corm of sword suckers calculated by Twyford and Walmsley (1973) were: 7 g kg^{-1}, 1.4 g kg^{-1} and 30 g kg^{-1} and in the shoot 13 g kg^{-1}, 2.4 g kg^{-1} and 50 g kg^{-1}. For small suckers, N, P and K mass fractions in the leaves were 20 g kg^{-1}, 3 g kg^{-1} and 38 g kg^{-1}, in the corm 6 g kg^{-1}, 1 g kg^{-1} and 28 g kg^{-1} and in the pseudostem 6 g kg^{-1}, 1 g kg^{-1} and 45 g kg^{-1}, respectively. For the large suckers, N, P and K mass fractions in the leaves were 20 g kg^{-1}, 3 g kg^{-1} and 33 g kg^{-1}, in the corm 7 g kg^{-1}, 1 g kg^{-1} and 28 g kg^{-1} and in the pseudostem 7 g kg^{-1}, 1 g kg^{-1} and 40 g kg^{-1}, respectively. Uptakes by cycle 1, 2 and 3 plants were summed to obtain the total mat nutrient uptake. The nutrient conversion efficiency (*CE*; kg finger DM kg^{-1} nutrient in plant) for the individual banana plants at harvest was calculated for cycle 1 and 2 plants as:

$$CE \ \ for\, nutrient \ \ X = \frac{Total \ \ banana \ \ finger \ \ yield}{Total \ \ plant \ \ uptake \ \ of \ \ nutrient \ \ X} \qquad (1)$$

where total banana finger yield is the dry weight of banana fingers (kg ha^{-1}) (i.e. peel and pulp). Fresh banana yields are normally expressed as bunch yields, and these include the fingers and the peduncle. The proportion of the peduncle (in % FW at harvest) for Kisansa

cultivar is around 8%. Bunch yields (Mg ha^{-1} yr^{-1} FW) for crop cycle 1 plants were calculated based on the duration from planting to harvest, but yields of the successive crop cycles were based on the duration between consecutive harvests (i.e. between cycle 1 and 2, and between cycle 2 and 3). Bunch yield (Mg ha^{-1} yr^{-1} FW), individual bunch mass (kg $bunch^{-1}$ FW), plant height (m), girth at base (m), number of functional leaves and foliar nutrient mass fractions at flowering, number of fingers, total nutrient uptake and conversion efficiencies were subjected to analysis of variance (ANOVA) using Genstat − 10th edition and the standard error of difference (*s.e.d.*) was calculated (Payne et al., 2007).

3.2.6. Application of the QUEFTS (QUantitative Evaluation of the Fertility of Tropical Soils) model

The QUEFTS model (Janssen et al., 1990) was originally developed to calculate maize yield as a function of N, P and K supply from soil and fertilizer, while accounting for interactions among the nutrients (N, P and K). The model has been applied to other crops such as rice (e.g. Witt et al., 1999; Haefele et al., 2003) and wheat (Mingqiang et al., 2006). The application of the QUEFTS model to highland bananas was done in four steps. The first step involved the estimation of the indigenous soil supply of N (INS), P (IPS) and K (IKS). Regressions were calculated to obtain relationships for estimating INS (between total N uptake and total soil N in g kg^{-1} using treatment 0N−50P−600K), IPS (between total P uptake and extractable P-Mehlich-3 in mg kg^{-1} using treatment 400N−0P−600K) and IKS (between total K uptake and exchangeable K in $cmol_c$ kg^{-1} using treatment 400N−50P−0K). The soil data (total soil N, extractable P and exchangeable K) used for these regressions were those from the 0−16 cm soil samples.

Actual nutrient uptakes (i.e. UN, UP and UK) were calculated in step 2 as a function of the potential nutrient supply (i.e. SN, SP and SK), which is the sum of indigenous soil supply and effective supply of the nutrient from fertilizer considering the apparent fertilizer recovery fractions. N, P and K recovery fractions for cycle 1 plants and the whole mat at harvest stage of cycle 1 plants were computed on plot basis at harvest using the concept of apparent fertilizer recovery (Janssen and Guiking, 1990) as:

$$ARFN = \frac{N\,uptake_{(150N-50P-600K)} - N\,uptake_{(0N-50P-600K)}}{Applied\ N_{(150N-50P-600K)}} \quad (2)$$

$$ARFP = \frac{P\,uptake_{(400N-50P-600K)} - P\,uptake_{(400N-0P-600K)}}{Applied\ P_{(400N-50P-600K)}} \quad (3)$$

$$ARFK = \frac{K\,uptake_{\,(400N-50P-250K)} - K\,uptake_{\,(400N-50P-0K)}}{Applied\ K_{\,(400N-50P-250K)}} \quad (4)$$

where *ARFN*, *ARFP* and *ARFK* are the apparent N, P and K recovery fractions, respectively. Intermediate N and K rates (150N and 250K) and the maximum P rate (50P) were taken to represent points with maximum slope (maximum recovery) on the yield response curve. Fertilizer recovery fractions for the cycle 1 plants were used for the calibration of QUEFTS, although some nutrients are partitioned to the ratoons. However, the next crop (cycle 2) will also partition nutrients to the next crop (cycle 3) and so on.

In step 3, data (banana finger yield vs. total N, P or K uptake) were combined and used to obtain the boundaries showing maximum dilution (minimum uptake) and maximum accumulation (maximum uptake) of N, P and K in the banana plant in relation to banana finger yield. Due to the poor crop response to N and P fertilizer at Kawanda, N and P apparent recovery fractions were not considered suitable, so only data from Ntungamo (two crop cycles) were used for QUEFTS. Two yield estimates for each nutrient at maximum dilution and at maximum accumulation i.e. YND, YNA, YPD, YPA, YKD and YKA were obtained (Janssen et al., 1990). The maximum yield reported for this region was 11.1 Mg ha^{-1} finger DM (67 Mg ha^{-1} yr^{-1} FW, assuming that the peduncle is 8% of the bunch fresh mass and dry matter content of fingers was 18%, which compares well with 20% reported for AAA dessert bananas e.g. Turner, 2003). Below this yield, banana production is limited by either water or N, P and K supply.

Because these were nutrient omission trials, minimum N uptake (maximum N dilution) was obtained from treatment 0N−50P−600K and maximum N uptake (maximum N accumulation) from treatment 400N−50P−0K, because K was the most limiting nutrient. Minimum P uptake (maximum P dilution) was obtained from treatment 400N−0P−600K and maximum P uptake (maximum P accumulation) from treatment 400N−50P−0K. Minimum K uptake (maximum K dilution) was obtained from treatment 400N−50P−0K and maximum K uptake (maximum K accumulation) from treatment 400N−0P−600K, because P was the second most limiting nutrient. A number of methods can be used for boundary line analysis (e.g. Schnug et al., 1996; Witt et al., 1999). Here a simple method was used, where boundary points for the above treatments (maximum N, P and K accumulation and dilution) were used to generate a regression line from which parameters *a* (slope of line showing maximum accumulation), *d* (slope of line showing maximum dilution) and *q* (uptake at zero finger yield) were determined for N, P and K. In this

method, outliers are eliminated as in percentile analysis. Yield estimates for possible nutrient pairs considering the interactions (i.e. YNP, YNK, YPN, YPK, YKN and YKP) were combined into one mean yield estimate in step 4. Details of the model and the underlying assumptions are given by Janssen et al. (1990).

The QUEFTS model that was calibrated using data from Ntungamo, was then validated using data (soil analyses - 0−15 cm and cycle 1 yields) from a fertilizer trial in Mbarara, southwest Uganda (00°33'S, 30°36'E, 1380 m.a.s.l). The trial consisted of four treatments replicated four times: T1 (100N−50P−100K) with weevils, T2 (0N−0P−0K) with weevils, T3 (100N−50P−100K) with no weevils and T4 (0N−0P−0K) with no weevils. East Africa highland banana cultivar Enyeru was planted. Details of the experiment are given by Okech et al. (2004). Average N, P and K recovery fractions obtained at Ntungamo were used. Banana finger yields (kg ha^{-1} DM) computed by QUEFTS were compared with measured values from the trials using R^2 and the root mean square error (RMSE). The latter was calculated by the following equation:

$$RMSE = \sqrt{\sum_{i=1}^{n} \frac{(m_i - p_i)^2}{n}} \tag{5}$$

where n is the number of observations, m_i is the measured value and p_i is the computed value. The sensitivity of computed banana finger yield to changes in model parameters, total soil N (g kg^{-1}), extractable P (mg kg^{-1}) and exchangeable K ($cmol_c$ kg^{-1}) was tested after calibration as:

$$RPS = \frac{\partial O}{O} \Big/ \frac{\partial I}{I} \tag{6}$$

where *RPS* is the relative partial sensitivity, ∂O/O is the relative change in model output, and ∂I/I is the relative change in the input value. The original values of the model parameters *a* (slope of line showing maximum accumulation), *d* (slope of line showing maximum dilution), *q* (uptake at zero finger yield) and total soil N, extractable P-Mehlich-3 and exchangeable K were altered by −10, −5, 5 and 10 % to assess the sensitivity of the model.

The QUEFTS approach was also used to estimate optimal fertilizer requirements for highland banana. The nutrient requirements were calculated based on a target yield. If the indigenous soil nutrient supply can meet the crop's nutrient requirements for a target

yield, then no fertilizer is applied (Smaling and Janssen, 1993). Target yield with nutrient requirements above indigenous soil nutrient supply will require additional fertilizer. However, not all the fertilizer applied is utilized by the crop, therefore apparent fertilizer recovery efficiencies were taken into account when calculating the quantity of fertilizer to be applied. The relationships between the quantity of fertilizer to be applied (F_{applied}), nutrient uptake (NU_{target}) at the target yield (Y_{target}), indigenous soil nutrient supply ($N_{\text{indigenous}}$), conversion efficiency (CE) and the apparent recovery fraction of nutrients (ARF) are given by the following equations:

$$NU_{\text{target}} = \frac{Y_{\text{target}}}{CE} \tag{7}$$

where NU_{target} are the plant nutrients in plant biomass at harvest for the target yield (kg ha^{-1} DW), Y_{target} is the target yield (kg ha^{-1}), CE is the conversion efficiency of nutrient X (kg banana finger kg^{-1} nutrient in plant biomass). If $N_{\text{indigenous}} \geq NU_{\text{target}}$, $NU_{\text{target}} = N_{\text{indigenous}}$, no fertilizer would be required. If $N_{\text{indigenous}} \leq NU_{\text{target}}$, then the amount of fertilizer to be applied to supply NU_{target} for a set Y_{target} can be calculated as follows:

$$F_{\text{applied}} = \frac{(NU_{\text{target}} - N_{\text{indigenous}})}{ARF} \tag{8}$$

where $N_{\text{indigenous}}$ is the indigenous soil nutrient supply (kg ha^{-1}), ARF is the apparent recovery fraction of fertilizer nutrient (kg nutrient in plant biomass kg^{-1} of fertilizer nutrient applied) and F_{applied} is the quantity of fertilizer to be applied (kg ha^{-1}) to reach the target yield.

However, crops do not take up all the nutrients supplied. In balanced nutrition (balanced supplies of N, P and K) of highland banana, actual nutrient uptake was 93% of the total effective supply (compared with 96% for cereals; Janssen, 2009). In addition, the yield may be slightly less than the product of the uptake and conversion efficiency. The relationship between Y_{target} and total nutrient supply, NU_{supply} derived for highland banana was:

$$Y_{\text{target}} = 0.86 \times NU_{\text{supply}} \times CE \tag{9}$$

where NU_{supply}, includes soil and fertilizer nutrient supply and 0.86 is ratio of yield computed based on the hyperbola giving yield combinations and yield with balanced nutrition for highland bananas (0.9 for cereals; Janssen, 2009) using QUEFTS.
The equation for the amount of fertilizer to be applied was obtained by substituting NU_{target} in equation 9 with NU_{supply} as follows:

$$F_{applied} = \left(\frac{\left(1.16 \times \frac{Y_{target}}{CE} \right) - N_{indigenous}}{ARF} \right) \quad (10)$$

3.3. Results

3.3.1. Yield and yield components

Bunch mass (kg bunch^{-1} FW) differed significantly between fertilizer treatments and between cycles and sites ($P < 0.001$). The maximum bunch mass increases above the control (0N–0P–0K) were less at Kawanda, 3.1, 4.7 and 6.2 kg for cycles 1, 2 and 3, respectively (control cycle 1 – 7.1 kg, cycle 2 – 9.0 kg and cycle 3 – 10.3 kg), as compared with Ntungamo, 12.4 and 16.0 kg for cycles 1 and 2, respectively (control cycle 1 – 3.9 kg and cycle 2 – 7.2 kg) (Table 2). Application of N and P without K (400N–50P–0K) gave no significant increase in bunch mass above the control at Ntungamo. Bunch yields (Mg ha^{-1} yr^{-1} FW) were significantly different between treatments, cycles and sites ($P < 0.001$) (Table 2). Maximum bunch yield increases above the control at Kawanda were 2.2, 7.2 and 11.2 Mg ha^{-1} yr^{-1} FW for cycles 1, 2 and 3 (control cycle 1 – 5.4, cycle 2 – 18.2 and cycle 3 – 15.3 Mg ha^{-1} yr^{-1} FW), and at Ntungamo 7 and 29.5 Mg ha^{-1} yr^{-1} FW for cycles 1 and 2, respectively (control cycle 1 – 2.1 and cycle 2 – 13.7 Mg ha^{-1} yr^{-1} FW).

Table 2. Yield and yield components of highland banana (cv. Kisansa) as affected by mineral fertilizer application over 3 crop cycles (C1-C3) at Kawanda, central Uganda and 2 crop cycles at Ntungamo, southwest Uganda.

Treatment / site	Kawanda									Ntungamo					
	Fingers (number bunch^{-1})			Bunch mass (kg bunch^{-1})			Bunch yield (Mg ha^{-1} yr^{-1})			Fingers (number bunch^{-1})		Bunch mass (kg bunch^{-1})		Bunch yield (Mg ha^{-1} yr^{-1})	
	C 1	C 2	C 3	C 1	C 2	C3	C 1	C 2	C 3	C 1	C 2	C 1	C 2	C 1	C 2
0N–0P–0K	71	82	93	7.1	9.0	10.3	5.4	18.2	15.3	53	71	3.9	7.2	2.1	13.7
0N–50P–600K	80	98	107	10.2	13.7	15.9	7.6	25.4	22.9	87	105	13.3	18.4	7.6	33.8
150N–50P–600K	73	82	107	8.1	10.8	14.9	6.1	19.2	22.4	89	120	15.2	23.2	8.9	39.6
400N–0P–600K	74	90	108	8.0	12.8	16.5	5.9	23.7	26.5	83	102	13.3	14.8	7.4	27.9
400N–50P–0K	75	86	101	7.8	10.2	12.9	5.7	19.7	18.9	56	74	5.0	7.3	2.6	13.0
400N–50P–250K	72	84	109	7.6	11.5	15.1	5.5	22.9	22.2	83	116	13.7	19.3	7.9	36.4
400N–50P–600K	72	85	101	7.9	11.7	15.3	5.7	22.1	22.5	100	121	16.3	22.7	9.1	43.2
Mean	74	87	104	8.1	11.4	14.4	6.01	21.6	21.5	79	101	11.5	16.1	6.5	29.7
s.e.d.	3.1	3.7	4.8	0.46	0.65	0.88	0.38	1.63	1.63	3.8	4.9	0.83	1.18	0.51	2.53
ANOVA-significance for the effects of:															
Site		***						***					***		
Cycle		***						***					***		
Site x Cycle		***						***					*		
s.e.d. between average of:															
Site		1.38						0.84					0.33		
Cycle		1.38						0.61					0.33		

C1, C2 and C3 are crop cycles 1, 2 and 3. ANOVA-significance and standard errors for only C1 and C2 do allow site comparison. *s.e.d.* is the standard error of difference. *** $P < 0.001$ and * $P < 0.05$.

Also, the number of fingers differed significantly between treatments, cycles and sites ($P < 0.001$), with the maximum increment due to fertilization above the control much larger at Ntungamo (47 and 50 fingers per bunch for cycles 1 and 2, respectively) compared with Kawanda (9, 16 and 16 for cycles 1, 2 and 3, respectively). Yield reductions were noted for crop cycles 1 and 2 at Kawanda due to increasing application of urea (0−400 kg ha^{-1} yr^{-1}). Average days from emergence to flowering, from flowering to harvest, and total crop cycle durations for all treatments combined were significantly larger at Ntungamo than Kawanda ($P < 0.001$), with averages of 567 and 461, 137 and 112, and 672 and 574 days, respectively (detailed data not presented).

3.3.2. Growth parameters at flowering

Girth at base at flowering (Table 3) was significantly different between fertilizer treatments and cycles ($P < 0.001$), but not different between sites ($P = 0.11$). The number of functional leaves at flowering differed significantly between cycles and sites ($P < 0.001$). At Kawanda, significant differences in the number of functional leaves within treatments at flowering were observed for crop cycle 2 ($P = 0.005$). There was a significantly larger number of functional leaves at flowering at Ntungamo ($P < 0.001$) than at Kawanda (Table 3).

3.3.3. Foliar nutrient mass fractions at flowering

Foliar N mass fractions at flowering (Table 4) differed significantly between cycles ($P < 0.001$), but not between sites, with values of 25.4 g kg^{-1} (cycle 1) and 18.5 g kg^{-1} (cycle 2) at Kawanda, and 26.5 g kg^{-1} (cycle 1) and 16.7 g kg^{-1}(cycle 2) at Ntungamo. Significant differences in fertilizer treatments ($P = 0.013$) were only noted for foliar N mass fractions for cycle 2 plants at Kawanda. Foliar P mass fractions were significantly different between cycles ($P < 0.001$), but not between sites. Average foliar P mass fractions at Kawanda were 1.16 g kg^{-1} (cycle 1) and 1.06 g kg^{-1} (cycle 2) and at Ntungamo 1.28 g kg^{-1} (cycle 1) and 0.96 g kg^{-1} (cycle 2). Foliar P mass fractions were significantly different ($P = 0.003$) for cycle 2 at Kawanda.

Table 3. Growth parameters for highland banana (cv. Kisansa) at flowering as affected by mineral fertilizer application over 2 crop cycles (C1-C2) at Kawanda, central Uganda and Ntungamo, southwest Uganda.

Treatment / site	Kawanda						Ntungamo					
	Height to axil of flag leaf (m)		Girth at base (m)		Functional leaves (number plant^{-1})		Height to axil of flag leaf (m)		Girth at base (m)		Functional leaves (number plant^{-1})	
	C 1	C 2	C 1	C 2	C 1	C 2	C 1	C 2	C 1	C 2	C 1	C 2
0N–0P–0K	2.48	2.93	0.58	0.63	6.5	5.9	2.26	2.55	0.50	0.53	4.8	5.5
0N–50P–600K	2.67	3.24	0.66	0.72	6.8	6.5	2.65	3.26	0.62	0.69	7.8	7.1
150N–50P–600K	2.65	3.09	0.62	0.67	6.6	6.2	2.76	3.47	0.64	0.74	7.4	7.4
400N–0P–600K	2.64	3.20	0.62	0.70	6.5	6.8	2.74	3.17	0.62	0.68	7.6	6.6
400N–50P–0K	2.54	2.97	0.60	0.65	6.4	6.3	2.26	2.70	0.49	0.55	5.2	5.3
400N–50P–250K	2.57	3.01	0.61	0.66	6.4	6.5	2.59	3.28	0.62	0.69	8.0	6.9
400N–50P–600K	2.63	3.14	0.59	0.68	6.6	6.7	2.81	3.48	0.65	0.75	7.7	7.3
Mean	2.59	3.08	0.61	0.67	6.6	6.4	2.58	3.13	0.59	0.66	6.9	6.6
s.e.d.	0.034	0.044	0.009	0.013	0.25	0.22	0.046	0.056	0.012	0.014	0.3	0.22
ANOVA-significance for the effects of:												
Site	*				***					ns		
Cycle	***				***					***		
Site x Cycle	***				ns					*		
*s.e.d. b*etween average of:												
Site	0.18				0.09					0.005		
Cycle	0.18				0.09					0.005		

C1 and C2 are the first and second crop cycles. ns = not significant. *s.e.d.* is the standard error of difference. *** $P < 0.001$ and * $P < 0.05$.

Table 4. Highland banana (cv. Kisansa) foliar nutrient mass fractions at flowering as affected by mineral fertilizer application over 2 crop cycles (C1-C2) at Kawanda, central Uganda and Ntungamo, southwest Uganda.

Treatment / site	N (g kg^{-1})		P (g kg^{-1})		K(g kg^{-1})		Ca (g kg^{-1})		Mg (g kg^{-1})	
	Cycle 1	Cycle 2	Cycle 1	Cycle 2	Cycle 1	Cycle 2	Cycle 1	Cycle 2	Cycle 1	Cycle 2
Kawanda										
0N–0P–0K	25.4	17.0	1.13	0.88	23.4	18.7	9.8	12.8	5.0	4.8
0N–50P–600K	25.6	15.9	1.22	0.99	26.7	23.3	7.7	12.0	4.5	3.8
150N–50P–600K	25.0	18.7	1.16	1.13	30.4	27.7	9.8	13.3	3.9	3.8
400N–0P–600K	25.1	20.2	1.14	1.12	29.0	28.1	9.1	12.8	3.9	3.0
400N–50P–0K	25.3	21.7	1.16	1.19	24.2	23.1	9.8	14.0	4.8	4.8
400N–50P–250K	25.2	18.1	1.17	1.07	28.3	24.1	10.0	13.6	4.5	4.3
400N–50P–600K	26.4	18.1	1.18	1.04	28.5	26.0	9.1	11.8	4.2	3.9
Mean	25.4	18.5	1.16	1.06	27.2	24.4	9.3	13.9	4.4	4.0
s.e.d.	0.07	0.14	0.004	0.006	0.34	0.32	0.12	0.11	0.05	0.07
Ntungamo										
0N–0P–0K	25.0	16.5	1.17	0.98	11.4	19.6	11.5	14.8	4.2	3.6
0N–50P–600K	26.8	17.6	1.35	1.05	28.2	21.4	10.7	14.5	4.0	3.7
150N–50P–600K	26.8	16.3	1.35	0.96	26.5	18.5	11.2	15.4	4.4	3.5
400N–0P–600K	26.7	17.7	1.29	0.94	27.6	18.8	9.8	12.4	4.0	2.7
400N–50P–0K	25.7	16.6	1.17	0.99	12.0	20.6	12.0	15.0	4.9	3.6
400N–50P–250K	27.9	17.7	1.35	1.07	23.4	17.7	11.9	15.8	4.6	4.2
400N–50P–600K	26.9	14.3	1.31	0.71	27.5	18.2	9.9	10.9	3.8	2.3
Mean	26.5	16.7	1.28	0.96	22.4	19.3	11.0	14.1	4.3	3.4
s.e.d.	0.104	0.24	0.007	0.013	0.26	0.40	0.08	0.16	0.05	0.05
DRIS norms		27.9		2.1		38.4		9.1		4.4
ANOVA-significance for the effects of:										
Site		ns		ns		***		***		*
Cycle		***		***		*		***		***
Site x Cycle		***		***		ns		ns		ns
s.e.d. between average of:										
Site		0.43		0.026		1.14		0.38		0.17
Cycle		0.43		0.026		1.14		0.38		0.17

Diagnosis and Recommendation Integrated System (DRIS) norms for East Africa highland banana according to Wairegi and Van Asten (2009). ns = not significant. *s.e.d.* is the standard error of difference. *** $P < 0.001$ and * $P < 0.05$.

Foliar K mass fractions differed significantly between sites ($P < 0.001$) and cycles ($P = 0.013$), with larger foliar K mass fractions at Kawanda, 27.2 g kg^{-1} (cycle 1) and 24.4 g kg^{-1} (cycle 2), compared with Ntungamo, 22.4 g kg^{-1} (cycle 1) and 19.3 g kg^{-1} (cycle 2). Significant differences in fertilizer treatments ($P < 0.001$) were only noted in foliar K mass fractions for cycle 1 plants at Ntungamo. Foliar Ca mass fractions did not differ between fertilizer treatments but were larger ($P < 0.001$) at Ntungamo for cycle 1 (11 g kg^{-1}) and cycle 2 (14.1 g kg^{-1}) plants as compared with Kawanda, cycle 1 (9.3 g kg^{-1}) and cycle 2 (13.9 g kg^{-1}). Foliar Mg mass fractions were significantly different between cycles ($P < 0.001$) and between sites ($P < 0.05$), with a lower mean for cycle 2 plants at Ntungamo (3.4 g kg^{-1}), as compared with foliar Mg mass fraction of 4.0 g kg^{-1} for cycle 2 plants at Kawanda.

Table 5. Average N, P and K uptake for highland banana mats (cycle 1, 2 and 3) at harvest stage of the cycle 1 plants calculated for control plots and plots with different combinations of mineral fertilizer applied at Kawanda, central Uganda and Ntungamo, southwest Uganda.

Treatment / site	Kawanda			Ntungamo		
	Nitrogen (kg ha^{-1})	Phosphorus (kg ha^{-1})	Potassium (kg ha^{-1})	Nitrogen (kg ha^{-1})	Phosphorus (kg ha^{-1})	Potassium (kg ha^{-1})
0N–0P–0K	70.5	7.4	204.1	62.6	6.7	121.2
0N–50P–600K	78.3	9.5	332.1	111.4	13.2	419.8
150N–50P–600K	79.6	9.2	316.3	138.2	17.3	487.4
400N–0P–600K	74.7	8.9	302.6	120.7	13.9	415.4
400N–50P–0K	66.2	8.3	237.3	73.5	7.9	147.3
400N–50P–250K	70.9	8.5	256.3	135.9	15.7	367.2
400N–50P–600K	78.9	9.7	311.7	149.2	17.6	509.9
Mean	74.2	8.8	280.1	113.2	13.2	352.9
s.e.d.	3.67	0.43	15.5	6.9	0.85	21.1
ANOVA-significance for the effects of:						
Site		***		***		***
s.e.d. between average of:						
Site		0.38		3.05		11.7

s.e.d. is the standard error of difference. *** $P < 0.001$.

3.3.4. Total nutrient uptake

Total N, P and K uptakes for a mat (cycle 1, 2 and 3 plants) calculated at time of harvest of the cycle 1 plants were significantly different ($P < 0.001$) between fertilizer treatments and sites. Average total nutrient uptakes were greater at Ntungamo, as compared with Kawanda, with averages of 113.2 vs. 74.2 kg N ha^{-1}, 13.2 vs. 8.8 kg P ha^{-1}, 352.9 vs. 280.1 kg K ha^{-1} (Table 5).

3.3.5. QUEFTS model application to highland bananas

Indigenous N, P and K supply were estimated from regressions using total soil N (g kg^{-1}), extractable P (mg kg^{-1}) and exchangeable K ($cmol_c$ kg^{-1}) in the first step of applying QUEFTS to highland bananas. Mean INS values for cycle 1 plants at Kawanda were 39 kg ha^{-1} for N (range 23 to 54 kg ha^{-1}), 2.8 kg ha^{-1} for P (range 0.84 to 4.9 kg ha^{-1}) and 133 kg ha^{-1} for K (range 22 to 289 kg ha^{-1}). At Ntungamo, mean INS values for cycle 1 plants were 60.3 kg ha^{-1} for N (range 24 to 104 kg ha^{-1}), 6.3 kg ha^{-1} for P (range 2.4 to 12.1 kg ha^{-1}) and 66 kg ha^{-1} for K (range 8.3 to 135 kg ha^{-1}).

Average apparent recovery fractions of applied fertilizer in cycle 1 plants and the whole mat at Kawanda were close to zero for N and P, and small for K (0.117 and 0.144). At Ntungamo, the apparent recovery fractions of applied N, P and K fertilizer in the cycle 1 plants and the whole mat were larger than at Kawanda, but still very small for N (0.055 and 0.095) and P (0.019 and 0.049) as compared with K (0.36 and 0.49). The average actual uptakes calculated in step 2 for cycle 1 plants at Ntungamo site from indigenous supply and effective supply from fertilizer were 73 kg ha^{-1} for N (range 27 to 140 kg ha^{-1}), 5 kg ha^{-1} for P (range 2 to 11 kg ha^{-1}) and 273 kg ha^{-1} for K (range 28 to 613 kg ha^{-1}).

Average N, P and K conversion efficiencies were significantly higher for N and P at Kawanda, but lower for K ($P < 0.001$), compared with Ntungamo (Table 6). Average N and P conversion efficiencies for the first two crop cycles at Kawanda were 50.5 kg finger DM kg^{-1} N (range 2.1 to 114.0 kg finger DM kg^{-1} N) and 627.3 kg finger DM kg^{-1} P (range 45.2 to 1099.2 kg finger DM kg^{-1} P), compared with Ntungamo, 48.0 kg finger DM kg^{-1} N (range 3.9 to 129.0 kg finger DM kg^{-1} N) and 549.2 kg finger DM kg^{-1} P (range 53.6 to 1093.3 kg finger DM kg^{-1} P). Average K conversion efficiencies for the two crop cycles at Ntungamo were 12.1 kg finger DM kg^{-1} K (range 2.7 to 29.1 kg finger DM kg^{-1} K), compared with Kawanda, 9.4 kg finger DM kg^{-1} K (range 0.76 to 24.3 kg finger DM kg^{-1} K).

Table 6. N, P and K conversion efficiencies calculated using equation 1 from plant nutrient mass fractions and banana finger yield measured on trial plots for cycle 1 and 2 plants at Kawanda, central and Ntungamo, southwest Uganda.

Treatment / site	NUE (kg DM kg^{-1} N)		PUE (kg DM kg^{-1} P)		KUE (kg DM kg^{-1} K)	
	Cycle 1	Cycle 2	Cycle 1	Cycle 2	Cycle 1	Cycle 2
Kawanda						
0N–0P–0K	37.7	52.8	531.7	679.1	13.3	10.5
0N–50P–600K	49.1	51.4	536.6	773.2	9.0	7.2
150N–50P–600K	42.4	60.0	553.8	695.1	8.6	6.9
400N–0P–600K	45.8	58.3	531.6	732.7	8.3	7.1
400N–50P–0K	52.4	52.6	529.7	697.5	14.2	13.1
400N–50P–250K	42.7	54.5	522.3	644.8	10.0	8.9
400N–50P–600K	47.1	57.3	566.0	749.8	9.0	7.3
Mean	45.3	55.3	538.8	710.3	10.4	8.7
s.e.d.	2.10	2.47	16.38	22.8	0.51	0.52
Ntungamo						
0N–0P–0K	19.6	40.1	240.1	528.4	13.8	14.4
0N–50P–600K	48.8	70.9	503.3	714.6	10.9	9.2
150N–50P–600K	53.9	69.7	445.7	795.8	10.9	11.4
400N–0P–600K	41.2	58.4	453.8	790.1	10.3	9.9
400N–50P–0K	23.7	33.8	299.8	506.4	14.9	16.4
400N–50P–250K	35.7	56.7	402.4	697.7	13.8	15.2
400N–50P–600K	43.1	54.5	453.9	706.5	10.7	12.7
Mean	38.0	54.9	399.9	677.1	12.1	12.7
s.e.d.	2.29	2.22	17.7	24.7	0.66	0.61
ANOVA-significance for the effects of:						
Site		*		***		***
Cycle		***		***		*
Site x Cycle		***		***		***
s.e.d. between average of:						
Site		1.73		7.69		0.22
Cycle		1.73		7.68		0.22

s.e.d. is the standard error of difference. C1 and C2 are the first and second crop cycles. *** $P < 0.001$ and * $P < 0.05$

N and P conversion efficiencies were generally smaller for fertilizer treatments without K fertilization (0N−0P−0K and 400N−50P−0K), while the K conversion efficiencies were greatest for both these fertilizer treatments at both sites. Due to the small apparent fertilizer recovery fractions and small P and N uptakes at Kawanda, data from Ntungamo was used for the calibration of QUEFTS.

Table 7. Parameters and equations used for calculating banana finger yields from actual uptakes (cycle 1 and 2) and indigenous supply of nitrogen (cycle 1) - (UN and INS), phosphorus (UP and IPS) and potassium (UK and IKS) using data at Ntungamo, southwest Uganda.

Yield (kg ha^{-1})	Parameters			Equation	Equation
	a	*d*	*q*		
YNA	20.6		14.7	YNA = 20.6 x (UN − 14.7)	
YND		108.4	7.90	YND = 108.4 x (UN − 7.9)	INS = 58.02 x Total soil N
YPA	225.3		0.87	YPA = 225.3 x (UP − 0.87)	
YPD		881	0.17	YPD = 881 x (UP − 0.17)	IPS = 2.73 x Extractable P
YKA	4.5		15.6	YKA = 4.5 x (UK − 15.6)	
YKD		23.9	4.90	YKD = 23.9 x (UK − 4.9)	IKS = 230.5 x Exchangeable K

YNA and YND, YPA and YPD, YKA and YKD are banana finger yields (kg ha^{-1}) obtained when nitrogen, phosphorus and potassium in the plant is maximally concentrated and diluted, respectively. INS, IPS and IKS are indigenous nitrogen, phosphorus and potassium supply (kg ha^{-1}), total soil nitrogen (g kg^{-1}), extractable P-Mehlich (mg kg^{-1}), exchangeable K ($cmol_c$ kg^{-1}).

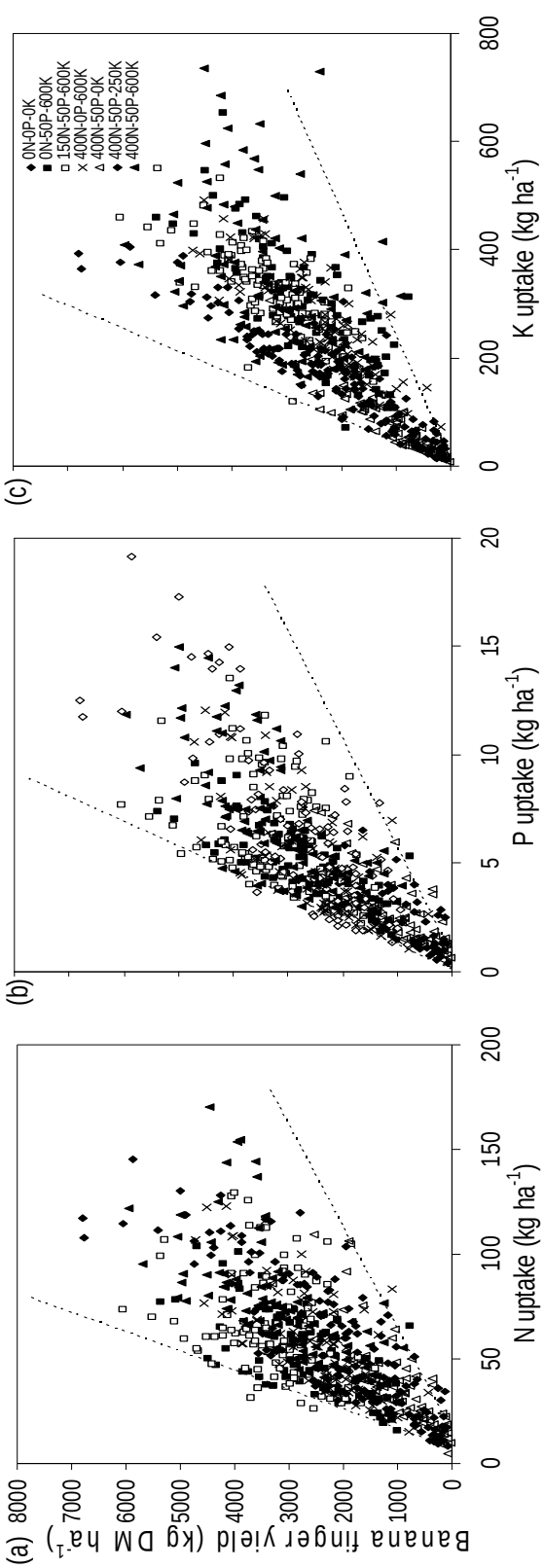

Figure 2. Relationship between total N uptake (a), total P uptake (b), K uptake (c) and banana finger biomass for cycle 1 and 2 plants measured in trial plots over 2 crop cycles at Ntungamo, southwest Uganda. Boundary points for maximum and minimum N, P and K uptakes were used to generate a regression line (for explanation see text) from which parameters *a* (slope of line showing maximum accumulation), *d* (slope of line showing maximum dilution) and *q* (uptake at zero finger yield) were determined.

The maximum and minimum N, P and K conversion efficiencies that define the boundary lines (maximum dilution and maximum accumulation) of nutrient uptake and banana yield were determined by using only the data from the Ntungamo site. They were estimated at 108.4 kg and 20.6 kg finger DM kg^{-1} N, 881 kg and 225.3 kg finger DM kg^{-1} P, and 23.9 kg and 4.5 kg finger DM kg^{-1} K (Table 7). These values encompassed well the variability in observed N, P and K uptakes and banana finger yield (kg ha^{-1} DW) - (Figure 2).

The minimum N, P and K uptake required to produce finger biomass at maximum dilution and maximum accumulation were 7.9 kg and 14.7 kg N ha^{-1}, 0.17 kg and 0.87 kg P ha^{-1}, and 4.9 kg and 15.6 kg K ha^{-1} (Table 7). The equations for calculating banana finger yields from uptake of nitrogen (UN), phosphorus (UP) and potassium (UK) in QUEFTS using data from Ntungamo site over two crop growth cycles and those for estimating INS, IPS and IKS are shown in Table 7.

The yield estimates predicted by QUEFTS compared well with measured values, with R^2 = 0.57 and RMSE = 648 kg ha^{-1} (Figure 3a). QUEFTS gave good predictions for the fertilizer treatments 0N−50P−600K, 400N−50P−600K and 150N−50P−600K (Figure 3a). The model was most sensitive to changes in parameter *d* (slope of line showing maximum dilution), with −10, −5, 5 and 10% changes of the parameter value resulting in relative partial sensitivity values (RPS) of 0.32, 0.39, −0.52 and −0.55, respectively of the output value. A RPS value of 0.0 implies that the change in input has no effect on output, whereas 1.0 implies that the change in input results in an equal change in output. The model was least sensitive to changes in *q* (uptake at zero finger yield), with relative partial sensitivity values of 0.01, 0.005, −0.05 and −0.05 of the output value for −10, −5, 5 and 10% changes of the parameter value. The model was most sensitive to changes in extractable P and available K, with −10, −5, 5 and 10 % changes in these model parameters resulting in RPS values of 0.21, 0.27, −0.39 and −0.43 for P and 0.002, 0.02, −0.06 and −0.07 for K of the output value. The overall results of the QUEFTS model validation against the observed finger yield (kg ha^{-1} DW) data from Mbarara were good with R^2 = 0.68 and RMSE = 562 kg ha^{-1} (Figure 3b). Agreement between measured and predicted finger yield on control plots was good, but the model over predicted yields from plots with high exchangeable K with and without fertilizer.

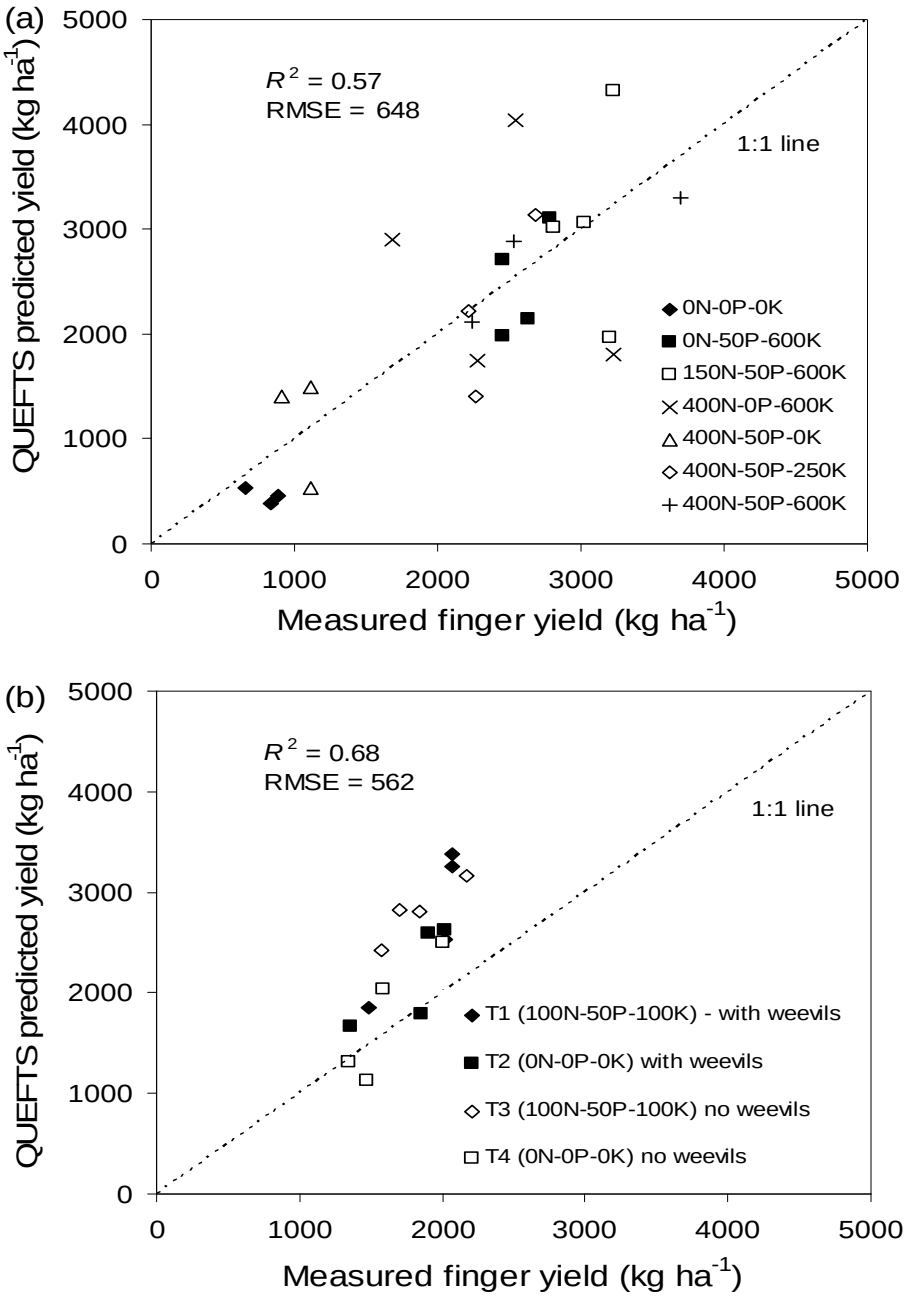

Figure 3. Comparison between banana finger yields measured on experimental plots versus yields computed using the model QUEFTS using soil chemical data, fertilizer application rates and recovery fractions from Ntungamo (a). Comparison between banana finger yields measured on experimental plots at Mbarara versus yields computed using the model QUEFTS that was first calibrated using data from Ntungamo (b). Soil chemical data and fertilizer rates used were from Mbarara and mean N, P and K recovery fractions obtained at Ntungamo were used.

3.3.6. Fertilizer recommendations using the QUEFTS approach

For Ntungamo, we used the maximum apparent N, P and K fertilizer recovery fractions obtained and indigenous soil nutrient supply to estimate the amount of fertilizers required for a range of target yields. For example a target yield of 30 Mg ha^{-1} would require 631 kg N ha^{-1}, 86 kg P ha^{-1} and 843 kg K ha^{-1} (Figure 4). Considering the low fertilizer recovery fractions resulting from moisture stress related to the poor soil physical properties at Kawanda, it seemed not appropriate to derive fertilizer recommendations for this site.

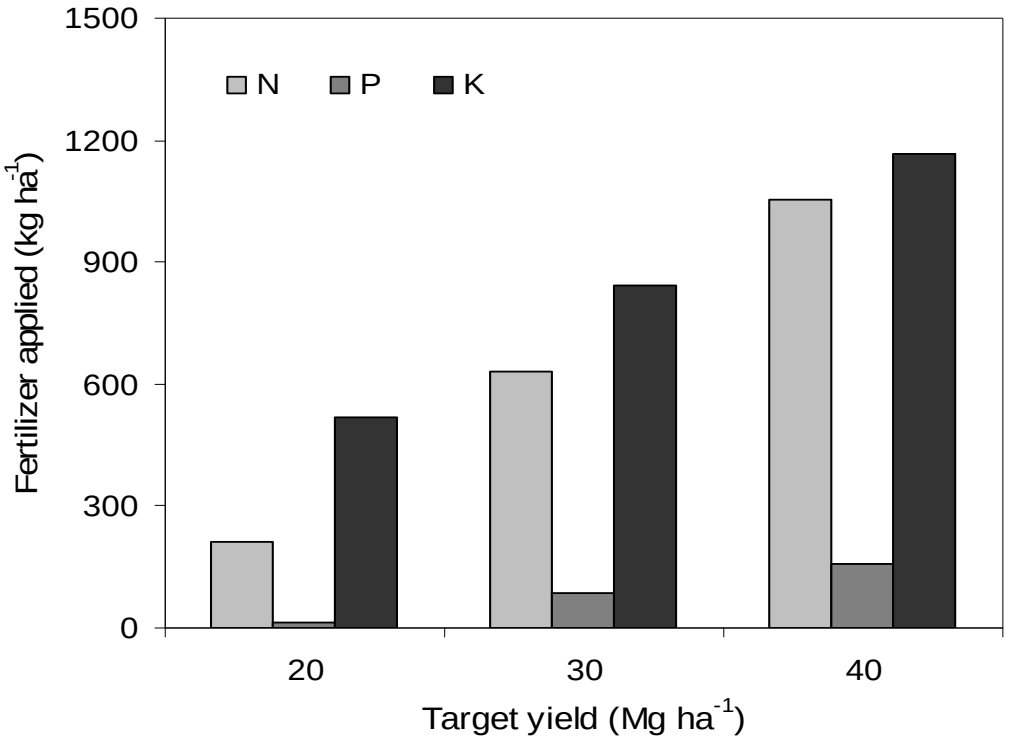

Figure 4. Fertilizers required for target banana yield at Ntungamo calculated using the N, P and K conversion efficiencies, the maximum apparent recovery fractions and indigenous soil supply.

3.4. Discussion

3.4.1 Effect of fertilizer on growth and yield components

Poor yields, shorter plants and lower number of fingers and functional leaves (Table 2 and 3) as observed on the control plots at both trial sites are attributed to poor soil fertility (Table 1). Potassium applications increased bunch mass especially at Ntungamo. Exchangeable K content (0.09 $cmol_c\ kg^{-1}$) at this site was below the critical value of 0.2 $cmol_c\ kg^{-1}$ reported by Delvaux (1995). The sandy clay loams at Ntungamo are presumably unable to satisfy the demand for this nutrient (cf. Purseglove, 1988). The addition of K fertilizer increased K availability in the soil solution resulting in better uptake and yields as noted for the treatment 400N–50P–250K − (Table 2 and 6). At Kawanda, the increases in bunch mass (kg $bunch^{-1}$ FW), bunch yield (Mg $ha^{-1}\ yr^{-1}$ FW), number of functional leaves and number of fingers (fingers $bunch^{-1}$) were smaller compared with Ntungamo (Table 2 and 3).

The weak response to fertilization at Kawanda seems to be related to low available soil water and clay accumulation (higher bulk density) in the B-horizon, which limits root exploration of this soil layer. This affects nutrient uptake, the number of functional leaves (photosynthetically active leaf area) during growth and at flowering and the number of fingers at flower initiation (cf. Turner, 1980; Stover and Simmonds, 1987; Robinson, 1996). Leaf senescence was also accelerated at Kawanda by a combination of black sigatoka (fungal foliar disease caused by *Mycosphaerella fijiensis*; data not shown) and soil moisture stress (Figure 1a) especially during the dry months leading to low assimilation and assimilate supply to fill the sink, hence poorly filled banana fingers compared with Ntungamo. Most plants at Kawanda reached harvest with no functional leaves left (data not shown). There was no difference noted in plant girth between the sites (Table 3), but cycle 3 plants at Kawanda received more rainfall (Figure 1a) and consequently performed better (Table 2). Other studies have emphasized the major importance of drought stress in highland banana systems (e.g. Taulya et al., 2005; Murekezi and van Asten, 2008). The better yield responses to added fertilizer at Ntungamo can possibly be explained by the coarser soil texture and lower bulk density, resulting in better root distribution (data not published), improved soil moisture availability, and consequently higher nutrient uptake (Table 6). Bunch yields at Ntungamo were reduced due to a longer crop cycle duration when compared to Kawanda. This is attributed to lower average daily effective temperature of 6.2 ^{o}C d, compared with 8.4 ^{o}C

d at Kawanda. Bunch mass increases with successive cycles at both sites are probably due to nutrient accumulation in the banana mat, and an improvement in soil physical properties and soil moisture conservation due to a self-mulch layer on the soil surface.

Yield increases with successive crop cycles noted (Table 2) could be attributed to a larger amount of available nutrients due to a transfer of nutrients from the harvested plant to the sucker, decomposition of crop residues and the fertilizers applied. Banana residues help provide mulch, which also conserves soil moisture. The yield increases due to fertilizer application obtained in our trial at Kawanda (Table 2) are larger than those reported for highland banana cultivar Nakyetengu at Kawanda: 1.75, 1.97 and 1.06 Mg ha^{-1} yr^{-1} FW for the treatments with 50N–15P–50K–12.5Mg kg ha^{-1} yr^{-1} (half of the blanket banana fertilizer recommendation), mulch (47 Mg ha^{-1} yr^{-1}) and a combination of mulch and fertilizer, respectively (Ssali et al., 2003). The fact that in that study mulch increased yield more as compared with fertilizer is in line with our observations that poor soil moisture availability due to suboptimal rainfall and limited root systems pose a major constraint to banana production and use of fertilizer. In established banana plantations (> 8 years) at Rubale, southwest Uganda, Smithson et al. (2001) reported a yield increase of 21.5 Mg ha^{-1} yr^{-1} FW with applications of 100N–25P–100K kg ha^{-1} yr^{-1} above a control of 45.8 Mg ha^{-1} yr^{-1} FW (with application of 25 kg P ha^{-1} yr^{-1}). This was partly attributed to high rainfall amounts, application of animal manure and the traditional mulching practices. This result also suggests that there is an important synergetic effect when mineral fertilizers are combined with organic inputs such as manure and mulch. In our trials, no external mulch was applied, only prunings and non-economic biomass from the banana plants at harvest were used as mulch. Since SOM content is low at Ntungamo, we therefore expect yields to further increase with successive crop cycles due to self-mulching, leading to improved chemical and physical soil properties.

3.4.2. Nutrient requirements and use by highland banana

Potassium was the most limiting nutrient for banana production. The addition of K fertilizer increased K availability and resulted in higher nutrient uptake and yields as illustrated by treatment 400N–50P–250K − (Table 2 and 6). Phosphorus seemed more limiting at Ntungamo with smaller yields for treatment 400N–0P–600K, although the initial soil P concentrations were higher than at Kawanda (Table 1). This may be attributed to more uptake of N and K, increasing the P demand (Table 6). The fertilizer treatments in cycle 2 with the largest yield at Ntungamo (150N–50P–600K, 400N–50P–

250K and 400N–50P–600K) had the lowest foliar N, P and K mass fractions (Table 4), indicating a dilution effect. Smithson et al. (2001) obtained similar results at Rubale, southwest Uganda where highest yields (67 Mg ha yr^{-1} FW) were obtained from plots with the lowest N and K foliar status. It has to be noted that all the foliar N, P and K values obtained in these trials were below the Diagnosis and Recommendation Integrated System (DRIS) norms established by Wairegi and Van Asten, (2009) from foliar samples collected from the banana growing regions of Uganda and those established by Wortman et al. (1994) for highland bananas in northwest Tanzania. However, the Ca values obtained in this study were higher than reported values, and the Mg values were comparable. The DRIS method uses nutrient ratios for interpretation of leaf analysis as compared with absolute nutrient concentrations. This does not capture the dilution phenomena of plant N (decrease in N concentration). Hallmark et al. (1987) modified DRIS to include ratios of nutrient concentrations to dry matter e.g. N/dry matter. Despite this shortcoming, the original DRIS method is commonly used.

Better N and P conversion efficiencies at Kawanda compared with Ntungamo suggest that N and P uptake are constrained probably by drought (soil moisture availability) at Ntungamo. Low N and P conversion efficiencies were observed in the control and 400N−50P−0K treatments at Ntungamo. These treatments produced the least yield, but K conversion efficiencies were largest for the same treatments. In these treatments, the K mass fraction in the banana plant is small, hence reaching maximum K dilution (Figure 2c) (cf. Smaling and Janssen, 1993). This implies that the amount of banana finger biomass produced per unit of K in plant biomass was maximum. Nutrient synergies were clear at Ntungamo with K limitation (400N−50P−0K) constraining the uptake of N and P, and P limitation (400N−0P−600K) having more effect on K uptake compared with N limitation (0N−50P−600K) − (Table 5). In general, nutrient uptakes in our trials were less than the values (388 kg N ha^{-1}, 52 kg P ha^{-1} and 1438 kg K ha^{-1}) reported by Lahav and Turner (1983) for AAA dessert banana plants yielding 50 Mg ha^{-1} FW at a density of 2400 plants ha^{-1}. However, if expressed per unit Mg FW bunch yield, uptakes in our study were larger for N, but similar for P and K to those reported in Lahav and Turner (1983).

The average N conversion efficiency obtained for highland banana at both study sites were not much different from values reported for maize (42.3 kg grain kg^{-1} N) and wheat (40.1 kg grain kg^{-1} N) - (Mingqiang et al., 2006). However, P conversion efficiency was twice as large for banana (587 kg finger DM kg^{-1} P) as compared with maize (255 kg grain kg^{-1} P) and wheat (269 kg grain kg^{-1} P), and K efficiency was much less (10.8 kg

finger DM kg^{-1} K) as compared with maize (50.6 kg grain kg^{-1} K) and wheat (43.1 kg grain kg^{-1} K). Similarly, the boundary lines (maximum dilution and maximum accumulation – Fig 2a) describing the envelope of banana finger yield (kg ha^{-1} DM) and N uptake (102.3 kg and 31.9 kg finger DM kg^{-1} N) were comparable with values reported for rice (96 kg and 42 kg grain kg^{-1} N; Witt et al., 1999, and 112 kg and 48 kg grain kg^{-1} N; Haefele et al., 2003). However, their K values (115 kg and 36 kg grain kg^{-1} K; Witt et al., 1999, and 102 kg and 32 kg grain kg^{-1} K; Haefele et al., 2003) were larger than values obtained in our study (26.5 kg and 7.1 kg DM kg^{-1} K). Smaller K boundary and conversion efficiency values can be explained by the differences in crop physiology and nutrient requirements. Bananas take up large quantities of K during growth (cf. Turner and Barkus, 1983; Purseglove, 1988; Zake et al., 2000). Mean K uptake in the treatment 400N−50P−600K was five times larger than uptake in the plots without K fertilizer.

Data from the Ntungamo trial was summarized by use of the QUEFTS model. QUEFTS predicted the poor yields from the control and the fertilizer treatment without K well, further emphasizing the importance of K fertilization in bananas. Agreement between observed and predicted yields for treatments receiving PK or NPK is attributed to the good response to fertilization at this site (Tables 2 and 3). High sensitivity of QUEFTS to parameter *d,* is attributed to the slope, with small changes in the value of *d* resulting in large changes in model output. The values of *q* are small with changes having little effect on model output. High sensitivity to changes in available soil K and extractable soil P emphasizes the importance of these nutrients in banana production in Ntungamo (Table 2). The over-predictions with QUEFTS of banana yields at Mbarara are due to the higher exchangeable K content, and possibly lower recovery fractions at Mbarara than at Ntungamo. Thus, the total supply of K is good but the response was not as large as observed at Ntungamo. The lack of agreement between measured and predicted finger yield may be explained by decreased nutrient uptake due to the low rainfall at Mbarara (1026 mm and 942.6 mm for 1997 and 1998) compared with Ntungamo (Figure 1b). In addition, nutrients other than NPK may have been limiting. The model QUEFTS assumes that yield is a function of N, P and K supply and ignores constraints of other nutrients e.g. Mg or moisture availability, which is highly variable depending on soil type. This paper presents the first attempt to calibrate QUEFTS for highland banana. Since cycle 1 plants were used for calibration, the transfer of dry matter to the cycle 2 plant either during its early stages of development or after harvest of the cycle 1 plant (from parts that stay alive after harvest) and nutrient supply through mineralization of crop residues are not captured by this model.

3.4.3 Improving nutrient management in highland banana systems

The N and P apparent fertilizer recovery fractions calculated in this study were low, especially at Kawanda. I suspect that this is due to low soil available water and restricted root depth (<40 cm). Prasertsak et al. (2001) reported 15% N recovery in banana plants (shoot, crop residues and roots) for urea applied on the soil surface, with 60% remaining in the soil and 25% lost from the system by run-off, leaching, ammonia volatilisation or denitrification in the wet tropics of Queensland, Australia (annual rainfall 1800−4000 mm and plant density 1300 mats ha^{-1}). In our trials, urea was applied in dissolved form and split fertilizer applications were used to reduce N losses, but recovery values are still lower. This implies that the applied fertilizer remains unused in the soil, temporarily or permanently, or is lost (Dobermann and White, 1999). Leaching losses from soils with a low cation exchange capacity in Martinique were reported to be 165 kg N ha^{-1} yr^{-1} under higher rainfall (1400−2000 mm yr^{-1}) – (Godefroy and Dormoy, 1990).

Larger K recovery fractions at both trial sites are due to the importance of this nutrient in banana growth. However, the apparent K recovery fractions are less than the 75% reported by Lopez and Espinoza (2000), suggesting that other factors such as soil moisture availability may have limited K uptake and thus the banana yield. Under intensive management in central America (Costa Rica and Honduras), maximum recovery fractions are estimated at 50% N, 30% P and 75% K. Using the QUEFTS modelling approach and the above recovery fractions, 426 kg N ha^{-1} + 55 kg P ha^{-1} + 1576 kg K ha^{-1} are required to produce 70 Mg ha^{-1} FW. These values are not much different from fertilizer application rates (300−450 kg N, 50 kg P and 1200 kg K ha^{-1}) in high yielding plantations e.g. in Costa Rica (Robinson, 1996). Given the very small apparent fertilizer recovery fractions at Kawanda, single application of fertilizer without improved soil moisture management (e.g. mulching) does not appear to be a wise option. At Ntungamo, the fertilizer rates required are large (Figure 4), making fertilizer use unprofitable given that the average farm gate price for bananas of USD 0.072 per kg FW (1USD = 2090 Ug.Shs.) and fertilizer prices of USD 50 per bag of 50 kg for most fertilizers (prices for 2008−09).

In order to make fertilizer use attractive to smallholder farmers, the recovery fractions of the applied fertilizer have to be increased to reduce the amount of fertilizer required (Figure 4). In addition, the placement of high quantities of urea 40−50 cm from the pseudostem as done in our trials seems to have problems especially in soils with poor available soil water as noted at Kawanda. Practices that increase soil moisture availability

in the highland region with moderate rainfall (<1200 mm yr^{-1}) like mulching, which allow better fertilizer recovery have to be encouraged (cf. Zake et al., 2000; McIntyre et al., 2000; Ssali et al., 2003. The addition of mineral fertilizer (100N−25P−100K; kg ha^{-1} yr^{-1}) to a relatively good soil (i.e. 0.7 $cmol_c$ kg^{-1} exchangeable K, 32 mg kg^{-1} extractable P and 12.6 g kg^{-1} soil organic carbon) raised bunch yields from 45.8 to 67 Mg ha^{-1} yr^{-1} at Rubale, southwest Uganda (Smithson et al., 2001). Irrigation can improve fertilizer recovery, but it is uncommon in smallholder banana based farming systems. In commercial banana plantations in other parts of the world, supplementary irrigation is done, resulting in shorter leaf emission intervals, larger pseudostem girth, and higher yields (Eckstein et al., 1998). A study by Bananuka (2001) showed that with supplemental irrigation to maintain soil moisture content around field capacity, highland banana yields of 59 Mg ha^{-1} FW could be obtained. However, the author does not mention the amount of fertilizer applied to obtain this yield. The profitability in year 2 was estimated at Ug.Shs. 2.064 million (USD 988), assuming a farm gate price of Ug.Shs. 100 per kg. This shows that by combining fertilization and increasing soil moisture availability, apparent recovery fractions can be increased resulting in larger banana yields on smallholder farms in Uganda.

3.5. Conclusions

Highland banana yields and plant performance continued to improve with successive crop cycles when fertilizers were applied. Per unit dry matter yield, highland bananas take up a similar amount of N, half the amount of P, and five times the amount of K, when compared with cereals. Perhaps not surprising, K proved to be the most limiting nutrient for banana growth at the trial sites. Foliar nutrient contents across sites and fertilizer treatments were below existing DRIS norms and smaller foliar K mass fractions at flowering were linked to larger bunch and biomass yields. Fertilizer recovery fractions measured in this study were below values published for AAA dessert bananas in central America, particularly for N and P, due to differences in crop management. The QUEFTS model for highland bananas used in this study proved to compute fertilizer response at a third site reasonably well, but poor fertilizer recovery rates strongly reduce the attractiveness of fertilizer application for smallholder farmers. This is unfortunate, since the combination of further increasing population pressure and negative nutrient balances further increase pressure on yields and food security. More research will be needed to

better understand the effect of soil physical properties and drought stress on yields and fertilizer recovery rates in highland bananas. At the current fertilizer input and farm gate banana prices, fertilizers can probably only be recommended to farmers when coupled with practices that increase soil moisture availability, such as mulching and irrigation.

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CHAPTER 4

Modelling the potential production of East Africa highland banana (*Musa* spp., AAA-EAHB cv. Kisansa) using LINTUL BANANA 1 model

This chapter will be submitted in modified form to Agricultural Systems as:

K. Nyombi, P.A. Leffelaar, M. Corbeels, P.J.A. van Asten, K.E. Giller, 2009. Modelling the potential production of East Africa highland banana (*Musa* spp., AAA-EAHB cv. Kisansa) using LINTUL BANANA 1 model.

Abstract

A dynamic radiation and temperature-driven physiological growth model for potential production of East Africa highland banana, LINTUL BANANA 1, was developed. The model considers a synchronized banana plantation with a mat consisting of two to three plant generations; Plant 1 (mother plant), Plant 2 (sucker 1) and Plant 3 (sucker 2), growing over a duration of more than one year. The plants shade each other, with lower plants (2 and 3) receiving less radiation. Data for model parameterization were collected from trials at Kawanda, central Uganda and Ntungamo, southwest Uganda. Dry matter increase was calculated based on intercepted photosynthetically active radiation (PAR), a constant light use efficiency (LUE) and dry matter transfers between plants. Partitioning factors for the shoot, shoot parts and roots are defined as a function of the phenological development stage of the crop. Leaf area index increase (GLAI) was simulated as a function of temperature in the juvenile stage and through leaf dry mass and specific leaf area (SLA) in the maturation stage. Computed potential bunch production was higher at Ntungamo 20 Mg ha^{-1} DW (111 Mg ha^{-1} FW), compared with Kawanda 18.25 Mg ha^{-1} DW (100 Mg ha^{-1} FW), due to a longer growth period and leaf duration, resulting into more radiation interception. Computed values compared well with measurements from banana fields under optimal growing conditions at comparable leaf area index values (20.3 Mg ha^{-1} DW or 113 Mg ha^{-1} FW). Leaf dry matter and leaf area index at flowering were larger at Ntungamo (4.4 Mg ha^{-1} DW and 5.3), compared with Kawanda (3.8 Mg ha^{-1} DW and 4.5). Sensitivity analysis was done to assess the effects of changes in parameters (light use efficiency (LUE), light extinction coefficient (k), specific leaf area (SLA) and relative death rates of leaves (r_d)) and initial dry matter values (DM1I and DM2I) on model output. At Ntungamo, the sensitivity of bunch DM, leaf DM and leaf area index at flowering to changes in LUE1 (1 refers to the mother plant) were 1.36, 0.67 and 0.67; for k1 0.42, -0.16 and -0.16; for SLA1 0.37, -0.14 and 0.69; and for r_d1 -0.89, -0.29 and -0.30, respectively. A sensitivity of e.g. 1.36 means that a 1% increase of LUE results in a 1.36% increase in bunch DM. At Kawanda, the sensitivity of bunch DM, leaf DM and LAI at flowering to changes in LUE1 were 1.30, 0.60 and 0.60; for k1 0.35, -0.24 and -0.25; for SLA1 0.30, -0.22 and 0.61; and for r_d1 -0.61, -0.10 and -0.11, respectively. The changes in initial total dry matter of the plants had small effect at both sites. It is clear that management options that increase LUE and reduce r_d (e.g. by fertilization) are important for increasing yield.

Key words: calibration, radiation use efficiency, sensitivity analysis, crop growth

4.1. Introduction

East Africa highland bananas (*Musa* spp., AAA-EAHB) are an important staple starch food and cash crop for about 100 million people in the Great Lakes region (i.e. Uganda, Tanzania, Rwanda, Burundi, parts of eastern Democratic Republic of Congo, and Bukoba and Kilimanjaro areas of Tanzania). Yields of highland banana in Uganda are low, due to poor soil fertility, moisture stress, pests, diseases and poor crop husbandry practices (NARO, 2000; Gold et al., 1999). The importance of water as an abiotic constraint limiting yields in highland banana production systems has increased over time, due to variability in annual rainfall amounts and reduced access to mulch materials (Zake et al., 2000; McIntyre et al., 2003; Taulya et al., 2006). As a first step to improving production, a complete understanding of the highland banana system is important. This will allow the quantification of the potential production. Potential crop production is obtained under optimal soil moisture conditions with adequate supply of nutrients and in the absence of pests, diseases or weeds, being determined by solar radiation, temperature, crop phenology, physiology and canopy architecture (Evans and Fischer, 1999).

An established banana plantation consists at any given time of plants at different stages of growth that each develop at their own rate. An individual banana mat consists of a mother plant with lateral shoots (suckers) growing from buds on the corm (true stem), which produce the next inflorescences. Under good management, two or three generations of plants; Plant 1 (mother plant), Plant 2 (sucker 1) and Plant 3 (sucker 2) form a mat. The appearance of the inflorescence marks the end of leaf production and the start of bunch finger filling. At bunch maturity, when the fingers are fully filled, the shoot of the mother plant is removed. Depending on management, the mat production cycle can be continued over 30 years (Speijer et al., 1999), compared with commercial plantations in other parts of the world where only 2−3 crop cycles are harvested and fields re-planted.

The application of existing banana models to this perennial highland banana system is difficult. The standard crop growth simulator model (STICS) which simulates crop growth as well as soil water and nitrogen balances driven by daily climate data, was adapted and used to simulate banana growth in the French West Indies (Brisson et al., 1998). However, STICS cannot be used to estimate potential production and does not capture banana plantation dynamics (three generations of plants). The SIMBA-POP model based on the cohort population concept was used to predict phenological patterns of the population and harvest dynamics for banana cultivar ‘Grand Nain’ (*Musa* spp., Cavendish sub-group) in the West Indies (Tixier et al., 2004). The SIMBA-POP model is

based on development with no physiological details. Kooman and Jones (1995) modified a relatively simple general crop growth model developed by Spitters and Schapendonk (1990) and used it to simulate banana growth for a single crop cycle, with dry matter partitioning to one sucker in Honduras. The CENTURY model (plant-soil-environment) developed by Parton et al. (1987) to simulate plant growth and organic matter dynamics in temperate regions was adapted to simulate East Africa highland banana growth and carbon dynamics, but did not give very good results (Woomer et al., 1998).

Therefore, the LINTUL BANANA 1 model was developed considering (i) the physiology of the highland banana crop; (ii) the plant dynamics (i.e. three plant generations, Plant 1, 2 and 3 at different stages of growth) with the leaves of the three plants forming three canopy levels. It is based on the light use efficiency (LUE) approach introduced by Spitters and Schapendonk (1990) in the LINTUL model – Light INTerception and UtiLisation Simulator. Crop growth models based on the radiation interception and light use efficiency (LUE) approach have been used on annual crops, such as ryegrass (*Lolium perenne* L.) (LINGRA; Schapendonk et al., 1998), wheat and corn (*Zea mays* L.) (STICS; Brisson et al., 1998) and trees or forests e.g. eucalyptus (*Eucalyptus globulus*) (G'DAY; Corbeels et al., 2005).

The goal of this study was to increase our understanding of how potential production is attained in East Africa highland banana. This was to enable the quantification of potential production and the yield gaps between potential and actual production. The objectives of this study were to: (i) develop a model to estimate highland banana potential production; (ii) explain variations in potential production at two contrasting sites in Uganda; and (iii) make phenotype and management recommendations based on the sensitivity analysis.

4.2. LINTUL BANANA 1 model description

LINTUL BANANA 1 is a growth simulation model for the potential production of East Africa highland bananas. The model assumes a mature (established) banana plantation, synchronised with two or three plant generations, Plant 1 (mother plant), Plant 2 (sucker 1) and Plant 3 (sucker 2) constituting a mat, growing over a duration of more than one year. The canopy is divided into three leaf levels, with lower plants (2 and 3) receiving less radiation as a result of shading by plant 1. Biomass production is modelled as the product of light interception and a constant light use efficiency for the site (kg MJ^{-1} PAR), with

biomass partitioning coefficients that are defined as a function of the phenological development stage of the banana plant (c.f. Spitters and Schapendonk, 1990). The processes in LINTUL BANANA 1 are (i) phenological development; (ii) light interception and use; (iii) leaf area development and death; (iv) dry matter production and transfer between plant 1 and 2, and between plant 2 and 3; (v) shoot-root and shoot dry matter partitioning. Partitioning of dry matter to the shoot and root and within the shoot are separated in order to be able to incorporate effects of water limitation on root-shoot partitioning later.

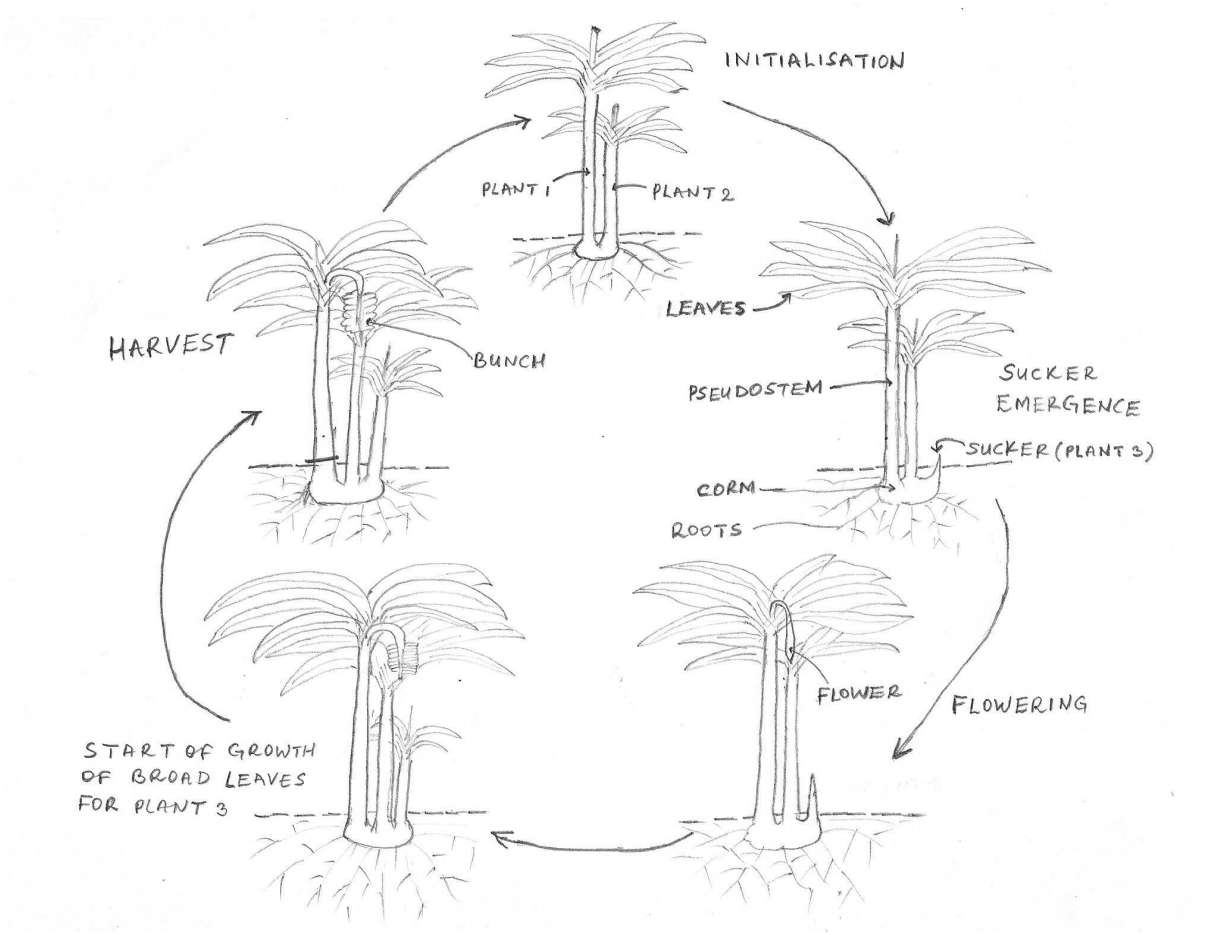

Figure 1. Scheme of the highland banana system showing the phenological stages and plants. Plant 1, Plant 2 and Plant 3 constitute a mat. At bunch maturity, Plant 1 is cut away (indicated by a small line at the base of plant 1 at harvest) leaving Plant 2 and 3.

The model is implemented in the Fortran Simulation Translator, FST (Rappoldt and van Kraalingen, 1996 and 2008). Plant development stages such as sucker emergence,

start of growth of functional leaves of plant 3, end of partitioning of dry matter to plant 3, flowering, and harvest are implemented through events triggered by the phenological development stage. At physiological maturity, harvest of bunches (plant 1) takes place, plant 2 becomes the new plant 1 and plant 3 becomes the new plant 2, with the new sucker (plant 3) emerging later in the growth process. Figure 1 shows the growth cycle considered. LINTUL BANANA 1 requires daily weather data (maximum and minimum temperature – ^{o}C) and total radiation – MJ ha^{-1} d^{-1}.

4.2.1. Model assumptions

Conditions are assumed to be optimal with respect to soil moisture and nutrient supply with no pests, diseases and weed competition. Plant 3 emerges with no functional leaves (cf. Stover and Simmonds, 1987), and is assumed to completely depend on plant 2 for a certain period (here: 0−360 °C d). During the following period, here 360−960 °C d, it is dependent on its own photosynthesis (following the start of the growth of functional leaves at 360 °C d) and a reducing amount of newly produced DM is supplied by plant 2.

Plant 3 is initiated as part of the corm of plant 2, with differentiation taking place over time (Figure 1). Root growth for plant 3 is assumed to start after emergence, with the fraction of dry matter allocated to roots increasing between[1] 0−360 °C d, and decreasing after the start of the growth of functional leaves to zero at 2663 °C d (flowering). No new banana roots emerge after shooting (flowering) – (Turner, 1970, Robinson, 1996), hence there is no dry matter partitioning to the roots after flowering. Since plant 3 forms the third canopy layer, it is heavily shaded by plant 1 and 2. Its increase in dry matter is dependent on partitioning from plant 2 (plant 2, which is also shaded by plant 1) and its own photosynthesis. Due to these effects, the growth in dry matter of plant 3 is small. Therefore, the relative death rates of leaves and roots for plant 3 are assumed to be zero. Banana roots of the mother plant after harvest are known to support the new mother plant (Walmsley and Twyford, 1968). Since it is not easy to quantify this, this effect is not added into the model. From the experimentation, there is uncertainty in the relative death rate of leaves (r_d or RDR) values due to drought, values are computed directly for the sites. It has been noted in commercial banana plantations that high LAI (> 4) of mother plants may retard growth and lengthen the cycle duration of the next crop harvest (Robinson, 1996). This effect is not added into LINTUL BANANA 1.

[1] In the further text specific values of physiological age are mentioned, but these parameters can be adapted to other banana cultivars.

4.2.2. Crop phenology

Crop development was based on temperature. The durations between the development stages are a function of the temperature sum (TSUM), computed as follows:

$$T_{\text{sum}} = \sum_{i=1}^{n} (\textit{average temperature day}_i - \textit{base temperature}) \quad (1)$$

where average temperature is calculated as (maximum + minimum temperature)/2 and the base temperature for banana growth is 14 °C (Robinson, 1996). In the model, plant development rate is proportional to integrated temperature (average temperature−base temperature) over time. Bananas are generally day-neutral in their response to day length, but photoperiods of less than 12 h are associated with a slight reduction in the rate of bunch initiation (Turner et al., 2008). This model does not incorporate photoperiodism and was developed for sites close to the equator.

4.2.3. Light interception and use efficiency

In LINTUL BANANA 1, the banana canopy was separated into three canopy levels (plant 1, 2 and 3). The amount of photosynthetically active radiation intercepted (MJ ha^{-1} d^{-1}) was calculated for the three levels following Beer-Lambert law: the incoming light passing a leaf level was reduced by $e^{-(ki \times Li)}$, where i is 1, 2 and 3 for the different leaf levels, respectively, and outgoing light was thus the input for the next leaf level. The amount of light intercepted was calculated by the difference between in- and outgoing light. The upper leaf level receives the daily total radiation (*DTR*, MJ ha^{-1} d^{-1}), half of which is the fraction of PAR (Doorenbos and Pruitt, 1984), *k*i and *L*i are the light extinction coefficient (ha soil ha^{-1} leaf) and leaf area index (ha leaf ha^{-1} soil) of plant level i.

4.2.4. Leaf area development

Leaf area index development in highland bananas was divided into two stages: the juvenile stage and the maturation stage. The juvenile stage was again divided into two parts; the first, with plant 3 having no functional leaves (Growth of leaf area index = 0), and the second part, starting with formation of functional or broad leaves. During the second part, leaf area increases exponentially as a function of the temperature

(360>TSUM3<960). The assumption is that leaf size and the rate of leaf emission are constrained by temperature through its effect on cell division and extension (Spitters et al., 1989). The growth rate of the leaf area index during this phase was calculated as:

$$\left(\frac{\mathrm{d}L}{\mathrm{d}t}\right) = r_g \times L \tag{2}$$

where d*L*/d*t* is the growth rate of LAI (ha leaf ha^{-1} soil d^{-1}), r_g is the relative growth rate, which is a product of the relative growth rate of leaf area during the juvenile phase (RGRL, expressed as $(°Cd)^{-1}$) and the daily effective temperature – DTEFF, and *L* is the leaf area index (ha leaf ha^{-1} soil). In the maturation stage, banana growth was assumed source-limited and the growth of leaf area index was calculated as the product of the growth rate of leaf dry matter and the specific leaf area (SLA) (van Keulen and Seligman, 1987) as follows:

$$\left(\frac{\mathrm{d}L}{\mathrm{d}t}\right) = \left(\frac{\mathrm{d}W}{\mathrm{d}t}\right) \times F_{lv} \times SLA \tag{3}$$

where d*L*/d*t* is the growth of leaf area index (ha leaf ha^{-1} soil d^{-1}), F_{lv} is the fraction of total dry matter partitioned to leaves, and *SLA* is the specific leaf area (ha leaf kg^{-1} leaf DM). The net change in LAI (ha leaf ha^{-1} soil d^{-1}) during growth was calculated as the difference between growth and death rates of LAI. The death rate of LAI (ha leaf ha^{-1} soil d^{-1}) was calculated using the relative death rate, r_d (d^{-1}) due to aging.

$$\frac{\mathrm{d}L}{\mathrm{d}t} = L \times r_d \tag{4}$$

Death of leaves due to shading occurs at LAI > 4 (Anonymous, 1997), but in the trials, LAI was lower, therefore death of leaves was only attributed to leaf aging. The net growth of the weight of green leaves was calculated as the difference between growth and death rate of leaves. The death rate of leaves was calculated as follows:

$$\frac{\mathrm{d}Wlv_i}{\mathrm{d}t} = Wlv_i \times r_d \quad (5)$$

where $\mathrm{d}Wlv_i/\mathrm{d}t$ is the death rate of leaves (kg DM ha^{-1} d^{-1}), Wlv_i is the weight of green leaves for plant 1 and 2 (i = 1−2) in kg DM ha^{-1} and r_d is the relative death rate of leaves (d^{-1}). The weights of green and dead leaves (kg DM ha^{-1}) were obtained by integrating their rates over time.

4.2.5. Dry matter production and transfer

Light use efficiency models are based on the observation by Monteith (1977) that the relationship between dry matter produced and intercepted photosynthetically active radiation (PAR), for several agricultural crops with crop growth not limited by water or nutrient supply, was linear. The slope of this relationship is the light use efficiency – LUE (kg DM MJ^{-1} PAR). The physiological basis of the light use models taking a linear relationship between biomass produced and intercepted photosynthetically active radiation (PAR), when the relationship between leaf photosynthesis and intercepted PAR is non-linear, has been challenged (Medlyn, 1998). The reason for the linearity is that canopy structure allows incident PAR to be distributed such that most leaves are exposed to non-saturating radiation levels, hence a linear response of canopy photosynthesis to intercepted PAR (Sinclair and Muchow, 1999). Banana leaves have been reported not to be fully saturated even at 2000 μmol quanta m^{-2} s^{-1} (Robinson, 1996). In addition, integrating over time, for example a month or year, reduces the variability in canopy light use efficiency and increases the linearity of the relationship between the amount of biomass produced and total intercepted PAR (Spitters, 1990; Dalla-Tea and Jokela, 1991).The rates of plant dry matter increase are modelled as the product of the intercepted PAR and a constant LUE as follows:

$$\frac{\mathrm{d}WH_i}{\mathrm{d}t} = I_{\mathrm{int,i}} \times LUE_i \quad (6)$$

where $\mathrm{d}WH_i/\mathrm{d}t$ is the growth rate of the plant, i =1−3, from intercepted radiation (kg DM ha^{-1} d^{-1}), $I_{\mathrm{int,i}}$ is the amount of PAR intercepted by the individual plant, and LUE_i is the light use efficiency coefficient (kg DM MJ^{-1} PAR).

During banana growth, plant 1 provides dry matter to plant 2 (here: TSUM1 2262–2423 °C d), and plant 2 supports plant 3 (here: TSUM3 0–960 °C d). At flower initiation, plant 1 needs the assimilates to fill the bunch later, so it is assumed that support to plant 2 stops at this stage.

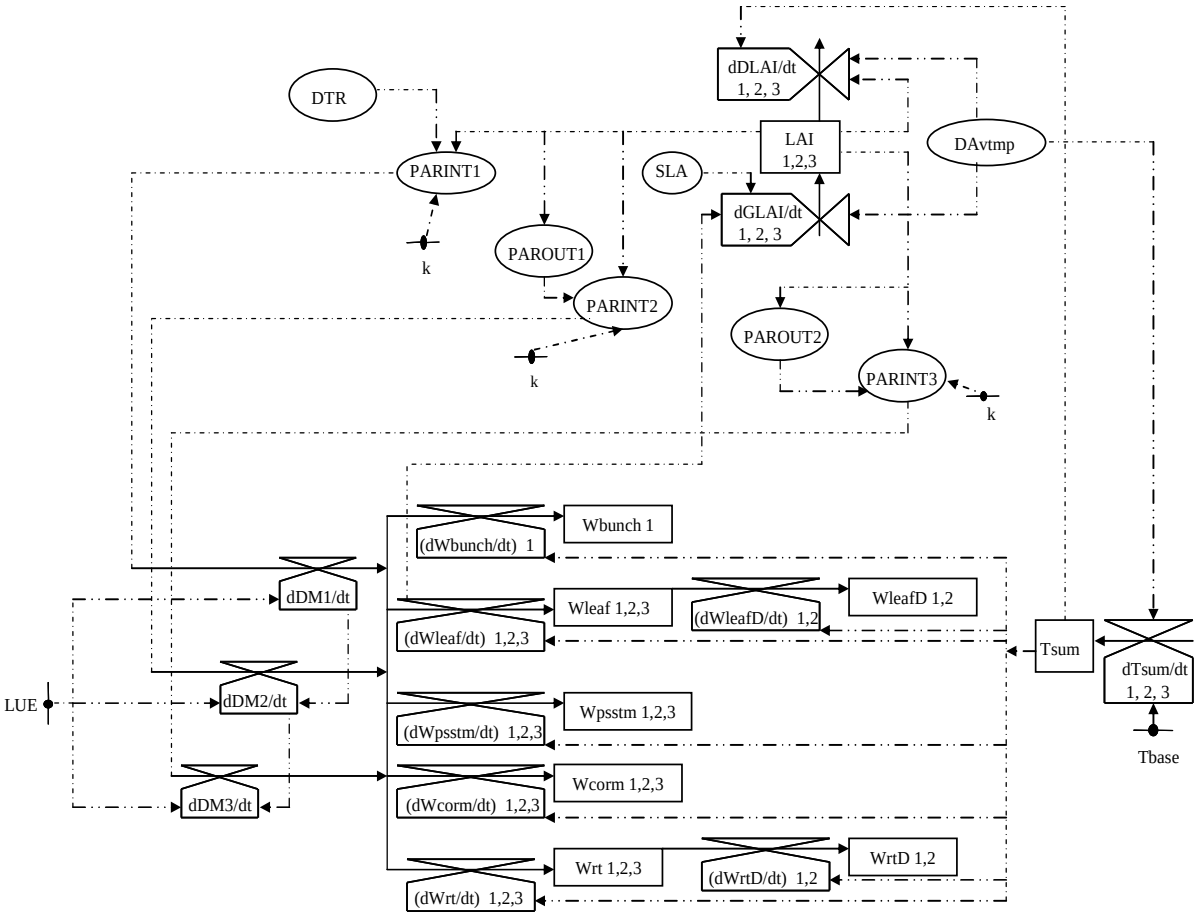

Figure 1. Relational diagram of LINTUL BANANA 1 for potential banana production (modified from Anonymous, 2007). DTR – daily total radiation, PAROUT1 – photosynthetically active radiation not intercepted by plant 1, PAROUT2 – photosynthetically active radiation not intercepted by plant 2, PARINT1,2,3 – photosynthetically active radiation intercepted, k – light extinction coefficient, LUE – light use efficiency, dDM1/dt, dDM2/dt, dDM3/dt – rates of biomass production, SLA – specific leaf area, Tbase – base temperature for growth, DAvtmp – daily average temperature, Wbunch 1 – weight of bunch, (dWbunch/dt) 1 – growth rate of bunch for plant 1, LAI – leaf area index, Tsum – temperature sum, dGLAI/dt – rate of increase in leaf area index, dDLAI/dt – rate of reduction in leaf area index due to death, (dWleaf/dt) – growth rate of leaves, (dWpsstm/dt) – growth rate of pseudostem, (dWrt/dt) – growth rate of roots, (dWcorm/dt) – growth rate of corm, (dWleafD/dt) – death rate of leaves, (dWrtD/dt) – death rate of roots, Wleaf – weight of green leaves, WleafD – weight of dead leaves, Wpsstm – weight of stem, Wrt – weight of roots, WrtD – weight of dead roots, Wcorm – weight of corm, and dTsum/dt – rate of increase in temperature sum for plants 1, 2 and 3. At harvest, plant 1 is cut away. Solid lines are material flows and dotted lines are information flows.

The fraction of dry matter partitioned to Plant 3, *FS*, was assumed to linearly decrease from 0.05 (*FSmax*) at TSUM2 1662 °C d, to 0 at TSUM1 = 2423 °C d (flower initiation stage). As a result of support to plant 2, the growth rate of dry matter of plant 1 was calculated as follows:

$$\frac{\mathrm{d}W1}{\mathrm{d}t} = \frac{\mathrm{d}WH1}{\mathrm{d}t} \times (1.0 - FS) \qquad (7)$$

where d*W1*/d*t* is the growth rate of plant 1 (kg DM ha^{-1} d^{-1}), d*WH1*/d*t* is the growth rate of plant 1 from intercepted radiation (kg DM ha^{-1} d^{-1}), *FS* is the fraction of dry matter partitioned to plant 2 by plant 1 during the period when it receives dry matter (TSUM1 (2262−2423 °C d), and (1−*FS*) is thus the part of the dry matter supporting Plant 1. The growth rate of dry matter of plant 2 (d*W2*/d*t*) was calculated based on two stages/processes; (i) where plant 2 fully supports plant 3 (TSUM3 0−360 °C d), with plant 3 having no functional leaves, and (ii) where a decreasing amount of dry matter is partitioned to plant 3 (TSUM3 360−960°C d). In addition, plant 2 receives dry matter from plant 1 during the period (TSUM2 960−1121 °C d). This approach is supported by a study by Eckstein et al., (1995a). The growth rate of dry matter of plant 3 (d*W3*/d*t*) was calculated based on two stages/processes; (i) where the sucker has no functional leaves, with the growth rate calculated as the product of the growth rate of plant 2 (d*W2*/d*t*) times *FS* (ii) where exponential growth of *L* takes place, with growth rate calculated as the sum of product of the growth rate of plant 2 (d*W2*/d*t*) times *FS* plus the growth rate of plant 3 due to radiation interception (d*WH3*/d*t*). During highland banana growth, leaves and roots do die. The net growth rates of dry matter of the three plants were calculated as the difference between their growth rates and the death rates of leaves and roots. Total dry matter produced by plants 1, 2 and 3 (DM1, DM2 and DM3, kg DM ha^{-1}) were obtained by integrating the net growth rates of plant dry matter over time.

4.2.6. Root-shoot and shoot dry matter partitioning

Dry matter produced during growth was partitioned between the shoot and roots. Plant 3 is initiated as part of the corm of plant 2, gradually differentiating into the corm of plant 3 and the pseudostem of plant 3 (Figure 1). Root growth is assumed to start after emergence, with root:shoot ratio of plant 3 increasing during the period 0−360 °C d due to increasing partitioning to roots (linear function Prt 1), calculated around the average Prt_{cal}

(Figure 3). The root:shoot ratio to be reached at TSUM3 360 °C d was set at a maximum of 0.2 (estimated from Blomme et al., 2008). The dynamics of the parallel shift up and down of the slope of the function α as a function of water stress is effected via intercept B, through Prt_{cal}.

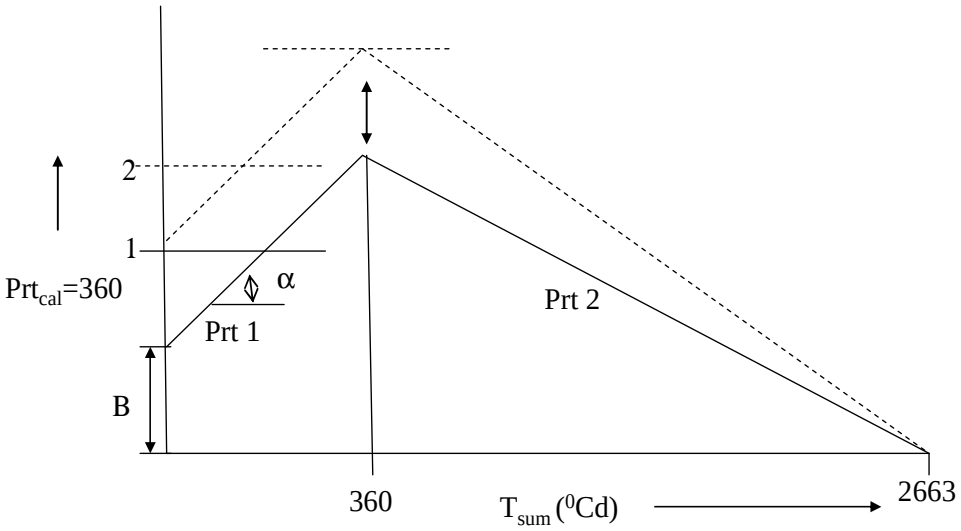

Figure 3. Root:shoot ratio during the simulation. On average the root:shoot ratio is Prt_w, but this value may increase from a lower one to the top at 360 ^{0}Cd (Prt 1). Thereafter the root:shoot ratio decreases down to zero at the Tsum of flowering (Prt 2). Slope $\alpha = A_{fixed}$ and B the intercept are explained in the text. The value of the horizontal lines, indicated by 1 and 2, signify the average partitioning that is desired during the simulation. The model is prepared to cope with a changing partitioning due to water stress through the possibility of a parallel shift of the line with slope α.This shift is dynamic, as indicated by the vertical small two-sided arrow.

From *TSUM*=360 °C d, a reducing fraction of dry matter is partitioned to the roots given by function Prt 2 (Figure 3). Partitioning to roots is zero after flowering. The growth rates of roots and shoot (kg DM ha^{-1} d^{-1}) were calculated as the product of the fraction of dry matter partitioned to the part and the total growth rate of dry matter. The net rates of change in root and shoot dry matter (kg DM ha^{-1} d^{-1}) were calculated as the difference in growth and death rates of root and shoot dry matter. The death rate of roots was calculated as follows:

$$\left(\frac{\mathrm{d}Wrtd_i}{\mathrm{d}t}\right) = Wrt_i \times r_{dr} \qquad (8)$$

where d$Wrtd_i$/dt is the absolute death rate of roots of plant, i = 1−3 (kg DM ha^{-1} d^{-1}), Wrt_i is the weight of roots of plant, i = 1−3 (kg DM ha^{-1}) and r_{dr} is the relative death rate (d^{-1}).

Shoot dry matter was partitioned amongst the leaves, pseudostem, corm and bunch (for plant 1) as a function of temperature sum. The growth rates of the shoot parts were calculated as:

$$\left(\frac{\mathrm{d}W_x}{\mathrm{d}t}\right) = \left(\frac{\mathrm{d}W_i}{\mathrm{d}t}\right) \times F_x \tag{9}$$

where $(\mathrm{d}W_x/\mathrm{d}t)$ is the growth rate of organ x (leaves, pseudostem, corm and bunch) (kg DM ha^{-1} d^{-1}) and F_x is the fraction of dry matter allocated to organ x, which is a function of the temperature sum (Figure 4). The weights of these organs during growth are obtained by integrating their growth rates over the growth period.

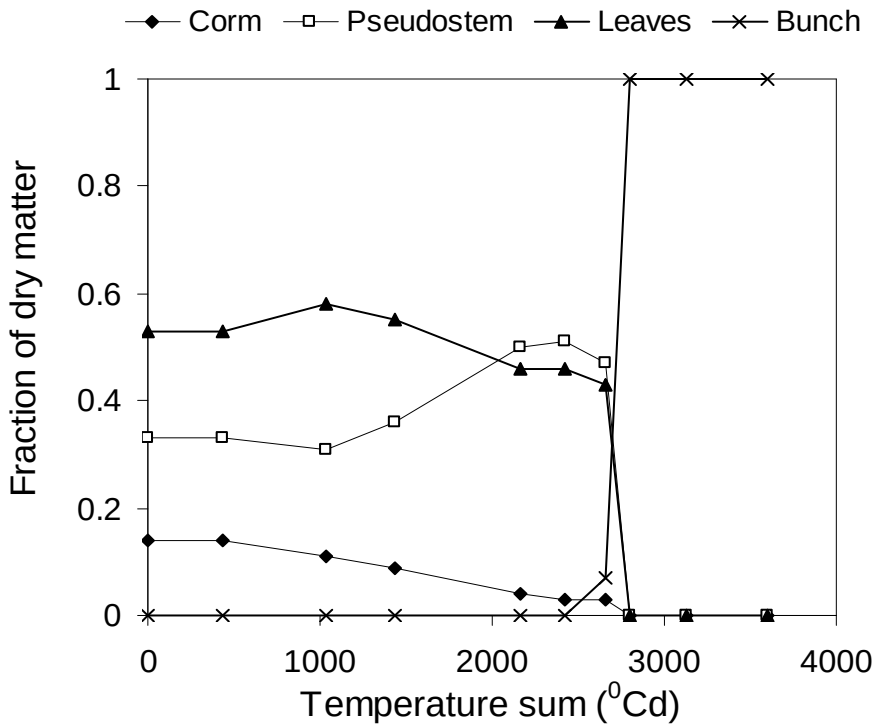

Figure 4. The partitioning of dry matter produced among above ground sinks, the corm, pseudostem, leaves and bunch as a function of thermal time (°C d) based on daily temperature.

Partitioning factors (allocation coefficients) were derived using a method described by Kropff et al., (1994a). The fraction of dry matter partitioned to the plant organ was calculated as:

$$F_x = \frac{(W_{t+1} - W_t)}{(Growth)} \quad (10)$$

where W_{t+1} is the weight of the organ after time interval t+1, W_t is the weight of the organ at time t, and *Growth* is the increase in dry matter (kg DM ha^{-1}) during the interval (t+1−t). The temperature sum (TSUM) corresponding to a stage was taken as the average of the TSUMs of the successive samplings where the weights of the organs were determined. The factors were based on destructively sampled plants at Kawanda. Pseudostem dry weight is maximum at flowering and leaf production ceases at flowering, hence all the dry matter is partitioned to the bunch after flowering. Results of the calculations are given in Figure 4.

4.3. Model parameterization

Data used for model calibration were collected from two trials located at Kawanda in central Uganda (00°25'N, 32°31'E, 1156 m.a.s.l) and at Ntungamo in southwest Uganda (00°54.53'S, 30°14.86'E, 1405 m.a.s.l). Average minimum and maximum temperatures during the experimental period at Kawanda were 17.0 and 27.4 °C and at Ntungamo 13.0 and 27.2 °C, respectively. The experiments are fully described in Chapter 2 and 3. The initial values and parameters used in LINTUL BANANA 1 are given in Table 1 and 2.

4.3.1. Crop phenology and growth data

The phenological stages in the model are sucker emergence, start of growth of functional leaves, end of exponential increase of LAI, flower initiation, flowering and harvest. Dates of sucker emergence, flowering and harvest were recorded. The start of growth of functional leaves and the end of the exponential phase were estimated by measuring area of individual leaves for selected plants. The duration from the start of flower movement from the corm tip (referred to here as flower initiation) to emergence was estimated. "Pregnant" banana plants were destructively sampled to locate the position of the

inflorescence along the pseudostem. These plants were compared with plants with similar emergence dates that reached the flowering stage. Floral initiation in banana is controlled by internal plant mechanisms, implying that flowering can take place at any time during the year. Plant height, girth at base and the number of functional (> 50% of leaf surface area green) and dead leaves were recorded at monthly intervals. Temperature sums (TSUM) between the different development stages were calculated using equation 1.

4.3.2. Light use efficiency (LUE)

The potential light use efficiency (LUE) for highland banana at a site was obtained as the slope of the regression line of dry matter accumulation (kg) and total intercepted PAR (MJ) calculated over an interval of 2 months during the rainy season. The best treatment (400N–50P–600K) was used to determine LUE. Daily values of photosynthetically active radiation intercepted (fraction of PAR intercepted times daily total incident PAR) were summed over the interval gave the total cumulative PAR intercepted.

The light extinction coefficient, *k* for highland banana was obtained as the slope of the relationship between $-1n$ ($PAR_{\text{below canopy}}$ / $PAR_{\text{above canopy}}$) and *L* measurements in highland banana plots with different fertilizer amounts at Kawanda and Ntungamo (Chapter 2). Leaf area was estimated using middle leaf area (MLA) times the number of functional leaves (Nyombi et al., 2009). Leaf area index (LAI) was calculated as the ratio leaf area to ground area covered by the leaves. Biomass accumulation during the interval was estimated using an allometric relationship for total dry matter, including roots [Total DM (kg) = 0.0001 $(\text{girth})^{2.38}$, R^2 = 0.98)]. This allometric relationship was also used to calculate initial values of dry matter for plant 1 and 2 used in the model. The total weight of dead leaves was calculated using equation 11 and the number of dead leaves during the interval was taken from the monthly growth monitoring data. Total DM produced during the interval was the sum of DM calculated using the allometric relationship plus the total weight of dead leaves.

4.3.3. Relative death rate of leaves (r_d)

Dead leaves were collected from plants at different stages of growth in the experiment at Kawanda to determine the relative death rate of leaves. Height (cm) and girth at base (cm) were measured at the moment of dead leaf collection. Leaves were oven dried at 70 °C for

48 h and dry weights (DW) were recorded. A relationship was found between individual leaf dry weight (LDW, kg) and plant height:

$$LDW = 7\times10^{-8}\,(height)^{2.51}\ (R^2 = 0.66) \quad (11)$$

The total weight of dead leaves during the monthly monitoring intervals was calculated as estimated leaf dry weight using equation 11, times the number of dead leaves during that interval. The total weight of dead leaves at a stage during growth was calculated as the sum of all dead leaves. For a given interval, the change in total weight of dead leaves was calculated as the difference between the weight of dead leaves at the end of the interval and the weight of dead leaves at the start of the interval. The difference between the weight of green leaves at the start of the interval and the weight of dead leaves during the interval gives the weight of green leaves left. Assuming exponential decay, relative death rate of leaves – r_d (d^{-1}) for a development interval was calculated. For plant 1, the interval 2262−2663 °C d was used because records of dead leaves from flowering to harvest were not so good. For plant 2, three intervals were used 960−1394 °C d, 1394−1826 °C d and 1826−2262 °C d and an average value obtained.

4.3.4. Relative death rate of roots (r_{dr})

Root death during the vegetative phase was based on experimentation by Moreau and Bourdelles (1963) using banana cultivar 'Gros michel' (*Musa* spp. AAA). The maximum lifespan of banana roots during the vegetative phase is about 4 months. Assuming exponential decay (with 7.3% of the original root dry matter left after 120 days), the calculated relative death rate was 0.0218 d^{-1}. The roots present at flowering remain alive during the reproductive phase to fill the bunch, with 92% of the roots still functional at harvest (Blomme, 2000). Assuming exponential decay with 92% of the original root dry matter left at harvest, the relative death rate values were calculated for the sites.

4.3.5. Relative growth rate of leaf area index (RGRL)

The relative growth rate of the leaf area index during the juvenile stage was determined using tissue-culture plants grown during a rainy period (3 months), with ample supply of N, P and K. Length and maximum width of all functional leaves were recorded at

monthly intervals. Individual leaf area was estimated as length times maximum width times 0.68 (Chapter 2). RGRL (°Cd)$^{-1}$ was calculated as follows:

$$RGRL = \frac{1n(LAI)_{t2} - 1n(LAI)_{t1}}{\Delta t} \quad (12)$$

where LAI_{t1} and LAI_{t2} are the leaf area index (ha leaf ha^{-1} soil) at the start and end of the interval, Δt is the change in temperature sum (°C d).

4.3.6. Specific leaf area (SLA)

Fully expanded leaves (1, 3, 5 and 7) were selected from plants at different stages of development from treatment (400N–50P–600K). Leaves were divided into 3 equal parts (lower or base, middle and upper or tip). For each part of the leaf, the mid-rib was removed (c.f. Garnier et al., 2001). A sample was obtained from the middle of each leaf part, and its length and width measured. Leaf samples were oven dried for 48 h at 70 °C (c.f. Poorter and Garnier, 1999) and dry matter weights were recorded. Specific leaf area was calculated as leaf area (m^2) divided by leaf dry mass (kg).

4.3.7. Sensitivity analysis

The sensitivity of modelled bunch DM, leaf DM and leaf area index (*L*) at flowering to changes in model parameters (SLA, *k*, LUE, r_d and RGRL for plant 1, 2 and 3) and initial dry matter values (DM1I AND DM2I) used in the model was tested. Parameters related to growth and death of leaves, canopy structure (reflected in *k*) and the use of intercepted PAR to produce dry matter (*LUE*) were selected because the model is based on the light interception and use. The initial dry matter values are used to initialize leaf area index. Static sensitivity at the end of the simulation was estimated by the central difference method as follows:

$$Sensitivity = \left(\frac{(O_{i=\max} - O_{i=\min}) / O_{i=default}}{(I_{\max} - I_{\min}) / I_{default}} \right) \quad (13)$$

where $O_{i=max}$ and $O_{i=min}$ are the outputs given by the increase and decrease in the input, $O_{i=default}$ is the output given by the default input $I_{default}$, I_{max} and I_{min} are the maximum and minimum values resulting from the change in input. Two levels of change in model input: ±2.5% and ±5% were used. Sensitivity as a function of time (dynamic sensitivity) was assessed using equation 13. Dynamic sensitivity was assessed because some parameters may not be sensitive at the end of the simulation, but may actually be sensitive during the simulation.

4.4. Results

4.4.1. Model parameterisation results

Sucker emergence at Ntungamo occurs at TSUM2 = 1302 °C d. The duration from sucker emergence to the start of growth of broad leaves was 360 °C d, with this exponential phase ending at 960 °C d (Table 2). Flowering occurs at 2663 °C d and flower initiation was estimated to occur at 2423 °C d at Ntungamo. Harvest occurs 937 °C d after flowering. The cumulative temperature sums from sucker emergence to flowering (3383 °C d) and flowering to harvest (1109 °C d) were larger at Kawanda, compared with Ntungamo, due to extreme moisture stress during the dry season. Growth rates were reduced to zero during the dry spells, therefore the temperature sums for Ntungamo were used for this site.

The light use efficiency calculated during the rain season based on total dry matter was slightly higher at Kawanda (3.50×10^{-3} kg MJ^{-1} PAR), compared with Ntungamo (3.33×10^{-3} kg MJ^{-1} PAR). The relative death rates of leaves were lower during the period 960−2262 °C d for both sites, but higher from 2262−2663 °C d, probably due to the large leaf size and lower leaf numbers during the period prior to flowering (Table 2). Average specific leaf area (SLA) was 12 m^2 kg^{-1}.

Light competition in the model is reflected in Figures 5 a and b. The net rate of change in total dry matter of plant 2 (NDM2) is strongly dependent on the amount of radiation reaching it. Higher leaf area index of plant 1 resulted in less intercepted radiation by plant 2.

Table 1. Initial values of state variables used in LINTUL BANANA 1 model for the two trial sites, Kawanda[1], central Uganda and Ntungamo[2], southwest Uganda.

Abbreviation	Explanation	Value	Unit
TSUM1I	Initial temperature sum of plant 1	2262	°C d
TSUM2I	Initial temperature sum of plant 2	960	°C d
TSUM3I	Initial temperature sum of plant 3	0	°C d
DM1I	Initial dry matter of plant 1	5050[1], 4902[2]	kg DM ha^{-1}
DM2I	Initial dry matter of plant 2	1034[1], 1757[2]	kg DM ha^{-1}
DM3I	Initial dry matter of plant 3	0[1] , 0[2]	kg DM ha^{-1}
LAI*i*I	Initial leaf area index of plant 1 and 2	Function of initial shoot DM, fraction of green leaves, specific leaf area and partitioning to leaves	ha leaf ha^{-1} soil
L3I	Initial leaf area index of plant 3	0[1] , 0[2]	ha leaf ha^{-1} soil
Wrt*i*I, Wsh*i*I	Initial dry matter of roots and shoot of plant 1 and 2	Function of the initial total DM and the DM fraction to roots and shoot	kg DM ha^{-1}
Wcorm*i*I, Wpsstm*i*I, Wleaf*i*I	Initial dry matter of the corm, pseudostem and leaves of plant 1 and 2	Function of the initial shoot DM and fraction of DM partitioned to the organ	kg DM ha^{-1}
Wrt3I, Wsh3I, Wcorm3I,Wpsstm 3I, Wleaf3I	Initial dry matter of roots, shoot, corm, pseudostem and leaves of plant 3.	0.0 (Sucker emerges later in the growth process at TSUM2=1302 °C d)	kg DM ha^{-1}
Wbunch1I	Initial dry matter of the bunch of plant 1	0.0	kg DM ha^{-1}
WleafD*i*I	Initial dry weight of the dead leaves of plant 1 and 2	Function of total DM of leaves, shoot DM and the fraction of dead leaves	kg DM ha^{-1}
Pcorm*i*I, Ppsstm*i*I, Pleaf*i*I, Pbunch*i*I	Initial proportion of dry matter in corm, pseudostem leaves and bunch for plant 1 and 2	Function of shoot DM and DM partitioned to the organ	-
DummyPbunch*i*I	Initial proportion of dry matter in bunch for plant 2 and 3	0.0 (Only plant 1 produces a bunch thus 'dummy')	-
Pcorm3I, Ppsstm3I, Pleaf3I	Initial proportion of dry matter in corm, pseudostem and leaves for plant 3	0.0	-
FrtRED*i*I	Initial fraction of reducing dry matter to the roots of plant 1 and 2	Calculated in Prt2 function subroutine based on the temperature sum	-

Table 2. Parameters used in LINTUL BANANA 1 model for the two trial sites, Kawanda[1], central Uganda and Ntungamo[2], southwest Uganda

Parameters	Explanation	Value	Unit
SLA	Specific leaf area	0.0012	ha leaf kg^{-1}DM
LUE	Light use efficiency	0.0035[1], 0.0033[2]	kg MJ^{-1} PAR
k	Light extinction coefficient	0.7	ha soil ha^{-1} leaf
TBASE	Base temperature	14	°C
TSUMSUC	Temperature sum of plant 2 for the start of growth of plant 3	1302	°C d
STGRLV	Temperature sum for the start of growth of photosynthetically active leaves of plant 3	360	°C d
TSUM3stop_exp	Temperature sum above which exponential growth of leaf area stops	960	°C d
Lstop_exp	Leaf area index above which exponential leaf area growth stops	0.88	ha leaf ha^{-1} soil
TSUMendfulldepe	Temperature sum at the end of full dependence of plant 3 on plant 2, plant 3 starts to photosynthesize	1662	°C d
TSUMshfhv	Temperature sum of plant 2 at harvest of plant 1 (also the shift, plant 2 becoming plant 1)	2298	°C d
TSUMfloinit	Temperature sum at flower initiation	2423	°C d
TSUMflower	Temperature sum at flowering	2663	°C d
TSUMHARV	Temperature sum at harvest	3600	°C d
RGRL	Relative growth rate of leaves	0.0077	$°Cd^{-1}$
FSmax	Maximum fraction of dry matter that goes from sucker 1 to sucker 2 in the stage where sucker 2 does not have functional leaves	0.05	(kg DM sucker 2) / (kg DM sucker 1)
r_{dr}	Relative death rate of roots	0.0218 (up to 2663 °C d) 2663−3600 °C d, 0.000758[1] and 0.000556[2]	d^{-1}
r_d	Relative death rate of leaves of plant, i = 1−3.	Plant 1, 0.022[1], 0.0214[2] , plant 2, 0.0116[1], 0.0094[2]	d^{-1}
Fleaf_green	Fraction of green leaves at initialisation	Plant 1, 0.52[1], 0.56[1] , plant 2, 0.86[1], 0.75[2]	-

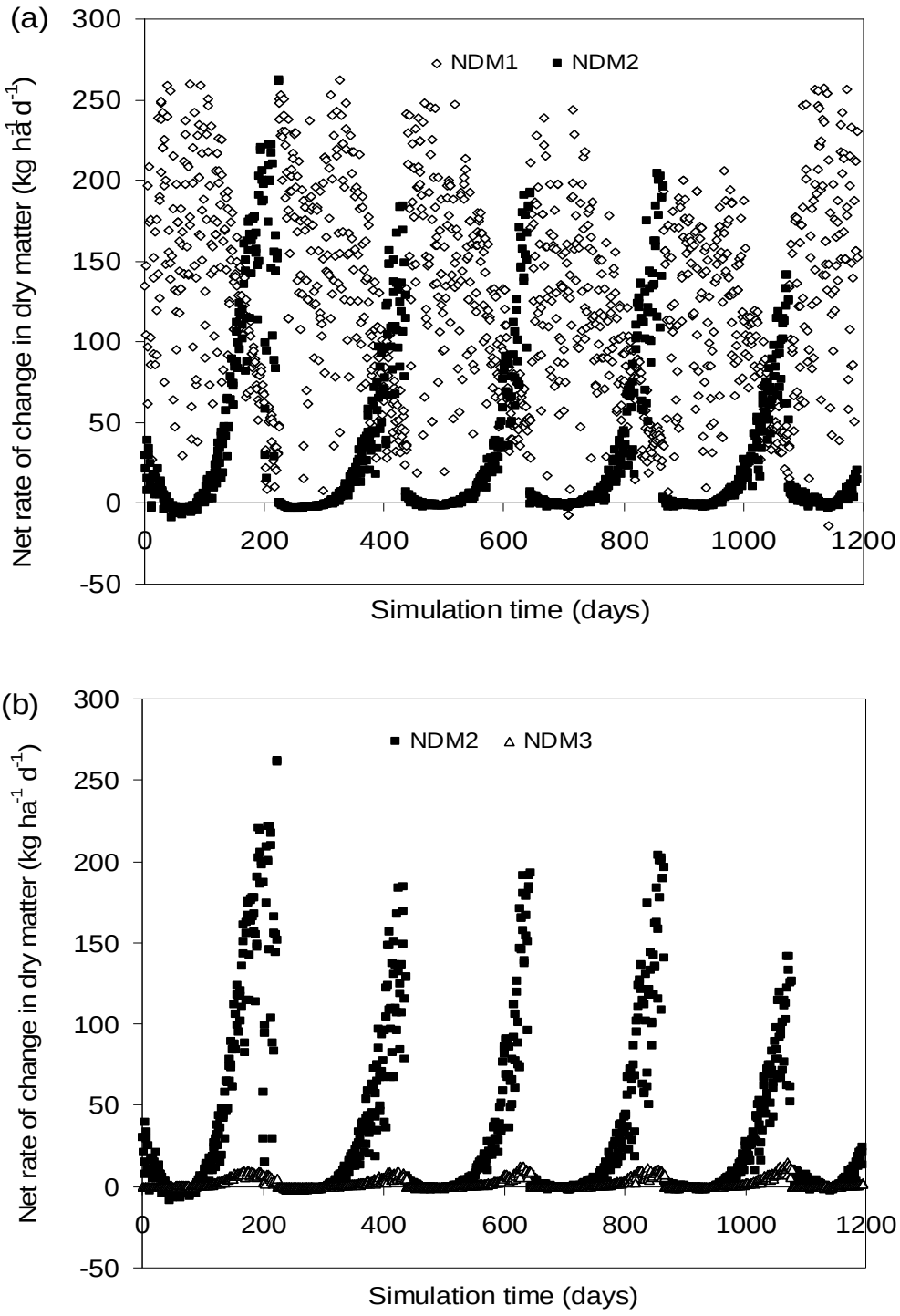

Figure 5. Relationships between the net rate of change in dry matter for plant 1 (NDM1) and plant 2 (NDM2) showing the maximum net rate of change in dry matter per day and variability in NDM1 (a) and between plant 2 (NDM2) and plant 3 showing the effect of shading (NDM3) (b).

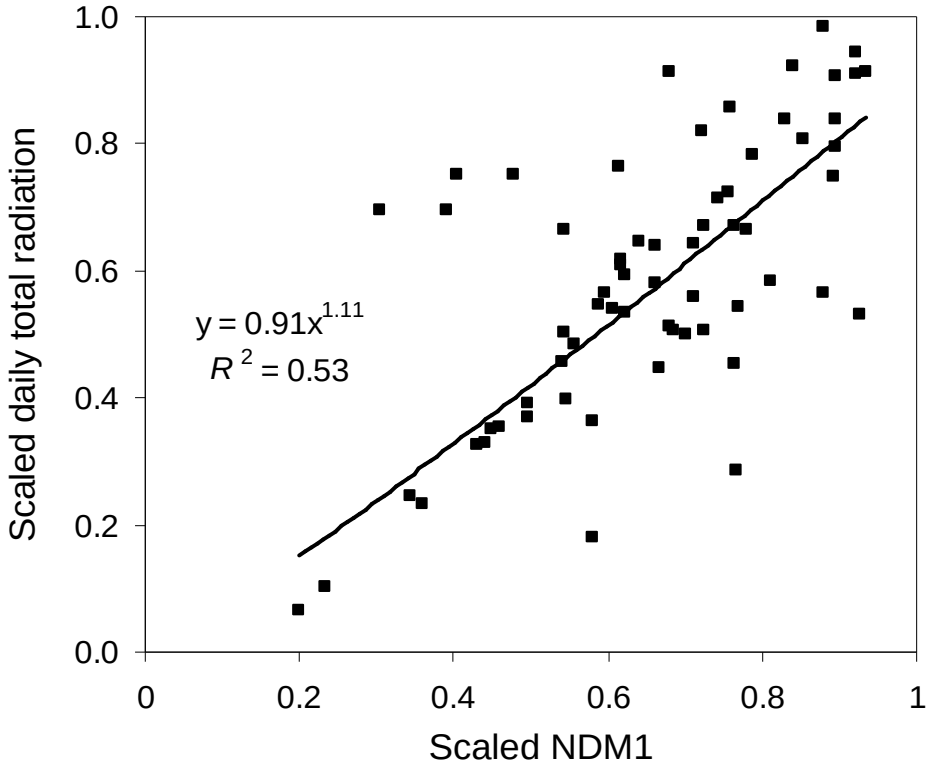

Figure 6. Relationship between scaled daily total radiation and the scaled net rate of change in dry matter of plant 1 (NDM1) during the simulation period TSUM1 2262−2663 °C d.

Radiation interception by plant 2 later increased as a result of death of *L* of plant 1. The relationship between scaled daily total radiation and scaled net rate of change in the dry matter of plant 1 (NDM1) is given in Figure 6. A higher value of scaled total radiation (daily total radiation/maximum total radiation) implies a higher NDM1. This confirms that the pattern of NDM1 values is due to variations in daily total radiation (DTR). Plant 3 emerges later in the growth process and is fully dependent on plant 2 during the first stage and reducing partitioning from plant 2 and its own photosynthesis during the second stage. As a result, the rate of change in total dry matter (NDM3) is small (Figure 5b).

4.4.2 Bunch DM, leaf DM and leaf area index at flowering

The economic yield (bunch dry matter), leaf dry matter and leaf area index (*L*) at flowering were considered. The leaf dry matter was chosen because the growth of *L* is calculated from leaf dry matter (equation 3). Since the model is based to LUE approach,

production is mainly determined by *L*. The bunch dry matter value calculated for Ntungamo was higher (20 Mg ha^{-1}) than the value at Kawanda (18.25 Mg ha^{-1}). Leaf DM values and LAI at flowering were 3.8 Mg ha^{-1} and 4.5 for Kawanda, and 4.4 Mg ha^{-1} and 5.3 for Ntungamo.

4.4.3. Sensitivity analysis at the end of the simulation

The sensitivity analysis showed that LUE, SLA, r_d and *k* had a large influence on the bunch DM, leaf DM and *L* at flowering, whereas the initial dry matter (DM1I and DM2I) had the least effect, at both sites (Table 3 and 4). In addition, the effect was dependent on the plant taken due to the effect of the canopy levels. The sensitivity values of bunch DM, leaf DM and *L* at flowering obtained for ±2.5% and ±5% changes in parameter and initial values are similar (Table 3 and 4), implying that a ±2.5% deviation around the default value is a good choice.

A higher SLA for plant 1 (SLA1) resulted in increased bunch DM and *L* at flowering, but reduced leaf DM at flowering (Table 3 and 4). The increase is explained by the direct relationship between SLA and *L* (equation 4) which results in higher LAI (increased radiation interception), resulting in higher bunch DM. The overall reduction in leaf DM at flowering is attributed to light competition, with higher SLA resulting in increased *L* for plant 1, which results in less radiation reaching plant 2 and 3. A higher SLA for plant 2 resulted in smaller increase bunch DM and leaf DM, but a larger increase in *L* at flowering. A change in SLA for plant 3 has minimum effect because the plant is dependent on partitioning from plant 2 (TSUM3 0−360 °C d), with the increase in *L* dependent on temperature during the exponential phase (TSUM3 360−960 °C d).

A higher *k*1 resulted in increased bunch DM, but reduced leaf DM and *L* at flowering (Table 3 and 4). This is attributed to increased radiation interception by plant 1, hence higher bunch DM, but increased shading of plant 2 and 3, resulting in reduced leaf DM and *L* at flowering. A higher increase in *k*2 resulted in smaller increase bunch DM, but a higher increase in leaf DM and *L* at flowering. Plant 3 is heavily shaded by plant 1 and 2, with changes in *k*3 having no effect.

Increased LUE for plant 1 (LUE1) resulted in a more than proportional increase in bunch DM, a higher leaf DM and *L* at flowering. Dry matter production in LINTUL BANANA 1 is strongly related to LUE (equation 7), with a 1% increase of LUE resulting in a 1.30% and 1.36% increase in bunch DM at Kawanda and Ntungamo respectively.

Table 3. Simulated bunch dry matter (bunch DM, Mg ha^{-1}), leaf dry matter at flowering (leaf DM, Mg ha^{-1}) and leaf area index of plant 1 at flowering (*L*, ha leaf ha^{-1} soil) at reference conditions at the end of a simulation over five harvests and the sensitivity (%/%) of the model output to changes in specific leaf area (SLA, ha leaf kg^{-1}), light extinction coefficient (*k*, ha soil ha^{-1} leaf), light use efficiency (kg MJ^{-1}), relative death rate of leaves (r_d, d^{-1}), initial dry matter (DM*i*I, kg ha^{-1}) and relative growth rate of leaf area index (RGRL, °Cd^{-1}) for plants 1, 2 and 3 at Kawanda, central Uganda. A sensitivity of 1.36 means that a 1% increase of input results in a 1.36% increase in output and a sensitivity of -0.24 means that a 1% increase of input results in a 0.24% reduction in output.

	Bunch DM (Mg ha^{-1})		Leaf DM at flowering (Mg ha^{-1})		LAI at flowering (ha leaf ha^{-1} soil)	
Reference output	18.25		3.8		4.5	
Levels of change	±2.5%	±5%	±2.5%	±5%	±2.5%	±5%
Partial sensitivities						
SLA1	0.304	0.301	-0.219	-0.226	0.615	0.611
SLA2	0.103	0.103	0.127	0.129	0.290	0.285
SLA3	0.0149	0.0147	0.0381	0.0397	0.0351	0.0395
*k*1	0.359	0.354	-0.241	-0.238	-0.237	-0.272
*k*2	0.0694	0.0695	0.188	0.189	0.193	0.193
*k*3	0.0009	0.0009	0.0063	0.0042	0.00	0.00
LUE1	1.300	1.297	0.604	0.596	0.606	0.593
LUE2	0.108	0.108	0.300	0.300	0.307	0.299
LUE3	0.0010	0.0014	0.0063	0.0063	0.00	0.00
r_d1	-0.617	-0.616	-0.104	-0.105	-0.114	-0.105
r_d 2	-0.0554	-0.0554	-0.144	-0.145	-0.149	-0.154
DM1I	0.0048	0.0044	0.0190	0.0180	0.0263	0.0219
DM2I	0.0072	0.0072	0.0180	0.0190	0.0176	0.0219
RGRL3	0.0653	0.0725	0.168	0.185	0.184	0.206

A higher increase in LUE for plant 2 resulted in smaller increase in bunch DM, but a higher increase in leaf DM and *L* at flowering, due to the direct relationships between LUE and DM production, and leaf DM and *L*. Plant 3 is heavily shaded by plant 1 and 2, with changes in LUE having no effect.

Increased r_d1 resulted in reduced bunch DM, leaf DM and *L* at flowering. This is attributed to the reduction in leaf DM and *L*, hence reduced radiation interception. An increase in r_d for plant 2 (r_d2) resulted in smaller decrease in bunch DM, but a higher decrease in leaf DM and *L* at flowering.

Table 4. Simulated bunch dry matter (bunch DM, Mg ha^{-1}), leaf dry matter at flowering (leaf DM, Mg ha^{-1}) and leaf area index at flowering (*L*, ha leaf ha^{-1} soil) at reference conditions at the end of a simulation over five harvests and the sensitivity (%/%) of the model output to changes in specific leaf area (SLA, ha leaf kg^{-1}), light extinction coefficient (*k*, ha soil ha^{-1} leaf), light use efficiency (kg MJ^{-1}), relative death rate of leaves (r_d, d^{-1}), initial dry matter (DM*i*I, kg ha^{-1}) and relative growth rate of leaf area index (RGRL, °Cd^{-1}) for plants 1, 2 and 3 at Ntungamo, southwest Uganda.

	Bunch DM		Leaf DM at flowering		LAI at flowering	
	(Mg ha^{-1})		(Mg ha^{-1})		(ha leaf ha^{-1} soil)	
Reference output	20.0		4.4		5.3	
Levels of change	±2.5%	±5%	±2.5%	±5%	±2.5%	±5%
Partial sensitivities						
SLA1	0.372	0.369	-0.140	-0.139	0.690	0.686
SLA2	0.0829	0.0824	0.0820	0.0824	0.240	0.247
SLA3	0.0111	0.0109	0.0306	0.0328	0.0300	0.0262
*k*1	0.422	0.422	-0.159	-0.158	-0.157	-0.161
*k*2	0.0506	0.0507	0.147	0.146	0.150	0.153
*k*3	0.00079	0.00059	0.0018	0.0022	0.00	0.00
LUE1	1.360	1.360	0.675	0.669	0.675	0.667
LUE2	0.091	0.090	0.273	0.273	0.277	0.270
LUE3	0.0006	0.0005	0.0027	0.0018	0.00	0.00
r_d1	-0.898	-0.898	-0.295	-0.294	-0.307	-0.292
r_d 2	-0.0406	-0.0406	-0.118	-0.118	-0.120	-0.123
DM1I	0.0123	0.0125	0.0207	0.0216	0.0225	0.0112
DM2I	0.0019	0.0016	0.0063	0.0058	0.0075	0.0112
RGRL3	0.0464	0.0466	0.126	0.125	0.120	0.127

A higher DM1I resulted in a relatively small increase of bunch DM, leaf DM and *L* at flowering. It is attributed to the fact that the increase was small as compared with the amount of bunch DM, leaf DM and *L* at flowering. Changes in DM2I had a negligible effect. A higher RGRL3 resulted in a smaller increase in bunch DM, and higher increase in leaf DM and *L* at flowering, due to the direct relationship between GLAI and RGRL3 during the juvenile stage (equation 3).

The effect of changes in the fraction of dry matter (*FSmax*) partitioned to the sucker was assessed only for the Ntungamo site. Changes (±2.5% and ±5.0%) gave sensitivity values 0.0083 and 0.0087 for bunch DM, 0.0234 and 0.0234 for leaf DM, and 0.0675 and 0.0225 for leaf area index at flowering.

4.4.4. Dynamic sensitivity

Changes (±2.5%) in LUE1 (light use efficiency for plant 1), LUE2 (light use efficiency for plant 2), DM1I (initial dry matter for plant 1) and DM2I (initial dry matter for plant 2) were used to assess dynamic sensitivity. Sensitivity to change in LUE1 is not constant during the simulation (Figure 7a). Changes in sensitivity for plant 2 due a change in LUE2 could be attributed to differences in starting points (dry matter and LAI) at the point of the shift (when plant 2 becomes the new plant 1) and the LAI values of plant 1 during the simulation (Figure 7b). Sensitivity is fairly constant for changes in DM2I (Figure 7d) and DM1I after the first harvest (Figure 7c).

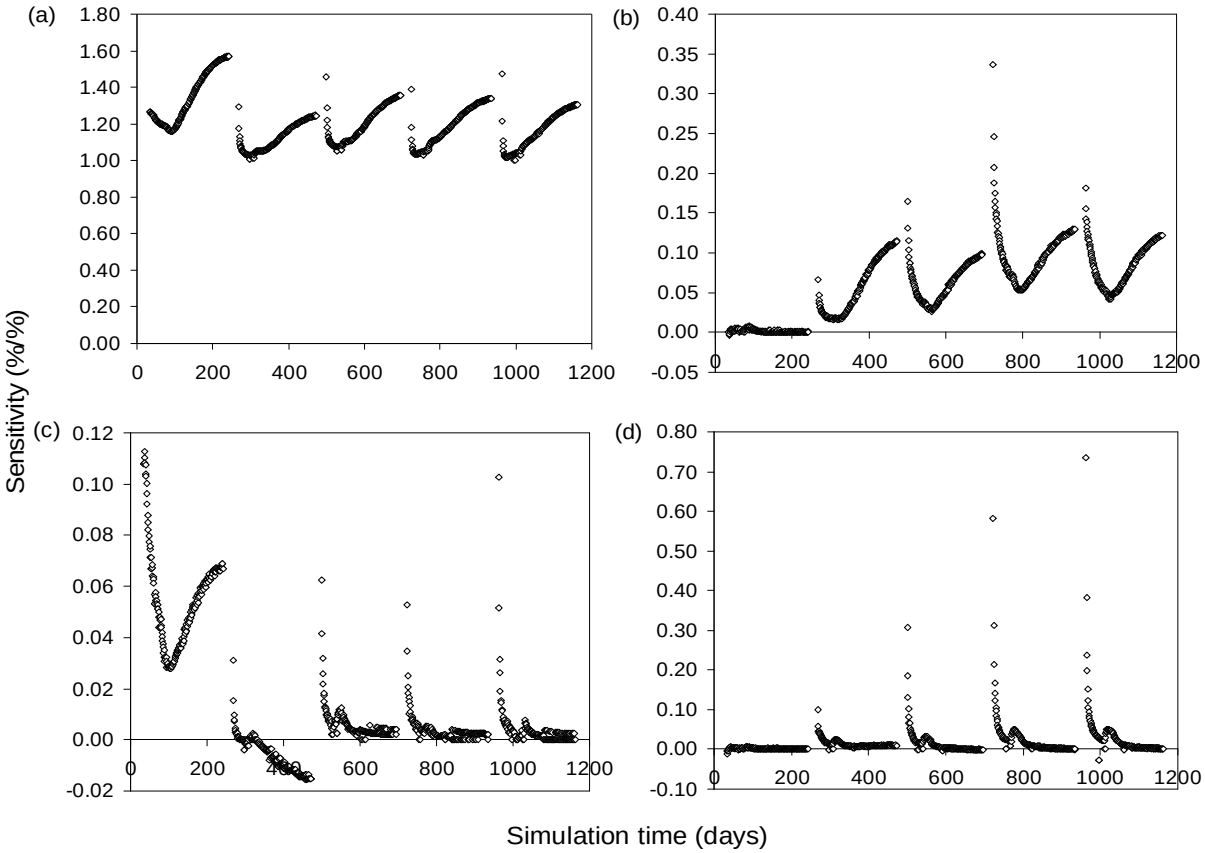

Figure 7. Dynamic sensitivity over 5 harvests for Ntungamo site with light use efficiency of plant 1 (a) and 2 (b) increased 2.5%, and with the initial dry matter of plant 1 (c) and 2 (d) increased by 2.5%.

4.5. Discussion

The model developed by combining the concept of the light use efficiency (LUE), specific leaf area (SLA) and banana growth dynamics (dry matter transfer between plants) was used to predict banana bunch dry matter for the potential situation. Validation of this model for East Africa highland bananas was not possible, with the highest yields (60−70 Mg ha^{-1} yr^{-1} FW or 10.8−12.6 Mg ha^{-1} DW) reported on research station (Tushemereirwe et al., 2001) and in a farmers' field in Rubale, southwest Uganda (Smithson et al., 2001) still below the calculated potential yield. This could be attributed to yield limiting and reducing factors. However, the bunch dry matter calculated by the model compares well with a yield of 113 Mg ha^{-1} FW (20.3 Mg ha^{-1} DW, assuming a dry matter content of 18%) reported for banana cultivar 'Robusta' (AAA group, Cavendish subgroup) at spacing of 1.8 x 1.8 m (density 3,086 plants ha^{-1}) with LAI > 4, grown with a 800-gauge thick black polyethylene film under irrigated conditions (Bhattacharyya and Madhava Rao, 1985). In the trials, the spacing was 3.0 x 3.0 m, but production is mainly determined by the leaf area index. Using the LUE approach, Turner (1998) calculated potential banana yields for cultivar 'Grand Nain' (*Musa* AAA) of 105−111 Mg ha^{-1} FW in the Jordan valley, assuming a daily total radiation average of 16 MJ m^{-2} d^{-1}, a light extinction coefficient 0.8, light use efficiency 3.0 g MJ^{-1}, daily average temperature 22 °C, harvest index 0.4 and dry matter content of fruits 0.15. Thus, the yields computed by the model are comparable to yields reported above.

Using data from Lassoudiere (1978a,b) for banana cultivar 'Poyo' (*Musa* spp., Cavendish subgroup) grown from corm pieces on a 'virgin organic soil' in Ivory Coast (average daily temperature range 23−28 °C), Turner et al. (2008) calculated a cumulative temperature sum ranging from 2600−3000 °C d from planting to flower emergence. For later flowering plants due to stress at different locations, the cumulative temperature sum ranged from about 2800−3600 °C d. These values are comparable to 2663 °C d calculated for the Ntungamo site, where moisture stress was not so strong, and Kawanda where moisture stress was strong. The durations from flowering to harvest calculated at Ntungamo (937 °C d) and Kawanda (1110 °C d) compared well with 900 °C d reported by Ganry (1978) for bunches of banana cultivar Cavendish to reach commercial grade.

The bunch dry matter calculated by the model shows that East Africa highland bananas are potentially high yielding plants (Table 3 and 4, reference output). Differences in bunch DM between sites are attributed to the effect of temperature on growth duration, with lower temperature at Ntungamo increasing the length of time that the crop can

intercept radiation, resulting in slightly higher bunch DM (cf. Muchow et al., 1990). Comparison of the calculated values and the reported bunch weights (< 4.0 Mg ha^{-1} DW) on smallholder farms in Uganda reveals a big yield gap between potential and actual yields.

The model was very sensitive to SLA, due to its use to compute the growth of leaf area index (equation 3) in the maturation phase. High model sensitivity to SLA has been reported for another model that also computed the GLAI based on SLA e.g. CONGRO (Pronk et al., 2003). This shows the importance of having good estimates of this parameter. SLA has been related to the amount of light absorbed by the leaf and the diffusion pathway of CO_2 through its tissues, with fast growing species having higher SLA (Syvertsen et al., 1995). When compared with SLA values reported for high yielding wheat cultivars 27.6−33.5 m^2 kg^{-1} (Rebetzke et al., 2004), the average SLA value used in the model is lower. However, the average value obtained for highland banana (12 m^2 kg^{-1}) was comparable to 8.7−13.6 m^2 kg^{-1} reported for banana cultivar 'Kolikuttu' (*Musa* spp., AAB) under different levels of shade in Sri Lanka (Rodrigo et al., 1997) and 10.0−14.9 m^2 kg^{-1} for a ratoon crop of banana cultivar 'Embul' (*Musa* spp., AAB) in Sri Lanka (Senevirathna et al., 2008). Within the East Africa highland banana cultivars, information regarding genotypic variation in SLA is scarce, but could provide potential for targeted selection and breeding. Kisansa cultivar was used in the trials because of its ability to give large bunches. For a banana cultivar SLA is dependent on a number of factors, e.g. plant nutrient status and light intensity (plant density). Israeli et al. (1995) reported acclimatisation of banana to maximise light capture under low light conditions by having thinner leaves (which implies a smaller *k* value), but increased chlorophyll content improves light capture. In this study, SLA measurements were done in the best treatment (400N−50P−600K) in an established banana plantation taking plants at different stages of growth and an average value was used (Table 2).

Higher *L* at flowering (5.3) at Ntungamo was attributed to the lower relative death rate of leaves (r_d) implying longer leaf duration, compared with Kawanda (Table 3 and 4). In this model, the r_d are only due to aging of leaves, because *L* in the trials was low to capture the effects of shading. The effect of shading in the model was mimicked by changing the r_d1, resulting in 0.61 and 0.9% reduction in bunch DM for every 1% change in r_d1 at Kawanda and Ntungamo. However, optimal *L* for light interception for most crops is between 4−4.5 (94−96% of radiation is intercepted according to Beer-Lambert). The incorporation of relative death rate due to shading could have a small effect on bunch DM. Higher *L* for plant 1 has no effect on the growth duration of the sucker in this model.

However, under field conditions high *L* of the mother plant has been observed to cause delayed growth of the sucker and a lengthened ratoon production cycle due to increased shading (Robinson and Nel, 1989). The effect of increased crop cycle length due to shading is not captured in this model.

As expected, bunch DM at both sites were strongly affected by LUE (Table 3 and 4). LUE values used in this model were determined using total plant dry matter, including roots and the leaves that die during the measurement interval (Table 2). LUE of agricultural crops varies between 1.09 and 4.41 g MJ^{-1} intercepted PAR for above ground biomass (Sinclair and Muchow, 1999). The addition of roots increases LUE, but the values used in the model are still within the range reported. LUE is influenced by site factors e.g. soil fertility (Sinclair and Horie, 1989), temperature (Thomas and Fukai, 1995), water availability (Collino et al., 2001), and management practices e.g. fertilization and irrigation. LUE was determined for best fertilized plots during the rain season in order to minimise the effect of moisture stress. The slightly higher LUE at Kawanda is probably related to a higher temperature, resulting in faster growth (cf. Thomas and Fukai, 1995; for barley and chickpea and Bell and Wright, 1992 for peanuts). The large effect of LUE on bunch DM implies that this parameter should be determined with maximum accuracy. Sensitivity analysis showed a large effect of LUE on bunch DM, emphasizing the importance of crop management (fertilization, pest control), if yields are to be increased.

4.6. Conclusion

The growth model LINTUL BANANA 1 developed provides good estimates of potential production in East Africa highland bananas. This model is, to the best of our knowledge, the first attempt to quantify the maximum possible yield of this crop as determined by prevailing weather conditions and crop characteristics. Given the importance of highland banana in the region, the model quantifies the maximum bunch DM and opens the quest for higher yields. It enables agronomists to determine the parameters that highly influence yield, to quantify the yield gaps, and enables breeders to select out traits for improvement. The model is strongly sensitive to LUE and parameters related to leaves like SLA and r_d.

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CHAPTER 5

Possible modifications to LINTUL BANANA 1 model in order to simulate water and nutrient-limited production

5.1. Introduction

East Africa highland bananas (*Musa* spp., AAA-EAHB) are an important staple starch food and cash crop in the Great Lakes region. Average yields on smallholder farms are low (< 16 Mg ha^{-1} yr^{-1}) (Gold et al., 1999; NARO, 2000; Wairegi et al., 2008). In order to increase banana yields, the growth and physiology of East Africa highland banana must be understood. This enables the calculation of the potential yields and the assessment of yield gaps (between potential and actual or attainable production). The LINTUL BANANA 1 model with basic processes such as radiation interception, conversion of radiation into daily dry matter, distribution of dry matter within the plant and dry matter transfers (from Plant 1 to Plant 2 and Plant 2 to Plant 3) was developed for potential production situations, and used to compute potential yields at two sites, Kawanda, central Uganda (1156 m.a.s.l) and Ntungamo, southwest Uganda (1405 m.a.s.l) (Chapter 4).

From the trials, water was identified as a major abiotic factor limiting banana production and the response to mineral fertilizers (Chapter 3). The major banana growing areas in the Lake Victoria basin and southwest Uganda, receive low and highly variable rainfall ranging 900−1400 mm per annum. The use of mulches for soil moisture conservation on smallholder farms is constrained by their availability, with less organic resources available from outfields due to increased land pressure (Bekunda and Woomer, 1996; Baijukya et al., 2005). Results from the trials showed that soil moisture availability had a large effect on the finger filling process, with bunches having the same number of fingers weighing less at Kawanda, compared with Ntungamo. In order to further understand the effects of soil moisture availability on highland banana growth and yield, a simple crop-soil balance can be added to the LINTUL BANANA 1 model to allow simulation of water-limited situations. Such a model would also be useful to quantify the amount of water needed through irrigation.

The limiting nutrients at two research sites were in the order K>P>N (Chapter 3). Potassium and nitrogen are the nutrients required in largest quantities for banana growth (Turner, 1985). Potassium is usually an abundant soil nutrient, but its availability in the soil depends on the presence of K-rich minerals (Sumner, 2000). In conditions of low potassium supply, photosynthesis, translocation and storage of assimilates and tissue water relations are affected (Marschner, 1986), resulting in low yields (Chapter 3). Nitrogen uptake (fertilization) increases leaf area index (LAI) and intercepted photosynthetically active radiation, and the light use efficiency (LUE), but with LUE response curves saturating at high leaf N contents (Sinclair and Horie, 1989). Soil nutrient

availability in banana plantations varies seasonally, due to soil, management and environmental factors (Delvaux, 1995). These factors influence nutrient uptake, utilization and biomass production. In Chapter 3, the static nutrient response model QUEFTS was calibrated and tested for highland banana. However, there is a need to incorporate crop-soil N and K availability into the model to capture crop and soil N and K dynamics during crop growth and be able to simulate N and K-limited production.

In this chapter, I propose how a crop-soil balance can be added to the LINTUL BANANA 1 model and the important processes (transpiration, evaporation, drainage, run-off and root exploration of new soil layers and the effects of banana residue mulch on evaporation, rainfall interception and run-off), in order to give LINTUL BANANA 2 for water-limited situations. In addition, some ideas on how to add crop-soil N and K availability to the LINTUL BANANA 1 model to be able to simulate N and K-limited production are proposed.

5.2. Possible modifications to LINTUL BANANA 1 in order to simulate water-limited production

5.2.1. Soil water balance

A simple soil water balance can be calculated by assuming a single soil layer, whose thickness increases with rooting depth (van Keulen, 1986). Root extension (primary, secondary and tertiary roots) leads to exploration of water in deeper soil layers, which are initially assumed to be at field capacity. In most models, vertical root growth is captured, but highland banana roots exhibit both vertical and extensive horizontal growth. The daily net rate of change in soil moisture amount (mm d^{-1}) can be calculated as:

$$\frac{dW}{dt} = [R + (dX / dt) + Irrig] - [InLAI + InDMmulch_{act} + Rn + Tran + Evapo + Drain] \qquad (1)$$

where dW/dt is the overall rate of change of soil water amount (mm d^{-1}), R is the amount of water added through rainfall (mm d^{-1}), dX/dt is the exploration rate of new soil water layers by root depth growth (mm d^{-1}), *Irrig* is water added through irrigation (mm d^{-1}), *InLAI* and $InDMmulch_{act}$ are the rainfall interceptions by the canopy and mulch (mm d^{-1}), *Rn*, *Tran*, *Evapo* and *Drain* are the water losses through run-off, transpiration, evaporation

and drainage (mm d^{-1}), respectively. The states, rates and information flows after addition of a crop-soil water balance to LINTUL BANANA 1 are detailed in Figure 2.

In a banana plantation, pruned dead leaves, leaves and pseudostems at harvest are applied as mulch. The maximum amount of water held by banana mulch (*DMmulchWSAT*, mm) is proportional to the quantity of banana mulch on the soil surface (Scopel et al., 2004) and can be calculated as follows:

$$DMmulchWSAT = \delta \times DMmulch \times 10^{-4} \quad (2)$$

where *DMmulch* is the amount of banana mulch on the soil surface (kg ha^{-1}), δ is the specific water retention capacity of banana mulch (kg H_2O kg $^{-1}$ DM). δ can be determined by soaking dry leaves and pseudostem in water for a specified period, draining to get rid of excess water and then weighing. Samples should be oven dried to obtain the dry weight. The specific water retention capacity (kg H_2O kg $^{-1}$ DM) of the leaves and pseudostem can be calculated as follows:

$$Specific\ water\ retention\ capacity = \frac{Weight\ after\ soaking - Dry\ weight}{Dry\ weight} \quad (3)$$

The maximum amount of rainfall that can be intercepted by a layer of banana mulch ($InDMmulch_{max}$, mm) depends on the amount of water held by mulch at that moment, *DMmulchW* (mm) and *DMmulchWSAT* (maximum amount of water that can be held) (Scopel et al., 2004).

$$InDMmulch_{max} = DMmulchWSAT - DMmulchW \quad (4)$$

The actual amount of rainfall intercepted by the surface banana mulch ($InDMmulch_{act}$, mm) is a function of the fraction of soil covered by banana mulch (*FSC*), limited by $InDMmulch_{max}$ and can be calculated as follows:

$$InDMmulch_{act} = \min\ (RAINS \times FSC,\ InDMmulch_{max}) \quad (5)$$

where *RAINS* is the rainfall amount on the surface of the banana mulch, corrected for losses through banana canopy interception and water runoff. The soil coverage by banana

mulch, *FSC* can be described by the equation below, which also accounts for the clumping and mutual shading by pieces banana mulch on the soil surface.

$$FSC = 1. - \exp(-\beta \times DMmulch) \quad (6)$$

where β is the area covered per unit dry weight of the banana mulch (ha kg $^{-1}$ DM). β was determined by spreading banana mulch (leaves and pseudostems in equal proportions 0.5:0.5), ranging e.g. from 0 kg, 0.2 kg, 0.4 kg, 0.6 kg, 0.8 kg and 1.0 kg over an area 1m^2. Photographs were taken and analyzed using WinRhizo Pro software (Regent instruments inc.) to determine the proportion of the area covered by the mulch. A relationship was established between the amount and cover of the banana mulch (Figure 2). With 2 Mg ha^{-1} of mulch, the fraction of soil surface covered is 57%, and 95% coverage is obtained with 6 Mg ha^{-1} of mulch (Figure 1).

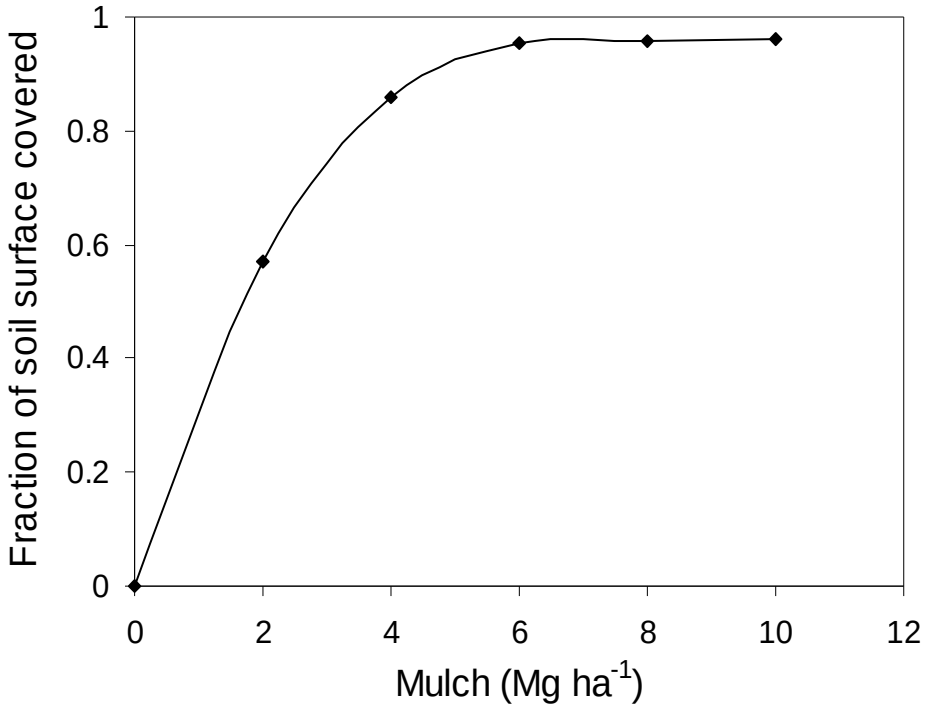

Figure 1. Relationship betweeen the fraction of soil surface covered and the quantity of banana mulch on the soil surface.

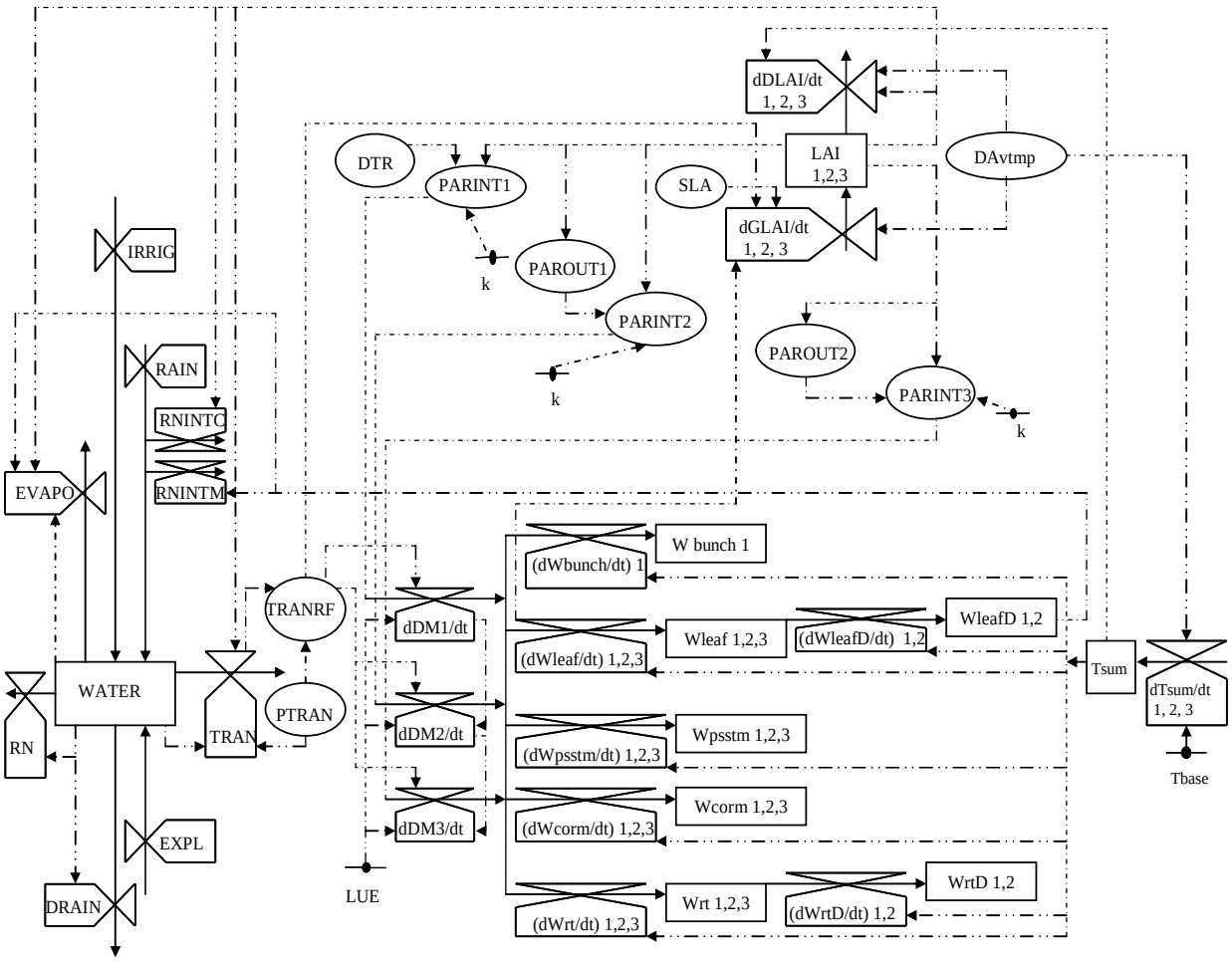

Figure 2. Relational diagram of LINTUL BANANA 2 for water-limited banana production (modified from Anonymous, 1997). RAIN – rainfall amount; RNINTC – intercepted rain by plant canopy; RNINTM – intercepted rain by mulch; EVAPO – evaporation; RN – run off; EXPLOR – water exploration; DRAIN – drainage; TRAN – transpiration; PTRAN – potential transpiration; TRANRF – reduction factor due to water stress; DTR – daily total radiation, PAROUT1 – photosynthetically active radiation not intercepted by plant 1, PAROUT2 – photosynthetically active radiation not intercepted by plant 2, PARINT1,2,3 – photosynthetically active radiation intercepted, k – light extinction coefficient, LUE – light use efficiency, dDM1/dt, dDM2/dt, dDM3/dt – rates of biomass production, SLA – specific leaf area, Tbase – base temperature for growth, DAvtmp – daily average temperature, Wbunch 1 – weight of bunch, (dWbunch/dt) 1 – growth rate of bunch for plant 1, LAI – leaf area index, Tsum – temperature sum, dGLAI/dt – rate of increase in leaf area index, dDLAI/dt – rate of reduction in leaf area index due to death, (dWleaf/dt) – growth rate of leaves, (dWpsstm/dt) – growth rate of pseudostem, (dWrt/dt) – growth rate of roots, (dWcorm/dt) – growth rate of corm, (dWleafD/dt) – death rate of leaves, (dWrtD/dt) – death rate of roots, Wleaf – weight of green leaves, WleafD – weight of dead leaves, Wpsstm – weight of pseudostem, Wrt – weight of roots, WrtD – weight of dead roots, Wcorm – weight of corm, and dTsum/dt – rate of increase in temperature sum for plants 1, 2 and 3. At harvest, plant 1 is cut away. Solid lines are material flows and dotted lines are information flows.

5.2.2. Drainage, runoff and irrigation

The rates of water drainage, runoff and irrigation (mm d^{-1}) can be calculated using the approach used in LINTUL2 model for water-limited production (Anonymous, 1997). Drainage of excess water above field capacity (WCFC, m^3 m^{-3}) is limited by the maximum drainage rate of the subsoil (DRATE, mm d^{-1}). A higher DRATE implies complete drainage. When the drainage is insufficient to keep soil water content below saturation (Water content < Water content at saturation, WCST), runoff occurs. But in the trials, a combination of trenches and mulch (pruned dead leaves during growth, leaves and pseudostems at harvest) controlled runoff. Therefore, runoff would be taken to be zero. The trials were carried out under rain-fed conditions, therefore no irrigation.

5.2.3. Potential rates of evaporation and transpiration

Potential rates of evaporation (PEVAP, mm d^{-1}) and transpiration (PTRAN, mm d^{-1}), in absence of limitations to the supply of liquid water to the evaporating surface, can be calculated using the Penman equations (Penman, 1948). A similar approach was used in the LINTUL2 model for water-limited production (Anonymous, 1997). The Penman equations are written as a weighted sum of two terms, a radiation term (for the soil, PENMRS and for the crop, PENMRC, MJ ha^{-1} d^{-1}), which supplies energy to vaporize water and the drying power term (PENMD, MJ ha^{-1} d^{-1}) to remove the vapor. The radiation term depends on the net radiation (NRAD, MJ ha^{-1} d^{-1}), the latent heat of vaporization (LHVAP, MJ kg^{-1}) and the weighting factor (SLOPE / (SLOPE+PSYCH). The SLOPE (kPa $°C^{-1}$) is the tangent of the relation between saturated vapour pressure, SVP (kPa) and temperature (°C), and PSYCH is the psychrometer constant. Net radiation is calculated as the balance between the incoming short-wave radiation from the sun minus 15−25% reflection and the net outgoing long-wave radiation from the earth's surface (RLWN, MJ ha^{-1} d^{-1}). The albedo value for the crop surface is usually 0.25 and the value for the mulch has to be estimated.

In a banana plantation, the net radiation absorption rate by the soil, NRADS (MJ ha^{-1} d^{-1}) is reduced by the presence of mulch (*DMmulch*), through a reduction in the amount of radiation reaching the soil surface. The amount of radiation reaching the soil surface through a layer of banana mulch (*DTR2*, MJ ha^{-1} d^{-1}) is a function of the mulch area index (*MAI*), and can be calculated using a Beer's law equivalent (Scopel et al., 2004) as follows:

$$DTR2 = DTR1 \times \exp(-\sigma \times MAI) \quad (7)$$

$$MAI = \beta \times DMmulch \quad (8)$$

where *DTR1* is the incident solar radiation (MJ ha^{-1} d^{-1}), σ is the extinction coefficient for net radiation in the banana residue layer, *MAI* is the mulch area index, β is the area covered per unit dry weight of the banana mulch (ha kg^{-1} DM) and *DMmulch* is the amount of mulch on the soil surface. The state variable *DMmulch* is filled dynamically by prunings (dead leaves) and instantly by leaves (green and dead) and pseudostem dry matter at harvest. The amount of mulch on the soil surface ($DMmulch_t$, kg ha^{-1}) can be calculated assuming exponential decay as follows:

$$DMmulch_t = DMmulch_{t0} \times \exp(-RDcR \times t) \quad (9)$$

where $DMmulch_{t0}$ is the amount of mulch on the soil surface at t=0 (kg DM ha^{-1}), *RDcR* is the relative decomposition rate (d^{-1}) of banana mulch (Lekasi et al., 1999) and *t* is the time in days.

The drying power of air decreases with air humidity (vapour pressure, kPa) and increases with wind speed (WN, m s^{-1}), measured at 2 m from the ground. The wind function (WDF, kg m^{-2} d^{-1} kPa^{-1}) for short closed grass crops can be used to estimate the conductance for transfer of latent heat and sensible heat from the surface to the standard height. The evaporative demand is partitioned between the soil and the crop (LAI, ha leaf ha^{-1} soil). Radiation not intercepted by banana crop will reach the soil and contribute to potential soil evaporation. The average extinction coefficient for visible and near infrared radiation is about 0.5, so soil evaporation is weighed by a factor $e^{-0.5LAI}$ and crop transpiration by $1 - e^{-0.5LAI}$. In LINTUL BANANA 1, there are three canopy levels, plant 1, plant 2 and plant 3. Plant 3 is small, potential transpiration can be assumed to be due to the canopies of plant 1 and 2.

5.2.4. Actual rates of evaporation and transpiration

The loss of water from the soil surface through evaporation is often a major component in the soil water balance of agricultural systems (Jackson and Wallace, 1999), especially in the case of banana plantations where full coverage of ground area by mulch is often not

achieved (Allen, 1990). The actual rates of evaporation (EVAP, mm d^{-1}) and transpiration (TRAN, mm d^{-1}) depend on the potential values, the soil water content (WC, m^3 H_2O m^{-3} soil) and the soil characteristics (the hydraulic conductivity of the soil). This requires soil water contents at saturation (WCST, m^3 H_2O m^{-3} soil), at field capacity (WCFC, m^3 H_2O m^{-3} soil), at wilting point (WCWP, m^3 H_2O m^{-3} soil) and at air dryness (WCAD, m^3 H_2O m^{-3} soil). Evaporation is important in the early stages of banana plantation establishment, and decreases with canopy development and increase in DMmulch. Evaporation decreases when soil water content becomes lower than field capacity and continues at a decreasing rate until air dryness. A critical water content (WCCR, m^3 H_2O m^{-3} soil), which lies between wilting point and field capacity has to be determined for highland banana below which actual transpiration (TRAN, mm d^{-1}) reduces as compared with the potential rate. The critical water content depends on crop characteristics expressed in the transpirational constant (TRANCO, mm d^{-1}). The soils at both sites were free draining, hence no effect of waterlogging on transpiration. The degree of water stress under which the crop grows can be expressed as a reduction factor TRANRF = TRAN / PTRAN (Figure 3).

5.3. Possible modifications to LINTUL BANANA 1 to simulate N and K-limited production

5.3.1. Soil-crop nitrogen and potassium availability

The nitrogen and potassium balances can be calculated as the difference between supply through mineralization and fertilizer, and the removal through crop uptake and losses. The daily net rate of change in N or K amount (kg ha^{-1} d^{-1}) can be calculated as follows:

$$\frac{dN}{dt} = N_{min} + \left(F_{applied} \times ARF\right) - \left(\frac{dNU}{dt}\right) - \left(\frac{dNL}{dt}\right) \qquad (10)$$

Where N_{min} is nitrogen supply through mineralization (kg ha^{-1} d^{-1}), ($F_{applied}$ x ARF) is nitrogen supply through fertilizer (kg ha^{-1} d^{-1}), $F_{applied}$ is the amount of fertilizer applied (kg ha^{-1}), ARF is the apparent fertilizer recovery fraction (determined in Chapter 3), dNU/dt is the rate of uptake by the crop and dNL/dt is the rate of loss. Nitrogen mineralization in a banana plantation can be determined using Raison tubes (Abril et al.,

2001). Details of the states, rates and information flows after addition of a crop-soil water balance to LINTUL BANANA 1 are shown in Figure 3.

5.3.2. Nitrogen and potassium uptake, demand and limitations on growth

The uptake of nutrients from the soil by the banana plant depends on (i) the crop N or K demand, which depends on the phenological stage and the total sum of individual plant organ demands and the amounts in the plant organs (actual versus maximum N or K concentration in the plant organ) (Gastal and Lemaire, 2002), (ii) Soil N or K availability (fertilization, potential soil N mineralization and soil K supply) (Jamieson and Semenov, 2000), (iii) Rooting depth (volume of soil exploited by roots), and (iv) Soil water status (depends the model assumptions whether water will be limiting or not). The total amount of N and K taken up by the crop is partitioned among the organs using the ratio of demand by the organ to total crop demand. In cereals, nitrogen uptake ceases at flowering (Sinclair and Amir, 1992), with N demand for the storage organs met by translocation from leaves, stems and roots. Similar assumptions could be made for highland banana. Crop N or K demand can be controlled by the critical N and K mass fraction ($\%N/K_{crt}$), which represents an optimum for biomass production (Figure 4). The actual N and K ($\%N/K_{act}$) is the accumulation above the residual content, $\%N_{res}$ which refers to nitrogen forming part of the cell structures. If N or K supply is unlimited, N or K will accumulate in the banana plant.

Nitrogen and potassium deficiency in highland banana results in reduced leaf area, increased leaf senescence and a longer crop cycle duration. Deficiencies have been reported to affect dry matter partitioning and the LUE in other crops e.g. maize, Uhart and Andrade, 1995. Effects of nutrient deficiencies on LUE and dry matter partitioning under field conditions have not been established for highland bananas. Nitrogen and potassium limitations can be quantified through the nitrogen and potassium nutrition indices (NNI or KNI) (Lemaire et al., 1989), defined as follows:

$$NNI = \frac{\left(\%N_{act} - \%N_{res}\right)}{\left(\%N_{crt} - \%N_{res}\right)} \tag{11}$$

where $\%N_{act}$ is the actual nitrogen mass fraction, $\%N_{res}$ is the residual nitrogen mass fraction, and $\%N_{crt}$ is the critical nitrogen mass fraction below which a plant experiences stress.

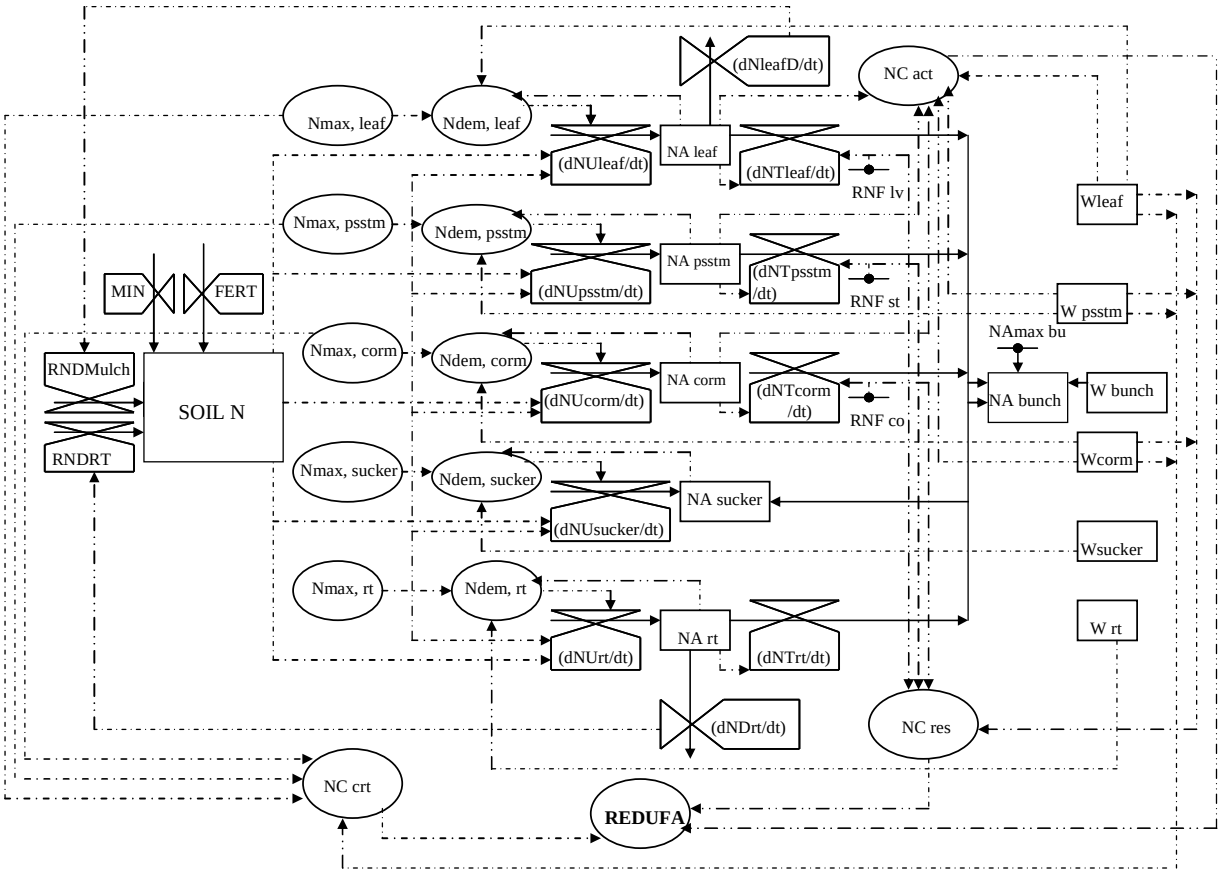

Figure 3. Relational diagram for nitrogen supply, uptake, translocation and contents in plant organs (modified from Shibu, 2007). SOIL N – amount of soil available nitrogen, MIN – nitrogen supply through mineralization, RNDMulch – nitrogen supply from mulch decomposition, RNDRT – nitrogen supply from dead roots, FERT – nitrogen supply through fertilization, Nmax, leaf – maximum nitrogen concentration in leaves, Nmax, psstm – maximum nitrogen concentration in pseudostem, Nmax, corm – maximum nitrogen concentration in corm, Nmax, sucker – maximum nitrogen concentration in sucker, Nmax, rt – maximum nitrogen concentration in roots, Ndem, leaf – nitrogen demand of leaves, Ndem, psstm – nitrogen demand of pseudostem; Ndem, corm – nitrogen demand of corm; Ndem, su – nitrogen demand of sucker, Ndem, rt – nitrogen demand of roots, (dNUleaf/dt) – rate of nitrogen uptake by leaves, (dNUpsstm/dt) – rate of nitrogen uptake by pseudostem, (dNUcorm/dt) – rate of nitrogen uptake by corm, (dNUsucker/dt) – rate of nitrogen uptake by sucker, (dNUrt/dt) – rate of nitrogen uptake by roots, NA leaf – nitrogen amount in leaves, NA psstm – nitrogen amount in pseudostem, NA corm – nitrogen amount in corm, NA sucker – nitrogen amount in sucker, NA rt – nitrogen amount in roots, (dNleafD/dt) – rate of nitrogen loss through death of leaves, (dNrtD/dt) – rate of nitrogen loss through death of roots, (dNTleaf/dt) – nitrogen translocation rate from leaves, (dNTpsstm/dt) – nitrogen translocation rate from pseudostem, (dNTcorm/dt) – nitrogen translocation rate from corm, (dNTrt/dt) – nitrogen translocation rate from roots, RNF lv – residual nitrogen concentration in leaves, RNF st – residual nitrogen concentration in pseudostem, RNF co – residual nitrogen concentration in corm, NC act – actual nitrogen concentration in leaves, pseudostem and corm, NC res – residual nitrogen concentration in leaves, pseudostem and corm, NC

crt – critical nitrogen concentration in leaves, pseudostem and corm, REDUFA – reduction factor (also nitrogen nutrition index), NA bunch – amount of nitrogen in bunch, Nmax bu – maximum nitrogen amount in bunch, Wleaf – weight of green leaves; Wpsstm – weight of pseudostem, Wbunch – weight of bunch, Wcorm – weight of corm, Wsucker – weight of sucker, Wrt – weight of roots. Solid lines – material flows and dotted lines – information flows.

If N/KNI is greater than 1, N or K availability in the soil will not limit banana growth. When NNI is lower than 1, banana growth is limited by nitrogen or potassium uptake. The K/NNI can be introduced as REDUFA (Figure 4), a factor affecting directly the growth and the death of LAI and the yield (bunches). Although the effects on growth could be modelled in a similar way, potassium is not incorporated in plant structures like nitrogen e.g. in proteins, it is a free cation counter balancing for nitrate uptake. Potassium plays an important role in phloem loading and translocation of assimilates (Marschner, 1986). In plants well supplied with potassium, the concentration of potassium, the osmotic potential of cell sap and the transport rate are higher, compared with levels in plants supplied with less potassium. Potassium deficiency therefore has a disproportionate effect on yield, as noted for plants not supplied with potassium at the Ntungamo site.

5.4. Concluding remarks

The steps that need to be taken to improve the capabilities (simulation of water and nutrient-limited production) of the growth model LINTUL BANANA 1 and its utility as a tool have been given. Due to the importance of highland banana in the region, these improvements should lead to increased understanding of banana growth, and the realization of crop's potential in order to meet the increasing food and cash demands of the population.

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CHAPTER 6

General discussion

6.1. Introduction

Soil fertility decline is a major problem leading to food insecurity in sub-Saharan Africa (Sanchez et al., 1997). Yields of major staple crops remain low, for example yields of maize are often around 1 Mg ha^{-1} of grain (Zingore, 2006), cassava 6.1−11.7 Mg ha^{-1} of fresh roots (Fermont, 2009) and bananas 9.7−25.5 Mg ha^{-1} yr^{-1} FW (Wairegi et al., 2008). In Uganda, more than 70% of the population depend on agriculture and live in rural areas. Despite the reduction in the number of undernourished people from 5.1 million (1995−97) to 4.1 million (2003−05), undernourishment is still a problem (Figure 1a). In 2008, emergency and food assistance from the World Food Program was valued at US$ 82.84 million (WFP, 2009) and from the Food and Agriculture Organisation valued at US$ 15 million (FAO, 2009). In addition, increasing population (Figure 1b) puts pressure on the available resources. Smallholder farmers are thus trapped in a circular spiral between food insecurity, poverty and low food and crop production. It is clear that increases in productivity of staple crops such as bananas or 'matooke' are required to reduce food insecurity and hunger, and raise incomes of the rural dwellers.

At the Africa Fertilizer Summit held in Abuja, Nigeria in 2006, it was proposed that mineral fertilizers are essential to hault the decline in soil fertility, to increase agricultural productivity and kickstart the African Green Revolution. The Government of Uganda envisages increased production of important staple food crops such as bananas as key to alleviating poverty and ensuring food security in rural parts of the country (GOU, 2000). The impetus for fertilizer use is mainly due to two factors (i) the failure of agricultural growth (<2% per annum) to match with population growth (3.3% per annum), and (ii) the reducing availability of organic nutrient sources (Bekunda and Woomer, 1996). However, the use of mineral fertilizers by banana farmers is still low (<5%) (Sseguya et al., 1999). In addition, soils are heterogenous in terms of the soil types and management, which may affect the response to fertilization (c.f. Zingore, 2006). There is a need to develop site-specific fertilizer recommendations that take into account the variability in soil chemical properties.

The goal of this research was to explore options for improving highland banana yields on smallholder farms in Uganda. This required a good understanding of the potential plant growth and its response to nutrients. To better understand banana growth, I first had to develop allometric relationships that describe the evolution of different plant parts (i.e. corm, roots, stem, leaves and bunch) during the plant life cycle (Chapter 2). Subsequently, the response of highland banana to mineral fertilizers was determined

(Chapter 3) and used to calibrate and test a static nutrient response model following the QUEFTS approach. In Chapter 4, plant growth data were used to develop and calibrate a new banana dynamic crop growth model that simulates potential yield based on radiation and temperature. In Chapter 5, I discuss and explore how the model can be extended to simulate water and nutrient-limited production.

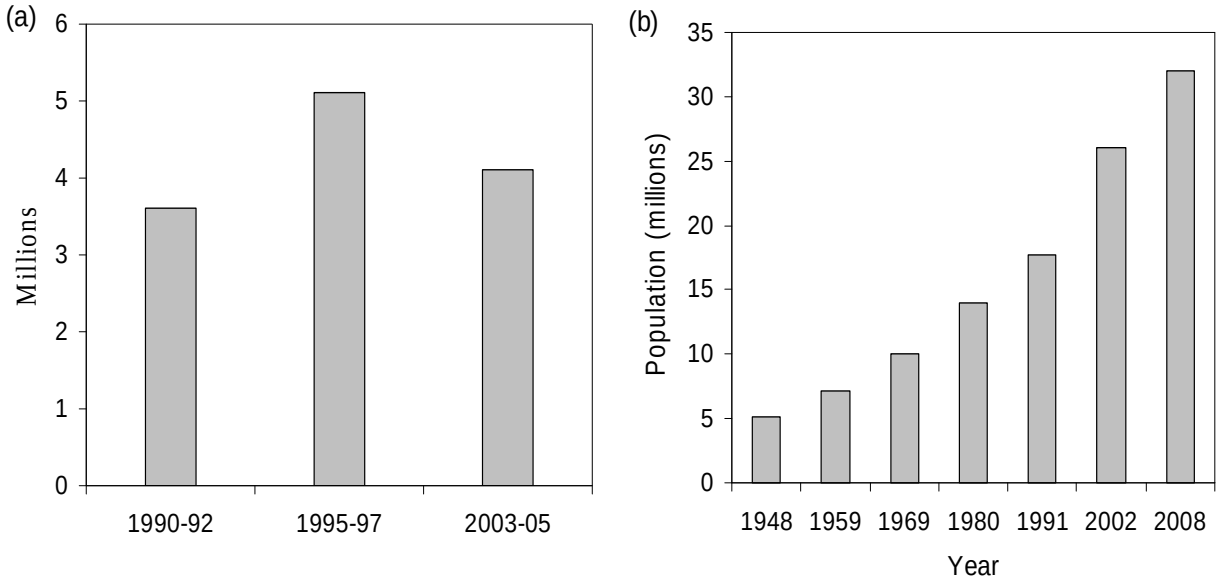

Figure 1. The number of undernourished people in Uganda as per the World Food Summit indicators (a); source: FAO, and the growth in population from 1948−2008 (b); source: Uganda Bureau of Statistics - UBOS.

In this last chapter (Chapter 6), I synthesize the results presented in the previous chapters and reflect on the broader implications of the research. Emphasis is placed on increasing banana yields (e.g. through improved crop management), which would help close the gaps between potential, and water and nutrient-limited yields, and thus contribute to improved food security in the East African highlands. The need to increase fertilizer recovery fractions to reduce the amount of fertilizer required for a target yield (Chapter 3) and the attractiveness of fertilizer use are further discussed. The knowledge gained from the crop growth modelling exercise (i.e. LINTUL BANANA 1, Chapter 4) and the contribution of the model to breeding and crop management are discussed. Finally, suggestions for future research on highland bananas are made.

6.2. Allometric growth relationships

Development and testing of crop growth simulation models requires data such as an estimate of leaf area index (LAI) and dry matter production and partitioning during growth. In Chapter 2, allometric relationships were derived and used to estimate aboveground biomass of different plant parts, and to initialize the dry matter values in LINTUL BANANA 1 model (Chapter 4). Girth at base was used as the predictor variable. I have shown that allometric relationships can be derived and used to assess plant growth and production, which will be useful in agronomic experiments and in on-farm research on banana systems. However, these relationships have to be coupled with knowledge on banana phenology in order to guide management decisions such as fertilizer applications, which improve biomass production and consequently the bunch weight (Chapter 2). Agronomists can provide banana farmers with tables indicating target girth at base at key stages during crop growth for different cultivars. If banana plant performance is below threshold values this would indicate reduced or poor management, thus requiring farmer intervention. This could assist in improved management of individual plants, through targeted applications of fertilizers or pest and disease control. By providing a means of quantifying the yield loss due to poor management, or by assisting farmers in measuring improvements in yield due to interventions, this would assist farmers in making decisions on whether investment in extra labour or fertilizer inputs are justified.

Banana is a major staple crop consumed on-farm and also marketed to the major urban centres in Uganda to provide income to the farmers. The estimation of bunch weights would facilitate the comparison of economic product (bunches) that at present are simply divided into categories such as small, medium and large for easy pricing and marketing. I have shown that girth at base measured at flowering can be used to estimate bunch fresh weights on farm (Chapter 2). Scientists in Uganda have lamented the lack of accurate information on banana yields on smallholder farms (Wairegi et al., 2009). Allometric relationships can be derived for other banana cultivars and used to quickly estimate the bunch weights or yields (Mg ha^{-1}), which can be used as a basis to assess management practices and food production at the national level. I noted differences in the allometric relationships between girth at base at flowering and bunch fresh weight for cultivars Mbwazirume and Kisansa. The allometric parameter ($\beta 1$) or the scaling exponent of the allometric relationship was much larger for Kisansa as compared with Mbwazirume. This has two implications (i) a larger increase in bunch weight with girth for cv. Kisansa, which may imply a higher increase in bunch weight per unit of nutrient

applied or improved crop management in general and (ii) allometric differences between the two banana cultivars resulting from differences in dry matter partitioning (cf. Niklas, 1995), which necessitates derivation of cultivar specific relationships. Knowledge of the differences in the allometric parameter ($\beta 1$) in highland banana cultivars could be further investigated in terms of (i) the yield (dry matter partitioning to the bunch) (ii) response to fertilization and (iii) sustainability, in terms of the amount of residues remaining in the field to act as mulch (that contribute to soil organic matter) and the amount of nutrients exported in bunches. Within the same cultivar, differences in allometric relationships (e.g. girth at base at flowering and bunches at harvest) could be attributed to response to poor management (e.g. inadequate fertilization) and soil moisture stress (Chapter 2). Comparisons across sites can provide insights into factors affecting growth and yields, as observed at our sites, with a small allometric parameter at Kawanda attributed to moisture stress and poor root exploration of the soil.

Leaf area index (LAI) determines the amount of radiation intercepted by the plant, and its estimation is crucial in growth assessment throughout the crop cycle. To quantify LAI, the area of a single leaf was first estimated as leaf length x maximum width x leaf area factor. The leaf area factor (ratio of actual leaf area to area obtained by multiplying the maximum width and length of the leaf) for highland banana cultivar Kisansa was 0.68. The value was lower (about 15 %) than reported values for other banana cultivars suggesting differences in leaf morphology within *Musa* species. Two simple models for total leaf area (TLA) estimation were developed based on the middle leaf area (MLA) and the number of functional leaves (n): (i) $MLA_{measured} \times n$ and (ii) $MLA_{predicted} \times n$. TLA measured using model (i), would require direct measurements of the middle leaf area (leaf length x maximum width x leaf area factor), which would be laborious. I have shown that more easy measurable morphological traits (plant height and girth) can be used first, to estimate middle leaf area (MLA), and then the total leaf area (MLA times the number of functional leaves). This allows agronomists to make rapid plant canopy assessments in the field, and facilitates management decisions such as sucker selection and de-suckering to maintain a given mat density. Knowledge of the LAI can be useful to estimate radiation interception, for example at LAI 4, 94% of the incident radiation is intercepted by the plant (if the light extinction coefficient, k = 0.7). At low LAI, especially in banana monocrops, more suckers 2−3 can be selected. However, with over 130 banana cultivars grown in Uganda (c.f. Karamura, 1998), it is important to derive TLA models for other cultivars.

6.3. Highland banana response to mineral fertilizers

The use of mineral fertilizers significantly increased bunch mass (kg bunch^{-1} FW), bunch yields (Mg ha^{-1} yr^{-1} FW) and the number of fingers at two trial sites (Kawanda and Ntungamo) in Uganda (Chapter 3). The increases were stronger at Ntungamo, compared with Kawanda. When N and P were applied without K (400N–50P–0K), there was no significant increase in bunch mass above the control at Ntungamo, which emphasizes the importance of adding potassium (cf. Turner and Barkus, 1983). Yield increases with K application were 6.5 and 30.2 Mg ha^{-1} yr^{-1} FW for crop cycles 1 and 2 at Ntungamo, and 0, 2.4 and 3.6 Mg ha^{-1} yr^{-1} FW for crop cycles 1, 2 and 3 at Kawanda.

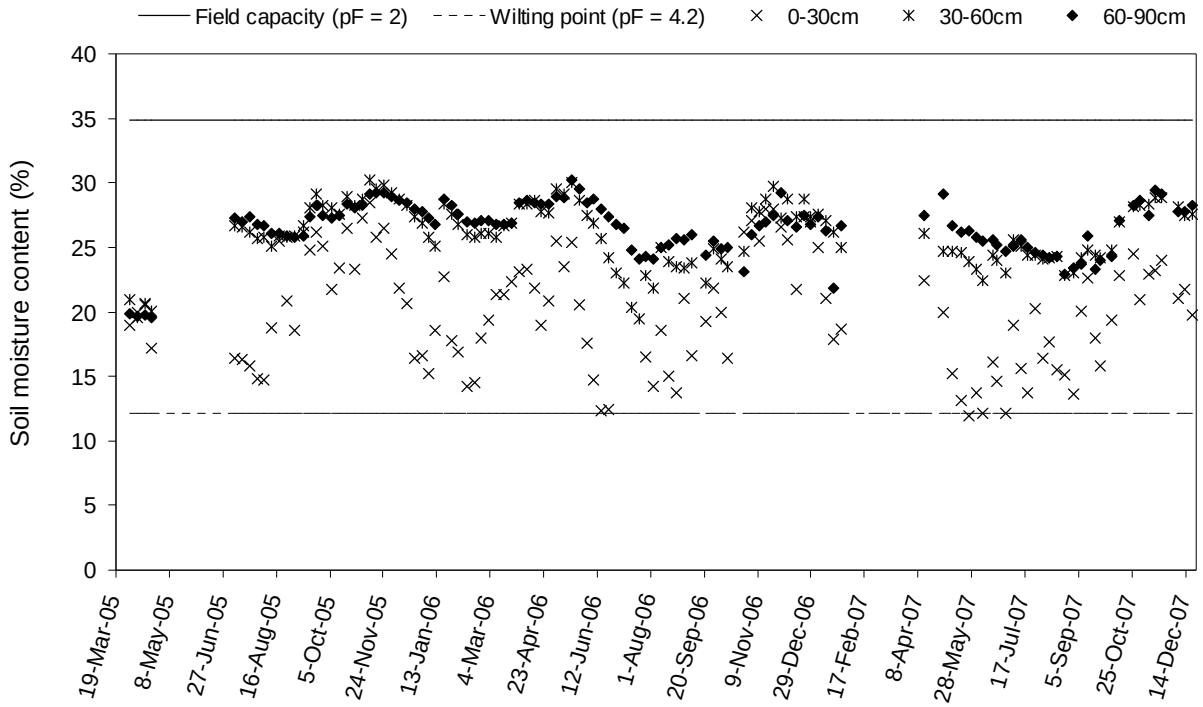

Figure 2. Variations in volumetric soil moisture contents during the experimental period at Ntungamo. Soil moisture measurements were done using Diviner2000 which was calibrated using gravimetric soil moisture measurements at the site.

The weak response to fertilization at Kawanda was attributed to a complex of factors such as low available soil water and higher bulk density (1.46−1.56 g cm^{-3}), which limited root elongation to explore soil nutrients. From field observations, most plants reached maturity with no functional leaves (remaining leaves had > 50% of their area yellow), bunches with the same number of fingers at Kawanda as those at Ntungamo were lighter due to

poorly filled fingers, and some bunches were choked (failure of the inflorescence to fully emerge), all being possible signs of moisture stress. At Ntungamo, an interaction of low soil organic matter content and low rainfall resulted in low fertilizer recovery fractions (Chapter 3). The variations in soil moisture contents for 0−30 cm, 30−60 cm and 60−90 cm soil layers were large (Figure 2) due to the seasonal variations in rainfall, transpiration and evaporation from the soil because no external mulch was applied and LAI was low. Soil moisture contents appeared to be limiting during the dry spells January to mid-March and mid-May to mid-August.

Low moisture contents of especially the 0−30 cm and 30−60 cm soil layers, where more than 90% of the roots are located (Kashaija et al., 2004), affected the response to fertilization (Figure 3).

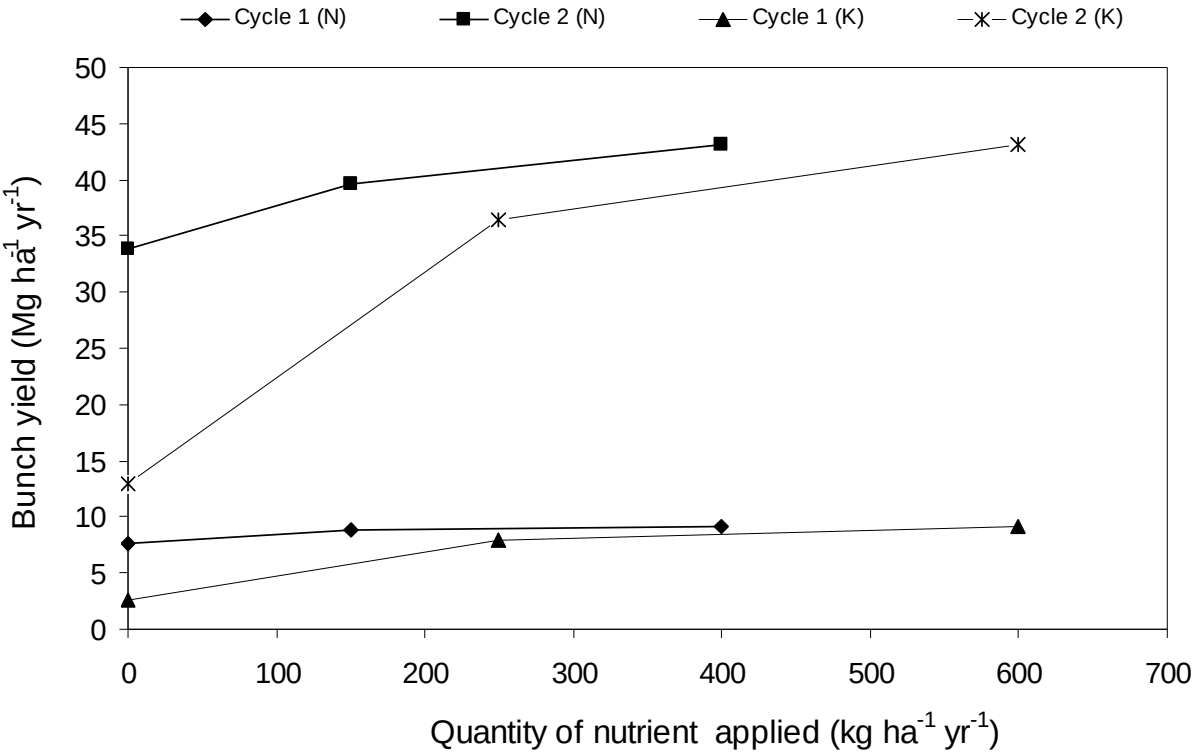

Figure 3. Response of highland bananas to applications of nitrogen (Urea) at 0, 150 and 400 kg N ha^{-1} yr^{-1} and potassium 0, 250 and 600 kg K ha^{-1} yr^{-1} at Ntungamo over two crop cycles. Bunch yields (Mg ha^{-1} yr^{-1} FW) for crop cycle 1 plants were calculated based on the duration from planting to harvest, but yields of the successive crop cycles were based on the duration between consecutive harvests (i.e. between cycle 1 and 2), resulting into differences in values for the two cycles. No response means that fertilizers remain unused in the soil or are lost.

McIntyre et al. (2000) reported that more water was removed from both the 0−30 cm and 30−50 cm depths in mulched banana plots due to a higher demand for water as a result of the increase in aboveground biomass. Bananas are sensitive to drought, with stress initiated at pF 2.3−2.4 in cultivar 'Williams' (Robinson and Alberts, 1986). For highland bananas, Cnops (2009) reported plants showing signs of stress at pF 2.5 and severe stress at pF 3.0. Based on soil moisture measurements (Figure 2), the small yield increases obtained at Ntungamo by increasing the N rate from 150 to 400 kg ha^{-1} yr^{-1} (0.2 Mg ha^{-1} yr^{-1} FW for cycle 1 and 3.6 Mg ha^{-1} yr^{-1} FW for cycle 2) and the K level from 250 to 600 kg ha^{-1} yr^{-1} (1.2 Mg ha^{-1} yr^{-1} FW for cycle 1 and 6.8 Mg ha^{-1} yr^{-1} FW for cycle 2) for treatment 400N−50P−600K are attributed to moisture stress for the plant. In comparison to other regions in the tropics (Costa Rica and Honduras) where moisture is not limiting (annual rainfall is above 3,000 mm), the yields (*Musa* AAA; Cavendish) with the maximum fertilizer rate used in our trials (400N−50P−600K) are about 80 Mg ha^{-1} (Stover and Simmonds, 1987). This emphasizes the argument that moisture stress is a major factor limiting production. The major banana growing areas in the Lake Victoria basin and southwest Uganda, receive low and highly variable rainfall ranging 900−1400 mm per annum.

6.4. Modelling banana growth

Using knowledge on the banana crop, a dynamic crop growth model to simulate potential yield was built (Chapter 4). The model, LINTUL BANANA 1, simulates basic processes such as radiation interception, conversion of radiation into daily dry matter, distribution of dry matter within the plant and dry matter transfers from Plants 1 (cycle 1) to Plant 2 (cycle 2) and from Plant 2 (cycle 2) to Plant 3 (cycle 3). Results suggest that the potential yield of East Africa highland bananas is > 100 Mg ha^{-1} FW (average of 5 crop cycles). Data for dry matter distribution during growth was obtained from plots that were fertilized and irrigated during dry periods to minimise effects of moisture stress and nutrient deficiency on dry matter distribution (Chapter 2). Light use efficiency (LUE) and specific leaf area (SLA) were determined for the best fertilized plots (400N−50P−600K) during the rain season. The potential bunch dry matter yields calculated by the model compared well with yields of banana plants (cultivar 'Robusta' (AAA group, Cavendish subgroup) at spacing of 1.8 x 1.8 m in India grown with an artificial mulch of 800-gauge thick black polyethylene film under irrigated conditions with LAI values > 4 (Bhattacharyya and

Madhava Rao, 1985). Thus, this gives confidence in the parameter values of LUE and SLA that were used. For models based on the light interception approach, LAI determines the amount of radiation intercepted and dry matter produced. Simulated LAI values at flowering at Kawanda (4.5) and at Ntungamo (5.3) ensured that > 95% of incident radiation (if the light extinction coefficient, k = 0.7) was intercepted. In our field trials, LAI was lower (Chapter 2) and moisture was limiting. It was therefore not possible to validate the model with our experimental data, thus potential yield values from other experiments (with other banana cultivars) were used for comparison. However, on-going research efforts under the Presidential Initiative on Banana Industrial Development (PIBID), which couple fertilization and irrigation to obtain the potential yield of highland banana should provide an opportunity for validating the model.

6.4.1. Crop physiology knowledge gained

In the LINTUL BANANA 1 model, the rates of increase in dry weights of plant parts (kg DM ha^{-1} d^{-1}) were 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. Dry matter partitioning results (Chapter 2) showed that banana plants (cv Kisansa) had leaves as the strongest sink at TSUM 1118 °C d and 1518 °C d, with increased partitioning to the pseudostem making it the strongest sink at 2125 °C d and at flowering (3383 °C d), and the bunch becoming the strongest sink at harvest (4326 °C d). Sucker initiation and emergence occurred between 1118 and 1518 °C d. Knowledge on sucker growth was used in LINTUL BANANA 1. Two stages of sucker growth were noted (i) where it is fully dependent on the mother plant and (ii) where it is dependent on its own photosynthesis and on a linearly reducing support from the mother plant. We noted that leaf production in highland bananas ceases at flowering, causing the plant to have fewer leaves at harvest.

The potential light use efficiency (LUE) for highland banana was obtained as the slope of the regression line of total dry matter accumulation (kg) and total intercepted PAR (MJ). LUE was 3.50 x 10^{-3} kg MJ^{-1} PAR at Kawanda, and 3.33 x 10^{-3} kg MJ^{-1} PAR at Ntungamo. This shows that bananas are fairly fast growing plants, with a high potential for biomass production, as shown in Chapter 4. The values for highland banana were within the reported range (1.09 and 4.41 g MJ^{-1} intercepted PAR) for agricultural crops (Sinclair and Muchow, 1999). Tsegaye and Struik (2003) reported LUE values 1.43−2.69 g MJ^{-1} PAR (aboveground DM) for Ensete (*Ensete ventricosum*) or 'false banana' at different sites in southern Ethiopia grown under rain-fed conditions, with N and P applied

at a total rate of 100 kg ha^{-1} yr^{-1} and K at a rate of 200 kg ha^{-1} yr^{-1}. The difference in LUE values between Ensete and highland bananas could be attributed to differences in physiology (Ensete is grown at higher altitudes 1500−3100 m.a.s.l) and the fact that values were calculated for the entire growth period including the dry period.

Specific leaf area, SLA (the ratio of leaf area and leaf mass) is an important crop characteristic or parameter related to leaf structure, growth and net photosynthesis. Average SLA for Kisansa was 12 m^2 kg^{-1}. In LINTUL BANANA 1, the growth of leaf area index was calculated as the product of the growth rate of leaf dry matter and the specific leaf area during the maturation stage. Knowledge on SLA in highland banana cultivars could provide potential for targeted selection and breeding aimed at increasing the growth rate and yield. Higher SLA has been related to faster growth in cereals (Rebetzke et al., 2004). However, increased SLA could increase radiation transmission through the canopy through (i) reduced leaf thickness and (ii) reduced leaf angle. Little work has been done on genotypic variation in SLA within the East Africa highland banana.

6.4.2. Contributions of the LINTUL BANANA 1 model to breeding and crop management

Crop growth modeling has over the years increased our understanding of how crops function and respond to the environment, hence contributing to crop improvement (e.g. the design of new rice types, Kropff et al., 1994b). Crop growth models can also be used to explore the importance of crop characteristics, such as physiological and morphological traits, and environmental characteristics, in a way that would not be possible in field experimentation or would take a long time or would be costly (Kropff et al., 1997). Models can allow us to make the knowledge gaps explicit (e.g. effects of increases in SLA, LUE and *k)*, hence aiding breeding and experimental designs to fill these gaps. Modelling can be used to explore effects of changes in morphological and physiological characteristics and for improving the management of experiments. Conventional breeding techniques in highland banana are difficult due to low male and female fertility resulting in low seed set per bunch (parthenocarpy) and germination rates (Ssebuliba et al., 2006). This slows down genetic improvement and therefore other techniques such as marker assisted breeding, marker assisted selection and genetic engineering are currently used with banana in Uganda.

Increased SLA (with other parameter and initial values not changed) resulted in increased bunch DM and LAI at flowering (Chapter 4). SLA has been related to the

amount of light absorbed by the leaf and the diffusion pathway of CO_2 through its tissues (Syvertsen et al., 1995), with plants with a higher SLA having higher growth rates e.g. wheat. Sensitivity analysis also showed that an increase in relative death rate of leaves (RDR) resulted in reduced bunch DM. The increase in RDR reduced the amount of dry matter in leaves, hence reduced LAI and radiation interception. Within the East Africa highland banana cultivars, genotypic variation is SLA (differences in growth rates) has to be established. Targeted selection and breeding could focus on plants with higher SLA and reduced RDR. In the trials, highland bananas had fewer leaves (5−11), as compared with 10−15 leaves commonly observed for the exotic banana cultivars. Increasing the value of LUE in the model resulted in a more than proportional increase in bunch DM, a higher leaf DM and LAI at flowering (Chapter 4). Actual LUE is largely influenced by site factors e.g. soil fertility and management practices e.g. fertilization and irrigation. Fertilization (especially N) affects the LUE through an increase in the leaf CO_2 assimilation per unit area (Sinclair and Horie, 1989). Drought affects growth via closure of the stomata, which reduces the intercellular CO_2 concentration (Ramachandra et al., 2004). In LINTUL type models, both effects are usually included in the LUE, which lumps a number of processes. In designing and managing experiments, site factors have to be considered.

Sensitivity analysis showed that a higher light extinction coefficient, *k* resulted in increased bunch DM (Chapter 4). Morphological improvements through breeding banana plants with more horizontal and broad leaves could increase radiation interception and result in higher bunch DM. FHIA (Fundacion Hondurena de Investigacion Agricola) hybrid banana cultivars (*Musa* AAAA) e.g. FHIA 17 have more and horizontal leaves (higher *k*) and yield greater than 100 kg bunch^{-1} in Uganda and Tanzania. Higher leaf numbers are probably attributed to lower leaf death rates. Msogoya et al. (2006) reported that FHIA 17 was harvested 15−34 days later as compared with highland bananas in the Eastern Zone of Tanzania, but with bunches more than double those of highland banana. The difference in growth duration is small, but the big difference in yield is due to differences in canopy structure, leaf number and probably partitioning to the bunch.

6.5. Closing the yield gaps; opportunities and challenges

East Africa highland banana are mostly grown between 1000 and 2000 m.a.s.l (Stover and Simmonds, 1987), where they are a staple food and income source for over 100 million

people. Comparing potential production calculated using the model (Chapter 4) with actual banana production on smallholder banana farms gives the 'yield gap', which shows how much yield improvement is possible at a given location. Actual yields (Mg ha^{-1} $cycle^{-1}$) in the region, vary with 11−26 Mg ha^{-1} $cycle^{-1}$ in Uganda (van Asten et al., 2008), 21−43 Mg ha^{-1} $cycle^{-1}$ in Burundi, 25−53 Mg ha^{-1} $cycle^{-1}$ in Rwanda and 35−63 Mg ha^{-1} $cycle^{-1}$ in south Kivu, Democratic Republic of Congo (CIALCA, 2008). High production near the Albertine rift is attributed to the relatively young and fertile soils and high rainfall (> 1400 mm yr^{-1}) supporting higher plant densities (1800−3300 mats ha^{-1}) and lower pest (nematodes and weevils) and disease (black sigatoka) pressure. Rainfall and soil fertility were higher and pest and disease pressure near the albertine rift was lower than what was observed in the field trials that were the basis for the work presented in this thesis. Farmers in Rwanda, Burundi and Democratic Republic of Congo rated banana production constraints, with declining and low soil fertility first, drought stress second and pests and diseases third (CIALCA, 2008). Farmers in Uganda rated banana production constraints, with pests first, low soil fertility second, diseases third and drought forth (van Asten et al., 2009).

Past approaches such as fertilizer starter packs and subsidies promoted by governments, donors and NGOs have had short term impacts and collapsed when funding was stopped. In order to attain the Millenium Development goals, a target of 6% per annum agricultural growth has been established by The New Partnership for Africa's Development (NEPAD) under the comphrensive Africa agriculture development programme. However, despite the current initiatives in Uganda (such as Plan for Modernisation of Agriculture – PMA, National Agricultural Advisory Services – NAADS, Soil Fertility Initiative – SFI), agricultural production continues to grow at < 2% per annum. This raises a number of questions, (i) how can smallholders farmers intensify banana production systems?, (ii) do the current policies target increased availability and access to fertilizers and pesticides?, and (iii) can increasing access to markets and raising banana prices trigger re-investments into banana farming?

Experimental results in this study showed that the maximum yield (Mg ha^{-1} yr^{-1}) with the application of 400N−50P−600K kg ha^{-1} yr^{-1} was about 40% of the calculated potential bunch DM using the LINTUL Banana model (Chapter 4). This raises questions regarding the use of mineral fertilizers to close the yield gaps. The ability of a crop to take up nutrients depends on factors like moisture availability, root exploration of the soil volume and pests and diseases. Banana root density is negatively correlated to soil bulk density (Delvaux, 1995). The poor response to mineral fertilizers (low recovery fractions)

at our sites was attributed to soil moisture stress, poor root exploitation of the soil, and low soil organic matter content (Chapter 3). Strong synergy between the soil organic matter content (mulch and manure application) and mineral fertilizers has been reported by Smithson et al. (2001) in an established banana plantation, with a yield of 67 Mg ha^{-1} yr^{-1} at a density of 700 mats ha^{-1} at Rubale, southwest Uganda, with a fertilizer application of 100N−25P−100K kg ha^{-1} yr^{-1}. Addition of organic materials often leads to a better soil structure, improved water infiltration, increased root exploration of the soil (McIntyre et al., 2000), and increased faunal activity (Okwakol and Kagole, 1993). This improves the recovery of applied fertilizer, implying a smaller amount of fertilizers is required for a given target yield (Chapter 3).

From the trials, it is evident that mineral fertilizers cannot be singly used to close the yield gaps in the study region. With irrigation virtually not practiced on banana farms, the combined application of organic and mineral fertilizers is probably a better option for increasing yields due to the synergetic effects. However, low quantities of fertilizer imported, a liberalized market and high transportation costs from Mombasa to Kampala, raise the cost of fertilizers, making them unaffordable to farmers. Not suprising, banana farmers rated constraints to fertilizer adoption with the cost first, availability in nearby shops second, and uncertainty about the quality of fertilizer in the shops (van Asten et al., 2009). Despite the cost issues, Wairegi (2009) obtained a good and profitable on-farm response to fertilizers in central Uganda under farmer management, with fertilizer amounts averaging 71N, 8P, 32K kg ha^{-1} $year^{-1}$. Government policies should target increased availability and access to fertilizers (and pesticides) at affordable prices and the dissemination of research findings on crop response to fertilization through an extension service that packages research findings in a format that allows adoption (Omamo, 2003).

The profitability of mineral fertilizer use in highland bananas is strongly related to the distance to the urban market (van Asten et al., 2008; Bagamba, 2007). This has strong implications for adoption of mineral fertilizer. Bananas from southwest Uganda are transported to the main urban banana markets located in central Uganda, and the banana chain is so fragmented with many actors (farmer − bicycle traders − truck traders − truck transporters − market vendors). As a result, farmers receive about 44% of the market price (PIBID, 2008), which also hinders the adoption of mineral fertilizers. Production areas in central Uganda have a comparative advantage of proximity to the market, but production has reduced and has shifted to southwest Uganda (Gold et al., 1999). This could be attributed to land pressure, labour shortage and pests and diseases. However, as the economy develops, populations urbanize (rate of urbanisation − 4.4% per annum),

incomes increase, market infrastructure expands, and agriculture operates on a more commercial basis. The current degree of urbanization has already created urban banana markets, due to the traditional preferences for matooke, but this demand has not been translated into investments in crop management (e.g. use of mineral fertilizers), probably due to low banana farm-gate prices and other production constraints. In order to get better returns, farmers can be encouraged to form production and marketing cooperatives for improved banana marketing especially in southwest Uganda.

6.6. More suggestions for future research

Most of the research on East Africa highland bananas over the last two decades has focused on pests e.g. banana weevil and nematodes, due to the perception that they were a major production constraint. Although research on controlling the pests continues (e.g. inserting genes into highland banana for disease resistance, use of endophytes), farmers in the region currently recognise that low and declining soil fertility and moisture stress are the most important production constraints. This has been confirmed from recent farm surveys carried out under the CIALCA project (Rwanda, Burundi and Democratic Republic of Congo) and recent farm surveys in Uganda. The nutrients limiting banana production have been identified in field trials, but the responses to mineral fertilizers are low. There is a need to understand the factors and their interactions determining highland banana yield across altitude and rainfall gradients. At higher altitude and rainfall levels, the density and yields (Mg ha^{-1} yr^{-1}) are higher as noted in Kivu, Democratic Republic of Congo. There is also a need to explore interactions between plant density and agro-ecology.

Results presented in this thesis showed that the potential yield of East Africa highland bananas is more than 18 Mg ha^{-1} DW. Much as improvements (e.g. through breeding) in parameters related to leaf area increase and light interception (SLA and k) are important, better management of crop (fertilization coupled with soil organic matter management and soil moisture conservation) can improve the current yields. With irrigation, bananas could be cultivated in the low-land areas of East Africa, where rainfall is lower, but higher average temperatures imply faster growth, which may or may not have yield advantages. For regions with dry periods, the benefit-cost ratios of irrigation in order to maintain soil moisture pF < 2.5 need to be determined. Bananas generally flower during the two rainy seasons (March to mid−May and August to December) giving two

harvest peaks from June to August and December to February. However, when grown under optimal conditions, different banana plants can flower throughout the year (Robinson, 1996) and can provide a steady food supply and income source. Irrigation (during the dry periods), sucker selection, and knowledge on banana phenology can be used to target production during periods when production is low and prices high.

In this thesis, a crop growth model for bananas is presented and used to calculate potential bunch dry matter. More work should focus on adding modules to the model in order to simulate water, nitrogen and potassium-limited production (Chapter 5). However, the effects of water and nutrient limitations on dry matter partitioning during growth and LUE in highland banana are not well established. In addition, increased moisture and nutrient stress delays flowering and affects finger filling. This gap has to be addressed further when improving the model. The LINTUL BANANA 1 model has been parameterized using parameters or coefficients for cultivar Kisansa, yet over 130 highland banana cultivars are grown in Uganda. There is a need to determine coefficients or parameters for more cultivars.

In this thesis, I have taken the first steps towards development of a growth simulation model for highland banana. I have indicated the steps that need to be taken to expand the capabilities of this model, and its utility as a tool (Chapter 5). I hope in future the LINTUL BANANA 1 model will assist in the realisation of the full potential of the highland banana in order to meet the increasing food and income demands of the people of the Great Lakes Region.

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Appendices

Appendix 1

The listing of LINTUL BANANA 1 model

Appendix 1

The listing of LINTUL BANANA 1 model

```
***Definitions of subroutines and functions.

DEFINE_CALL GLA(INPUT,INPUT,INPUT,INPUT,INPUT,INPUT,INPUT,INPUT,...
                INPUT,INPUT,                                  OUTPUT)

DEFINE_FUNCTION Fsu2(INPUT,INPUT,INPUT,INPUT)

DEFINE_FUNCTION prt1(INPUT,INPUT,INPUT,INPUT,INPUT,INPUT,INPUT,INPUT)

DEFINE_FUNCTION prt2(INPUT,INPUT,INPUT,INPUT,INPUT,INPUT)

DEFINE_CALL INTERPOL(STRING,STRING,STRING,STRING,                      ...
                     INPUT_ARRAY,INPUT_ARRAY,INPUT_ARRAY,INPUT_ARRAY ,...
                     INTEGER_INPUT,INPUT,OUTPUT,OUTPUT,OUTPUT,OUTPUT)

***Definitions of Arrays for the functions that are linearly interpolated.
ARRAY PCOTB(1:K), PSTTB(1:K), PLVTB(1:K), PBUTB(1:K)

*********************************************************************************************

TITLE LINTUL BANANA 1

*LINTUL BANANA 1 is a model for optimal growing conditions, where dry matter production is
*simulated as a result of PAR interception and utilization with a constant light use efficiency -
*LUE, with dry matter transfers between plants incorporated.

*Crop - East Africa Highland banana (MUSA AAA-EAHB cv. Kisansa)

***Remarks
***This program assumes an established banana plantation.
***Initialisation should always be between TSUM1 2262 and 2423(referring to plant 1 - mother
***plant).In that physiological time period, plant 1 (mother plant) and plant 2 (sucker 1), are
***present, but not yet plant 3 (sucker 2). Thus, only plant 3 goes through the juvenile stage
***and the prejuvenile stage, where it has no functional leaves yet.
***Units used throughout the program are hectare (ha), kg, degree celcius (C),
***MJ for radiation and days (d).

INITIAL

*********************************************************************************************

***Parameters that should not be changed.

***The initial parameters TSUMi, LAIi, DMi, Wrti,Wshi, Wleafi, Wcormi, Wpsstmi, with i= 1 to 3,
***and Wbunch1 are related because they belong to a certain development stage and must thus be
***chosen in coherence.
***For example, if TSUM1I would be taken 2423 Cd (and TSUM2I=1121 and TSUM3I=0), switch SWFSU2
***should be 0.0, because DM1 is then not supplied anymore to DM2.

INCON TSUM1I          = 2262.
*Initial temperature sum of plant 1 (C d)
INCON TSUM2I          = 960.
*Initial temperature sum of plant 2 (C d)
INCON TSUM3I          = 0.
*Initial temperature sum of plant 3 (C d)

LAI1I           = Pleaf1I * SLA1 * Wsh1I * Fleaf_green1
*Initial leaf area index of plant 1 (ha leaf ha-1 soil)

LAI2I           = Pleaf2I * SLA2 * Wsh2I * Fleaf_green2
*Initial leaf area index of plant 2 (ha leaf ha-1 soil)

LAI3I           = Pleaf3I * SLA3 * Wsh3I * Fleaf_green3
*Initial leaf area index of plant 3 (ha leaf ha-1 soil): is always 0.0 at start
```

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***Dead leaves are hanging along the pseudostem of the plant, they hardly contribute to the
***shadow in the plant, and the functional part is only the green portion of the leaves.
***Thus, also the LAIi's are multiplied by the green fraction.

PARAM Fleaf_green1    = 0.56
*Fraction of green leaves on plant 1 at initialisation (2262 C d)
PARAM Fleaf_green2    = 0.75
*Fraction of green leaves on plant 2 at initialisation (960 C d)
PARAM Fleaf_green3    = 0.00
*Fraction of green leaves on plant 3 at initialisation (0 C d). Plant 3 emerges later in the
*growth process thus Fleaf_green3 is of no importance and taken zero

INCON DM1I            = 4902.
*Initial total dry matter of plant 1 (kg DM ha-1)

INCON DM2I            = 1757.
*Initial total dry matter of plant 2 (kg DM ha-1)

INCON DM3I            = 0.
*Initial total dry matter of plant 3 (kg DM ha-1)

INCON HarvestDM_I     = 0.0
*Initial value of the integral keeping track of "harvested" dry matter of all above ground plant
*parts
*These contain the dry matter of pseudostem, leaves (both green and dead) and bunch at the moment
*of harvest (3600 C d), plus the pruned dead leaves, all in (kg DM ha-1)
*The corm is not harvested

INCON DMmulch_I       = 10000.0
*Initial amount of mulch (kg DM ha-1)
*Initialised in accordance with an established plantation by running the simulation and the mulch
*appears to start each time around 10000 kg/ha = 1 kg/m^2, which is in the order of magnitude of
*the small experiment to assess soil coverage by mulch done

INCON HarvestWpsstm_I = 0.0
*Initial value of the integral keeping track of "harvested" dry matter of pseudostem
INCON HarvestWLeaf_I  = 0.0
*Initial value of the integral keeping track of "harvested" dry matter of green leaves
INCON HarvestWLeafD_I = 0.0
*Initial value of the integral keeping track of "harvested" dry matter of dead leaves
INCON HarvestWbunch_I = 0.0
*Initial value of the integral keeping track of "harvested" dry matter of bunches

INCON HarvestDM_pru1I = 0.0
*Initial value of the integral keeping track of pruned leaf dry matter of plant 1
INCON HarvestDM_pru2I = 0.0
*Initial value of the integral keeping track of pruned leaf dry matter of plant 2
INCON HarvestDM_pru3I = 0.0
*Initial value of the integral keeping track of pruned leaf dry matter of plant 3
*Actually, we assume that leaves of plant 3 do not die

*HarvestDM_pruiI, added to keep track pruned leaves of plant i=1-3, to enable balance shoot dry
*matter of the indivudual plants
*WleafDi is re-set to 0.0 after pruning and HarvestWLeafD captures the total pruned leaves and
*harvested leaves

PARAM TSUMSUC         = 1302.
*Temperature sum referring to physiological time of plant 2, when plant 3 starts to grow
PARAM STGRLV          = 360.
*Temperature sum for the start of growth of photosynthetically active leaves of plant 3
*TSUM3=360 corresponds to TSUM2=1662 of plant 2
PARAM TSUMendfulldepe = 1662.
*Temperature sum at the end of complete dependence of plant 3 on plant 2 (C d)
PARAM TSUMshfhv       = 2298.
*Temperature sum of plant 2 at harvest of plant 1 (C d). Hereafter, the function FSU2RED2_2 must
*be read by TSUM1, whereas before that physiological time it was read by TSUM2. Therefore, it is
*there called FSU2RED2_1
PARAM TSUMfloinit     = 2423.
*Temperature sum at flower initiation  of plant 1 (C d)
PARAMETER TSUMflower  = 2663.
```

```
*Temperature sum at flowering of plant 1 (C d)
PARAM TSUM3stop_exp   = 960.
*Temperature sum at which exponential leaf area growth of plant 3 stops (C d)
PARAM LAIstop_exp     = 0.88
*LAI above which exponential leaf area growth stops. Used in subroutine GLA.

PARAMETER psh_wish    = 1.0
*Desired partitioning to the roots: psh_wish must stay 1.0
Wrt3I                 = 0.0
*Initial dry matter of roots of plant 3 (kg DM ha-1)
Wsh3I                 = 0.0
*Initial dry matter of shoot of plant 3 (kg DM ha-1)

INCON Wcorm1H_I = 0.0
*Initial value of the weight of the corm at harvest
INCON Wcorm1_at_Harvest_I  = 0.0
*Initial value of the integral keeping track of the weight of corm of plant 1 at harvest
INCON Corm1_to_Wsh1I = 0.0
*Initial amount of dry matter re-distributed from corm of harvested plant to the shoot of
*the new plant 1 (kg DM ha-1)
INCON Corm1_After_HarvI      = 0.0
*Initial value of the weight of corm after harvest (kg DM ha-1)
INCON Corm1_Lost_After_HarvI = 0.0
*Initial value of the weight of corm lost after harvest (kg DM ha-1)

PARAM Plant_distance  = 3.0
*Distance between plants (m) taking a 3*3 spacing to calculate the # of leaves per plant as an
*indication. This # can easily be compared to field observations.

***The SET variables connect to events, especially to emergence and the start of growth of plant
***3, and to accumulation of harvested products.
***The switch SWFSU2 must be taken 1.0, because it regulates that there is some dry matter, that
***is produced by plant 1, going to plant 2. This switch is normally set to 1 after the harvest,
***but since we start just in the middle of crop development it is still on (so it is 1.0) from
***the "previous" harvest.
***The same holds for SWFrt1, the switch that indicates that Function prt2  should be read
***between 360 C d and 2663 (Tsumflower(ing)). Before 360 C d, function prt1 is read.
***Because of the initialization timing between 2262 and 2423 C d, SWFrt1 should be on (so equal
***to 1.0).

SET SWemerg3          = 0.0
SET SWstdm3           = 0.0
SET SWFSU2            = 1.0
SET SWFrt1            = 1.0

***Balances
INCON ZERO            = 0.0

*******************************************************************************************

***Parameters that can be changed.

PARAM TBASE           = 14.
*Base temperature for banana growth (degree C)

***General remark: the RGRLi, Ki, LUEi, SLAi, RDRi and LWRi, where i = 1,2,3, have been given
***separate names, so that in e.g. a sensitivity analysis, these could be simply adapted. In
***principle, however, these parameters are similar for i = 1, 2 and 3.

PARAM RGRL1           = 0.0077 ; RGRL2 = 0.0077 ; RGRL3 = 0.0077
*Relative growth rate of leaf area index during the exponential growth phase (Cd-1)
PARAM K1              = 0.7
*Light extinction coefficient for plant 1 (ha soil ha-1 leaf)
PARAM K2              = 0.7
*Light extinction coefficient for plant 2 (ha soil ha-1 leaf)
PARAM K3              = 0.7
*Light extinction coefficient for plant 3 (ha soil ha-1 leaf)
      LUE1            = 3.33 * 1.E-3
      LUE2            = 3.33 * 1.E-3
      LUE3            = 3.33 * 1.E-3
```

```
*Light use efficiency for plant 1, 2 and 3 (kg MJ-1 PAR)
PARAM SLA1            = 0.0012 ; SLA2  = 0.0012 ; SLA3  = 0.0012
*Specific leaf area of plant 1, 2 and 3 (ha leaf kg-1 leaf DM)

PARAM RDR1            = 0.0214
*Relative death rate of leaves of plant 1 (d-1)
PARAM RDR2            = 0.0094
*Relative death rate of leaves of plant 2 (d-1)
PARAM RDR3            = 0.00
*Relative death rate of leaves of plant 3 (d-1)
*Plant 3 is heavily shaded by plant 1 and 2, therefore GDM3 and GWleaf3 are small,therefore RDR
*for plant 3 is taken to be zero
PARAM Days_between_prunings = 30.
*Days_between_prunings affects the pruning of leaves and is a management parameter, here set
*at 30 days

PARAM RDcR            = 0.0175
*Relative decomposition rate of mulch (d-1)
*Estimated as average of relative decomposition rates of dry leaves and pseudostems from
*experiments during the rain season by Lekasi et al., 1999. Decomposition of crop residues in
*banana-based cropping systems of Uganda. Biological Agriculture and Horticulture 17,1-10.

PARAM RDRrt1_After_Harv = 0.051
*Relative death rate of roots of plant 1 after harvest (d-1)
*After 3 months (90 days), only 1% of the roots are left
*RDRroots1 = 1n(0.01)/(-90) = 0.051
*Roots of harvested plant 1 will decay, and the roots of the next harvested plant are added to
*this pool of roots (roots of harvested plant 1 plus roots of new plant 1 harvested)

PARAM FSU2max         = 0.05
*Fraction of DM that goes from plant 1 to plant 2 during the stage where plant 2 does not have
*functional leaves (0<TSUM3<360) and fully obtains DM from plant 2 expressed in
*(kg DM plant-3) / (kg DM plant-2)

***Function introduced to capture the effect of water stress on dry matter partitioning over the
***roots and shoot.
***For potential production, there is no water stress

PARAM prt_wish_0  = 0.2
**Parameter prt_wish_0 is the assumed rt:sh ratio if there is no water stress.
*PARAM prt_wish_high = 0.4
PARAM prt_wish_high = 0.2
*Parameter prt_wish_high represents at the moment the highest rt:sh ratio if water stress occurs.
*This is rudimentary introduced in the start of the DYNAMIC section by an INSW, and will be
*adapted by the water stress factor, probably TRANRF later
*A prt_wish = 1.0 would mean that there is as much dry matter in the roots as in the shoot, and
*the fraction of the growth rate to be partitioned to the roots and shoot is
*(1/(1+1) = 0.5 and (1-0.5)=0.5). A value of 0.2 means that a fraction of 0.2 of dry matter is in
*the roots. The fraction to be partitioned from the actual growth rate to the roots is now
*0.2/(1+0.2)=1/6 and 1-1/6=5/6 to the shoot
*These calculations are automated in the function routines prt1(increasing DM partitioning to
*roots) and prt2 (reducing DM partitioning to roots)

*Desired partitioning to the roots: psh_wish must stay 1.0, it is therefore placed in the
*"not-to-be-changed-section" and here it is, as a reminder placed as a comment

      prt_cal         = prt_wish_0 / (psh_wish + prt_wish_0)
      Frtmax          = Factor * prt_cal

*     prt_wish_high = 0.4
*prt_wish_0 is introduced because of the initialization of prt_cal to mimick the water stress (or
*not) at the beginning of the simulation "_0", and to calculate the initialization of dry matter
*over root and shoot. (Technical remark: since prt_wish is dynamically used later, a new name
*must be specified , prt_wish_0 was chosen)
*prt_wish_high is the consequence of a maximum stress of water during the simulation
*Both prt_wish_0 and prt_wish_high will be controlled by water stress, in the versions for
*water-limited production
*In fact only prt_wish will be made a function of water stress
*Frtmax is used to initialize the start of the dry matter distribution over the plant organs,
*adjusted to the different initial TSUM's, using prt1 and prt2
*Parameter Factor was used to test the effect of water stress (1 means no stress)
```

```
*PARAM Factor          = 2.5
*PARAM Factor          = 1.8
*PARAM Factor          = 1.4
PARAM Factor          = 1.0

DummyRt               = prt1(TIME,STTIME,prt_wish_0,psh_wish,Frtmax,...
                                                    STGRLV,TSUM3I,TSUM3I)
*Function prt1 is called to calculate slope Afixed that is then placed in the COMMON/SLOPE/ in
*the function, and can be used by function prt2, in which this COMMON is also included

Wrt1I                 = FrtRED1I * DM1I
*Initial dry matter of roots of plant 1 (kg DM ha-1)
FrtRED1I              = prt2(prt_wish_0,psh_wish,TSUM3I,STGRLV,TSUM1I,TSUMflower)

Wrt2I                 = FrtRED2I * DM2I
*Initial dry matter of roots of plant 2 (kg DM ha-1)
FrtRED2I              = prt2(prt_wish_0,psh_wish,TSUM3I,STGRLV,TSUM2I,TSUMflower)

*Wrt3I                 = 0.0
*Initial dry matter of roots of plant 3 (kg DM ha-1)
*Note that this value must always be 0.0. It is therefore placed in the "not-to-be-changed-
*section" and here it is, as a reminder, placed as a comment.
*Wrt3I is always 0.0, because plant 3 emerges somewhere in the growth process, so after the shift
*it is also gone. This does not hold for the roots and shoots of plant 2 and the plant 1, which
*always have some initial positive value, calculated from the rt:sh ratio.
*The roots from plant 1 at harvest will NOT be harvested (is just not possible or at least is
*never done in practice).

*Difficult to estimate dead roots, we assume that there are no dead roots. Most studies report
*living roots, because dead roots rot away fast.

INCON Wrt1DI = 0.
*Initial weight of dead roots of plant 1 (kg DM ha-1)
INCON Wrt2DI = 0.
*Initial weight of dead roots of plant 2 (kg DM ha-1)
INCON Wrt3DI = 0.
*Initial weight of dead roots of plant 3 (kg DM ha-1)

INCON Wrt1_After_HarvI = 0.
*Initial weight of dead roots of plant 1 (kg DM ha-1) just after harvest

PARAM  RDRrt2 = 0.0218
*Relative death rate of roots of plant 2 (d-1)
PARAM  RDRrt3 = 0.0
*Relative death rate of roots of plant 3 (d-1)

Wsh1I                 = (1.0 - FrtRED1I) * DM1I
*Initial dry matter of shoot of plant 1 (kg DM ha-1)
Wsh2I                 = (1.0 - FrtRED2I) * DM2I
*Initial dry matter of shoot of plant 2 (kg DM ha-1)
*Wsh3I                 =  0.0
*Initial dry matter of shoot of plant 3 (kg DM ha-1)
*Note that this value must always be 0.0. It is therefore placed in the "not-to-be-changed-
*section" and here it is, as a reminder placed as a comment

PARAM RDRCorm1_After_Harv = 0.038
*Relative decomposition rate of the corm after harvest (d-1)
PARAM pcorm1_to_Wsh1      = 0.5
*Approximate proportion of corm dry matter of harvested plant 1 re-distributed to the new plant 1

*After about 4 months (120 days), 1% of the original corm dry matter will be left
*RDCRcorm = 1n(0.01)/(-120) = 0.038 d-1
*Assumption: No death of corm during growth

*There is corm-decay and corm redistribution after harvest of plant 1. If we take the (relative)
*decay rate to control the decrease of the corm as a whole (with 1% left after 4 months), the
*fraction "Corm1Dm_transferprop" goes to the plant1 Wsh1, and the remainder "(1 -
*Corm1Dm_transferprop)" goes to the organic matter of the soil, that is not further specified

Wcorm1I               = Pcorm1I  * Wsh1I
```

```
*Initial dry matter of corms of plant 1 (kg DM ha-1)
Wpsstm1I              = Ppsstm1I * Wsh1I
*Initial dry matter of pseudostem of plant 1 (kg DM ha-1)
Wleaf1I               = Pleaf1I  * Wsh1I *  Fleaf_green1
*Initial dry matter of green leaves of plant 1 (kg DM ha-1)
WleafD1I              = Pleaf1I  * Wsh1I * (1.0 - Fleaf_green1)
*Initial dry matter of dead leaves of plant 1 (kg DM ha-1)
Wbunch1I              = Pbunch1I * Wsh1I
*Initial dry matter of the bunch of plant 1 (kg DM ha-1)

CALL INTERPOL('PCOTB','PSTTB','PLVTB','PBUTB',...
               PCOTB ,PSTTB  ,PLVTB  ,PBUTB  ,...
               K,TSUM1I, Pcorm1I,Ppsstm1I,Pleaf1I,Pbunch1I)

Wcorm2I               = Pcorm2I  * Wsh2I
*Initial dry matter of corms of plant 2 (kg DM ha-1)
Wpsstm2I              = Ppsstm2I * Wsh2I
*Initial dry matter of pseudostem of plant 2 (kg DM ha-1)
Wleaf2I               = Pleaf2I  * Wsh2I *  Fleaf_green2
*Initial dry matter of green leaves of plant 2 (kg DM ha-1)
WleafD2I              = Pleaf2I  * Wsh2I * (1.0 - Fleaf_green2)
*Initial dry matter of dead leaves of plant 2 (kg DM ha-1)

CALL INTERPOL('PCOTB','PSTTB','PLVTB','PBUTB',...
               PCOTB ,PSTTB  ,PLVTB  ,PBUTB  ,...
               K,TSUM2I, Pcorm2I,Ppsstm2I,Pleaf2I,DummyPbunch2I)

Wcorm3I               = Pcorm3I  * Wsh3I
*Initial dry matter of corms of plant 3 (kg DM ha-1)
Wpsstm3I              = Ppsstm3I * Wsh3I
*Initial dry matter of pseudostem of plant 3 (kg DM ha-1)
Wleaf3I               = Pleaf3I  * Wsh3I *  Fleaf_green3
*Initial dry matter of green leaves of plant 3 (kg DM ha-1)
WleafD3I              = Pleaf3I  * Wsh3I * (1.0 - Fleaf_green3)
*Initial dry matter of dead leaves of plant 3 (kg DM ha-1)

CALL INTERPOL('PCOTB','PSTTB','PLVTB','PBUTB',...
               PCOTB ,PSTTB  ,PLVTB  ,PBUTB  ,...
               K,TSUM3I, Pcorm3I,Ppsstm3I,Pleaf3I,DummyPbunch3I)

TotWleafD_I           = WleafD1I + WleafD2I + WleafD3I
*Initial value of the integral collecting the dead leaves over time. This state is periodically
*harvested and becomes mulch. Also prunings come into this state.

ARRAY_SIZE K=20

PARAMETER PCOTB(1:19) = 0.,0.14, 440.,0.14, 1038.,0.11, 1434.,0.09, 2168.,0.04, 2423.,0.03,...
                        2663.,0.03, 2800.,0.00, 3132.,0.00, 3600.; PCOTB(20:K)=0.00

PARAMETER PSTTB(1:19) = 0.,0.33, 440.,0.33, 1038.,0.31, 1434.,0.36, 2168.,0.50, 2423.,0.51,...
                        2663.,0.47, 2800.,0.00, 3132.,0.00, 3600.; PSTTB(20:K)=0.00

PARAMETER PLVTB(1:19) = 0.,0.53, 440.,0.53, 1038.,0.58, 1434.,0.55, 2168.,0.46, 2423.,0.46,...
                        2663.,0.43, 2800.,0.00, 3132.,0.00, 3600.; PLVTB(20:K)=0.00

PARAMETER PBUTB(1:19) = 0.,0.00, 440.,0.00, 1038.,0.00, 1434.,0.00, 2168.,0.00, 2423.,0.00,...
                        2663.,0.07, 2800.,1.00, 3132.,1.00, 3600.;PBUTB(20:K)=1.00


*The partitioning functions are taken equal for all plants (plant 1, 2 and 3)
*If there are 10 coordinate pairs, there are 20 numerical values, and the ARRAY must be declared
*20 long (K=20)

***Run control. STTIME=1 corresponds to January 1. FINTIM=1200 means that the calculations
***continue for 1200 days

TIMER STTIME = 1.; FINTIM = 1200.; DELT = 0.25; PRDEL = 1.0
TRANSLATION_GENERAL DRIVER='RKDRIV' ; DELMAX = 0.25; TRACE = 4

*** Output
```

```
PRINT  TSUM1,LAI1,DM1,BalDmHlp1,Wcorm1,Wcorm1I, Wpsstm1,Wpsstm1I,PARINT1,Wleaf1,Leafnum_plant1,...
       Wleaf1I,Wbunch1,NDM1, NDM2, NDM3, Wbunch1I,Wsh1,GWsh1,WleafD1I,WshPlnt1Tot,Wrt1,...
       WrtD1_Tot,GWrt1,DWrt1, NWrt1, DWleaf1,Wcorm1H, Corm1_to_Wsh1,BalRtShHlp1,BalShHlp1,...
       HarvestDM1_Pru,TSUM2,LAI2,DM2,BalDmHlp2,Wcorm2,Wcorm2I, Wpsstm2,Wpsstm2I, Wleaf2,Wleaf2I,...
       Wsh2,WleafD2I,WshPlnt2Tot,Wrt2,WrtD2_Tot,DWleaf2,GWsh2,WleafD2,BalRtShHlp2,BalShHlp2,...
       HarvestDM2_Pru,TSUM3,LAI3,DM3,Wcorm3,Wcorm3I, Wpsstm3,Wpsstm3I, Wleaf3,Wleaf3I,...
       Wsh3,WleafD3I,WshPlnt3Tot,Wrt3,WrtD3_Tot,DWleaf3,GWsh3,WleafD3,BalRtShHlp3,BalShHlp3,...
       BalDmHlp4, TotWrtD, BalDmHlp5, BalRtShHlp1, BalRtShHlp2,BalRtShHlp3, BalRtShHlp4,...
       HarvestDM, HarvestWLeaf, HarvestWLeafD, HarvestWpsstm, WleafD1,HarvestWbunch, DMmulch,...
       TotWleafD,Wrt1_After_Harv,RtShratio1, RtShratio2, RtShratio3, Corm1_After_Harv,...
       Corm1_Lost_After_Harv, Corm1_to_Wsh1

*PRINT  HI1,HIoverall, DMTotdm, DMTotRtSh, RtShratioAll, SWemerg3, SWstdm3, SWFSU2,SWFrt1,...
*       FSU2RED2_1, FSU2RED2_2, FrtRED3, FrtRED2, FrtRED1, FrtGR, GDM1HLP, GDM1, GDM2HLP,...
*       GDM2, G2from2_1, G2from2_2, G2from1, GDM3, G3from2_1, G3from2_2, G3Photos,...
*       GWrt1, GWrt2, GWrt3, DTEFF, GLAI1, GLAI2, GLAI3,...
*       PARINT1, PARINT2, PARINT3, PARIN1, PARIN2, PARIN3, PAROUT1, PAROUT2, PAROUT3

DYNAMIC

*******************************************************************************************

***Environmental data, the driving variables of the system. Note: RDD in the weather file are
***in kJ m-2 d-1, but come to the FST program in J m-2 d-1.
WEATHER WTRDIR='C:\SYS\WEATHER\'; CNTR='UGA'; ISTN=2; IYEAR=2006
*     Reading weather data from weather file:
*     RDD    Daily global radiation        kJ m-2 d-1
*     TMMN   Daily minimum temperature     degree C
*     TMMX   Daily maximum temperature     degree C
*     VP     Vapour pressure               kPa
*     WN     Wind speed                    m s-1
*     RAIN   Precipitation                 mm

DTR            = (RDD/1.E+6) * 1.E+4
*To convert daily total radiation as generated from the weather system in
*J m-2 d-1 to MJ ha-1 d-1
DAVTMP         = 0.5 * (TMMN + TMMX)
*Daily average temperature (degree C)
DTEFF          = MAX (0., DAVTMP-TBASE)
*Daily effective temperature

*******************************************************************************************

***Water stress is now introduced (as if) by defining prt_wish as different from the initial
***setting.
***In this main program the INSW will be replaced by e.g. the TRANRF function.
prt_wish       = INSW(TSUM3-180.0,prt_wish_0,prt_wish_high)

*******************************************************************************************

***Balances
***For Dry Matter DM:
*All BalDmHlp1/2/4/5 should be 0.0000
*BalDmHlp5 is relative to BalDmHlp3
*BalDmHlp1 and 2 check the rates after and before splitting these over the plants
*BalDmHlp3 accumulates all principal rates of dry matter production, which are compared to the
*summed DMi's. BalDmHlp4 is the absolute difference; BalDmHlp5 is the absolute balance relative
*to the total (BalDmHlp3)
BalDmHlp1      = G2from1 + GDM1 - GDM1HLP
BalDmHlp2      = G2from2_1 + G2from2_2 + G3from2_1 + G3from2_2 - GDM2HLP
*DM1+DM2+DM3=DMTotdm should equal of the integral of GDM1HLP+GDM2HLP+G3Photos
BalDmHlp3      = INTGRL(ZERO, GDMTOT)
GDMTOT         = GDM1HLP + GDM2HLP + G3Photos

BalDmHlp4       = ((DMTotdm) + (TotWrtD) + (TotWleafD - TotWleafD_I) + ...
                  (HarvestDM1_Pru-HarvestDM_Pru1I) + (HarvestDM2_Pru-HarvestDM_Pru2I)) - ...
                  (BalDmHlp3) - (DM1I+DM2I+DM3I) + (HarvestWleafD-HarvestWleafD_I)

BalDmHlp5      = BalDmHlp4 / NOTNUL(BalDmHlp3)
***BalDmHlp3 must also be reset at harvest, but only with respect to the shoot part (DM1-Wrt1)
***This part should be subtracted, because that is harvested
```

```
***This is implemented in the EVENT section as (HELPDM1-HELPWrt1)

*****************************************************************************************

***Balances for Root and Shoot Dry Matter:
*BalRtShHlp1, 2 and 3 are individual balances with respect to the motherplant, plant 2 and plant
*3, respectively. BalRtShHlp4 is the overall balance check, including all 3 plant parts in one
*calculation.
*BalRtShHlp4 is the balance calculated relative to the total DM production
*All balances should be 0.0000.

BalRtShHlp1 = ( ((Wrt1+Wsh1+Corm1_to_Wsh1) - (Wrt1I+Wsh1I+Corm1_to_Wsh1I)) - (DM1 - DM1I) ) / DM1

BalRtShHlp2 = ( ((Wrt2+Wsh2) - (Wrt2I+Wsh2I)) - (DM2 - DM2I) ) / DM2

BalRtShHlp3 = ( ((Wrt3+Wsh3) - (Wrt3I+Wsh3I)) - (DM3 - DM3I) ) / NOTNUL(DM3)

BalRtShHlp4 = ( (DMTotRtSh - ((Wrt1I+Wrt2I+Wrt3I) + (Wsh1I+Wsh2I+Wsh3I)))-...
                  (DMTotdm   - (DM1I+DM2I+DM3I) - (Corm1_to_Wsh1-Corm1_to_Wsh1I)) ) / DMTotdm

***BalRtShHlp1 and BalRtShHlp4 were around zero before the splitting of the shoot into its
***different parts was done. Reason: before the splitting up in parts the shoot was harvested as
***a whole, and this was obvious from the line "NEWVALUE Wsh1 = HELPWsh2",where the whole of the
***Wsh1 is replaced by Wsh2 (at that moment contained in the variable HELPWsh2). But after the
***splitting up in corm, psstm, leaves and bunch, the corm is not harvested.
***It is remaining in the soil, instead. Therefore, the balances BalRtShHlp1 and BalRtShHlp4 are
***not working properly anymore. This could only be changed if a helpvariable would be introduced
***that also represents Wsh1 as a whole. This has not been done, however, so BalRtShHlp1 and
***BalRtShHlp4 are not correct anymore after the introduction of the different shoot parts.

***Balances for Shoot dry Matter partitioning:
*BalShHlp1, 2 and 3 are individual shoot balances with respect to plant 1, plant 2 and plant 3

*All balances should be 0.0000.

BalShHlp1   = (  ((Wcorm1 + Wpsstm1 + Wleaf1 + Wbunch1 + WleafD1 + Corm1_to_Wsh1)  - ...
                 (Wcorm1I+Wpsstm1I+Wleaf1I+Wbunch1I+WleafD1I+Corm1_to_Wsh1I)) - ...
                 ( (Wsh1 - Wsh1I) + (WleafD1-WleafD1I) + (HarvestDM1_Pru-HarvestDM_Pru1I)) ) /
Wsh1

BalShHlp2   = (  ((Wcorm2 + Wpsstm2 + Wleaf2 + WleafD2 )  - ...
                 (Wcorm2I+Wpsstm2I+Wleaf2I+WleafD2I)) - ...
                 ( (Wsh2-Wsh2I) + (WleafD2-WleafD2I) + (HarvestDM2_Pru-HarvestDM_Pru2I) ) ) / Wsh2

BalShHlp3   = (  ((Wcorm3 + Wpsstm3 + Wleaf3 + WleafD3 )  - ...
                 (Wcorm3I+Wpsstm3I+Wleaf3I+WleafD3I)) - ...
                 ( (Wsh3-Wsh3I)+(WleafD3-WleafD3I)+(HarvestDM3_Pru-HarvestDM_Pru3I) ) ) /
NOTNUL(Wsh3)


*** Crop development is temperature-sum driven
TSUM1           = INTGRL(TSUM1I, RTSUM12)
*Temperature sum of plant 1 (C d)
TSUM2           = INTGRL(TSUM2I, RTSUM12)
*Temperature sum of plant 2 (C d)
TSUM3           = INTGRL(TSUM3I, RTSUM3)
*Temperature sum of plant 3 (C d)

RTSUM12         =  DTEFF
*Rate of change of temperature sum for plant 1 and 2. These rates of change are not triggered by
*an emergence, because we start with an established banana crop consisting of plant 1 and 2
RTSUM3          =  DTEFF * SWemerg3
*Rate of change of temperature sum for plant 3
*This temperature sum starts to accumulate at emergence of plant 3, as indicated by SWemerg3
*It is triggered by TSUM2 - TSUMSUC, where TSUMSUC is taken as 1302 C d

EVENT
   ZEROCONDITION TSUM2 - TSUMSUC
***Switch to indicate emergence of plant 3
   NEWVALUE SWemerg3   = 1.0
ENDEVENT
```

```
*** Leaf area calculations and light interception
LAI1            = INTGRL(LAI1I, NLAI1)
*LAI1 - leaf area index of plant 1 (ha leaf ha-1 soil)
LAI2            = INTGRL(LAI2I, NLAI2)
*LAI2 - leaf area index of plant 2 (ha leaf ha-1 soil)
LAI3            = INTGRL(LAI3I, NLAI3)
*LAI3 - leaf area index of plant 3 (ha leaf ha-1 soil)

***Net increase of Leaf area index
NLAI1           = GLAI1 - DLAI1
*Daily net rate of change of LAI for plant 1 (ha leaf ha-1 soil d-1)
NLAI2           = GLAI2 - DLAI2
*Daily net rate of change of LAI for plant 2 (ha leaf ha-1 soil d-1)
NLAI3           = GLAI3 - DLAI3
*Daily net rate of change of LAI for plant 3 (ha leaf ha-1 soil d-1)

***Death rates of Leaf area index
DLAI1           = LAI1 * RDR1
*Death rate of leaf area index of plant 1 (ha leaf ha-1 soil d-1)
DLAI2           = LAI2 * RDR2
*Death rate of leaf area index of plant 2 (ha leaf ha-1 soil d-1)
DLAI3           = LAI3 * RDR3
*Death rate of leaf area index of plant 3 (ha leaf ha-1 soil d-1)
*RDR3=0, no death of leaves for plant 3

*******************************************************************************************

      CALL GLA(SLA1,Pleaf1,GWsh1,SWstdm3,TSUM1,TSUM3stop_exp,LAI1,...
               LAIstop_exp,RGRL1,DTEFF,                      GLAI1)
*Growth rate of LAI plant 1 (ha leaf ha-1 soil d-1)
      CALL GLA(SLA2,Pleaf2,GWsh2,SWstdm3,TSUM2,TSUM3stop_exp,LAI2,...
               LAIstop_exp,RGRL2,DTEFF,                      GLAI2)
*Growth rate of LAI plant 2 (ha leaf ha-1 soil d-1)
      CALL GLA(SLA3,Pleaf3,GWsh3,SWstdm3,TSUM3,TSUM3stop_exp,LAI3,...
               LAIstop_exp,RGRL3,DTEFF,                      GLAI3)
*The growth of the leaves for plant 3 due to photosynthesis does not directly start at emergence,
*but is retarded by a temperature sum (STGRLV) which corresponds with 360 C d (about two months).
*Plant 3 emerges with no functional leaves, and obtains the necessary DM to establish its weight
*(and leaf area growth, ha leaf ha-1 soil d-1) from plant 2 up to STGRLV=360 C d

EVENT
   ZEROCONDITION TSUM3-STGRLV
   NEWVALUE SWstdm3    = 1.0
***In this event section, the dry matter SWitch is set to indicate the end of the full support of
***plant 2 to plant 3. Switch SWstdm3 also indicates the start of the linear decrease of the
***contribution of DM of plant 2 to plant 3, and the start of photosynthesis of plant 3
***STGRLV is 360 C d
ENDEVENT

***Light interception by the banana canopy (three levels - plants 1, 2 and 3)
PARIN1          = 0.5 * DTR
*Total PAR incident for plant 1 (MJ ha-1 d-1)
*PAR is 50% of DTR, expressed in MJ ha-1 d-1. This fraction of 0.5 is well established
*(Sinclair & Muchow, 1999) and therefore hard-coded
*Sinclair, T.R., Muchow, R.C., 1999. Radiation use efficiency. Adv. Agron. 11, 215-265.
PAROUT1         = PARIN1 * EXP(-K1*LAI1)
*Total PAR transmitted by plant 1 (MJ ha-1 d-1)
PARINT1         = PARIN1 - PAROUT1
*Total PAR intercepted by plant 1 (MJ ha-1 d-1)

PARIN2          = PAROUT1
*Total PAR incident for plant 2  (MJ ha-1 d-1)
PAROUT2         = PARIN2 * EXP(-K2*LAI2)
*Total PAR transmitted by plant 2  (MJ ha-1 d-1)
PARINT2         = PARIN2 - PAROUT2
*Total PAR intercepted by plant 2  (MJ ha-1 d-1)

PARIN3          = PAROUT2
*Total PAR incident for plant 3  (MJ ha-1 d-1)
PAROUT3         = PARIN3 * EXP(-K3*LAI3)
```

```
*Total PAR transmitted by plant 3 (MJ ha-1 d-1)
PARINT3         = PARIN3 - PAROUT3
*Total PAR intercepted by plant 3 (MJ ha-1 d-1)

********************************************************************************************

***Crop growth or dry matter production
DM1             = INTGRL (DM1I, NDM1)
*Total dry matter of plant 1 (kg DM ha-1)
DM2             = INTGRL (DM2I, NDM2)
*Total dry matter of plant 2 (kg DM ha-1)
DM3             = INTGRL (DM3I, NDM3)
*Total dry matter of plant 3 (kg DM ha-1)

DMTotdm         = DM1 + DM2 + DM3

HarvestDM       = INTGRL(HarvestDM_I    , RHarvestDM)
*HarvestDM - "harvested" dry matter: contains the whole of the shoot part that is harvested, so
*the pseudostem, the leaves (both green and dead) and the bunch, Plus the pruned dead leaves.
*This state variable is shockwise filled by dead leaf weight material, usually from prunings, and
*filled instantaneously by the pseudostem material, green and dead leaves of plant 1 and bunch at
*harvest. Because of the shockwise additions, the continuous day-to-day rate (RHarvestDM) is set
*to zero.

RHarvestDM      = 0.0

*Cumulative weight of leaves of plant 1 pruned (kg DM ha-1)
HarvestDM1_Pru       = INTGRL(HarvestDM_pru1I    , RHarvestDM1_pru)
RHarvestDM1_pru      = 0.0
*Cumulative weight of leaves of plant 2 pruned (kg DM ha-1)
HarvestDM2_Pru       = INTGRL(HarvestDM_pru2I    , RHarvestDM2_pru)
RHarvestDM2_pru      = 0.0
*Cumulative weight of leaves of plant 3 pruned (kg DM ha-1)
*Actually no leaves die, used to help with the re-settings
HarvestDM3_Pru       = INTGRL(HarvestDM_pru3I    , RHarvestDM3_pru)
RHarvestDM3_pru      = 0.0

DMmulch  = INTGRL(DMmulch_I, DcRDMmulch)
*DMmulch - "harvested" dry matter  (kg DM ha-1)
*It contains the shoot part that is not of economic interest, so the pseudostem and the leaves
*(both green and dead)
*Harvest occurs at (TSUM1=3600 C d) and it is used for mulching the soil

*This state variable is more or less dynamically filled by dead leaf weight material,usually from
*prunings, and filled instantaneously by the pseudostem material and all remaining leaves (dead
*and green) at harvest of only plant 1 (so no dead leaves from plant 1 and 2 at harvest)
*Since the prunings take place at regular time intervals, usually each month, the state variable
*DMmulch is filled shockwise. Dead leaves are gathered in an extra state variable called
*"TotWleafD", which is WleafD1 + WleafD2 + WleafD3

DcRDMmulch = - RDcR * DMmulch
*Decomposition rate of mulch (kg ha-1 d-1) is take proportional to the amount present
*(exponential decay). This means that the assumption is that the different materials (pruned dead
*leaves, harvested green and dead leaves and pseudostem) have a comparable relative decomposition
*rate. The RDcR could be redefined later as a function of moisture content and temperature

************************************************************************************************
EVENT
   ZEROCONDITION TSUM1-TSUMfloinit
   NEWVALUE SWFSU2     = 0.0
***Switch SWFSU2 is put to 0 at flower initiation of plant 1 (at TSUM1=TSUMfloinit=2423 C d)
***At this physiological time the support of plant 1 to plant 2 is completely stopped

ENDEVENT

***Net rates of change of the weights of the dry matter due to the death of the leaves and roots
***To calculate this, the death rate of the leaf weights are directly used

NDM1            = GDM1 - DWDM1
NDM2            = GDM2 - DWDM2
NDM3            = GDM3 - DWDM3
```

```
DWDM1           = DWleaf1   +  DWrt1
DWDM2           = DWleaf2   +  DWrt2
DWDM3           = DWleaf3   +  DWrt3

*DWDMi is the sum of the death rates of leaves - kg ha-1 d-1(DWleafi) and roots (DWrti) for
*plant i = 1-3

***Plant 1
GDM1HLP         = PARINT1 * LUE1
*Total production of plant 1 (kg DM ha-1 d-1), from intercepted PAR(MJ ha-1 d-1) and a constant
*LUE (kg MJ-1 PAR), of which a part, indicated by the result of function-subroutine FSU2
*(that is substituted in the variable FSU2RED2_2), goes to plant 2
*The remainder (1.0 - FSU2RED2_2) goes to plant 1 via GDM1

GDM1            = ( 1.0 - FSU2RED2_2 ) * GDM1HLP

***Plant 2
GDM2HLP         = PARINT2 * LUE2
*Since plant 2 fully feeds plant 3 during a "period" from 0-360 C d, the total DM produced by
*plant 2 (defined in the help-variable GDM2HLP)is divided over plant 2 and 3 during that "period"
*This period starts, however, when emergence of plant 3 takes place, indicated by SWemerg3 that
*becomes 1.0, if TSUM2 > TSUMSUC(=1302 C d)
*The part of GMD2HLP that goes to plant 3 is ( SWemerg3*(1.0-SWstdm3) * FSU2max ) and the
*remainder goes to GDM2 itself: {1-( SWemerg3*(1.0-SWstdm3) * FSU2max )}
*Since, however, either G2from2_1 or G2from2_2 should be active in rate GDM2, G2from2_2 must be
*SWitched on with SWstdm3, whereas G2from2_1 must then be SWitched off by (1.0-SWstdm3)
*That makes it subsequently superfluous to also multiply by (1.0-SWstdm3) in the expression
*{1-( SWemerg3*(1.0-SWstdm3) * FSU2max )}, and therefore this has been removed

G2from2_1       = (1.0-SWstdm3)*( 1.0 - SWemerg3*FSU2max  ) * GDM2HLP

G2from2_2       =      SWstdm3 *( 1.0 -        FSU2RED2_1 ) * GDM2HLP
G2from1         =                              FSU2RED2_2   * GDM1HLP
GDM2            = G2from2_1 + G2from2_2 + G2from1
* Total rate of increase in weight of plant 2 (kg DM ha-1 d-1)

***Plant 3
G3from2_1       = ( SWemerg3 *(1.0-SWstdm3) * FSU2max ) * GDM2HLP
G3from2_2       =                             FSU2RED2_1 * GDM2HLP
G3Photos        =    SWstdm3 * (PARINT3 * LUE3)
GDM3            =  G3from2_1 + G3from2_2 + G3Photos
*Total rate of increase in weight of plant 3 (kg DM ha-1 d-1) due to
*(i)DM partitioning from plant 2 to plant 3 (G3from2_1) in the period of
*"no functional leaves" (0.0 < TSUM3 < 360),
*(ii)due to a decreasing amount of supply from plant 2 to plant 3 in the period that plant 3
*has photosynthesis but is still supported (G3from2_2), and
*(iii)due to photosynthesis of plant 3 itself. Since this should start only  after
*TSUM3 > 360 C d, it is put on with SWstdm3. Note that GLAI3 will have a value from emergence
*onwards, and that LAI3 also increases and will intercept light, because it is supported by
*plant 2, but it is functionally not working

FSU2RED2_1      = SWstdm3 * FSU2(FSU2max,TSUMfloinit,TSUMendfulldepe,TSUM2)
FSU2RED2_2      = SWFSU2  * FSU2(FSU2max,TSUMfloinit,TSUMendfulldepe,TSUM1)
*FSU2RED2_1 is the function that takes care of the linear decrease of the amount of newly
*produced DM2, so given by GDM2HLP, that is supplied by plant 2 to plant 3 in the period that
*plant 2 is not yet shifted to the status of  plant 1
*The function is then read by TSUM2 and it is a fraction between FSU2max and 0.0
*After the shift, at TSUM2=TSUMshfhv=2298 C d (coinciding with TSUM1=TSUMHARV=3600 C d), the
*function is read by TSUM1, because plant 2 has become plant 1, and will continue to supply dry
*matter up to its flower initiation at 2423 C d
*However, the dry matter now goes to plant 2 (previous plant 3) and comes from  plant 1 (previous
*plant 2). Thus, the rates have to be differently formulated, and that has been done in the above
*programming part.
*During the period TSUM2=1662 to 2298 C d, SWstdm3 is 1, otherwise, it is 0
*During the period TSUM1=2298 to 2423 C d, SWFSU2 is 1, otherwise, it is 0
*SWemerg3= 1 after TSUM2=1302, up to the harvest

*******************************************************************************************

***Crop total dry matter produced is divided over root and shoot
```

```
***Crop root growth or dry matter production of roots
Wrt1            = INTGRL (Wrt1I, NWrt1)
*Dry matter of roots of plant 1 (kg DM ha-1)
Wrt2            = INTGRL (Wrt2I, NWrt2)
*Dry matter of roots of plant 2 (kg DM ha-1)
Wrt3            = INTGRL (Wrt3I, NWrt3)
*Dry matter of roots of plant 3 (kg DM ha-1)
WrtTot          = Wrt1 + Wrt2 + Wrt3
*Total dry matter of roots of the whole of the banana plant (kg DM ha-1)

***Crop shoot growth or dry matter production of shoots
Wsh1            = INTGRL (Wsh1I, NWsh1)
*Dry matter of shoot of plant 1 (kg DM ha-1)
Wsh2            = INTGRL (Wsh2I, NWsh2)
*Dry matter of shoot of plant 2 (kg DM ha-1)
Wsh3            = INTGRL (Wsh3I, NWsh3)
*Dry matter of shoot of plant 3 (kg DM ha-1)
WshTot          = Wsh1 + Wsh2 + Wsh3
*Total dry matter of shoot of the whole of the banana plant (kg DM ha-1)

RtShratio1      = Wrt1  /NOTNUL(Wsh1)
RtShratio2      = Wrt2  /NOTNUL(Wsh2)
RtShratio3      = Wrt3  /NOTNUL(Wsh3)
RtShratioAll    = WrtTot/NOTNUL(WshTot)

DMTotRtSh       = WrtTot + WshTot

EVENT
   ZEROCONDITION TSUM1-TSUMflower
   NEWVALUE SWFrt1    = 0.0
***Switch SWFrt is put to 0 at flowering of plant 1 (at TSUM1=TSUMflower=2663 C d)
***At this physiological time root formation of plant 1 is assumed to completely stop
***For the plant 1, that is initialized after 360 C d (in fact between 2262 and 2423 C d) and
***ends at 3600 C d, this switch is the only important one
***For Sucker 1, that is initialized after 360 C d (in fact between 960 and 1121 C d)and ends at
***2298 C d (and then continues to be plant 1), this switch is also the only important one

ENDEVENT

***Net rates of change of the weights of the shoot due to the death of the leaves
***To calculate this the death rate of the leaf weights are directly used
***Below Part of corm1 goes to Wsh1 after harvest

NWsh1           = GWsh1 - DWsh1 + dCorm1_to_Wsh1
NWsh2           = GWsh2 - DWsh2
NWsh3           = GWsh3 - DWsh3
DWsh1           = DWleaf1
DWsh2           = DWleaf2
DWsh3           = DWleaf3
dCorm1_to_Wsh1  = pcorm1_to_Wsh1 * dCorm1_After_Harv

*A help variable

Corm1_to_Wsh1   = INTGRL( Corm1_to_Wsh1I, dCorm1_to_Wsh1)

*Integral to keep track of weight of the corm of plant 1 at harvest
Wcorm1H             = INTGRL(Wcorm1H_I, RWcorm1H)
RWcorm1H            = 0.0

***Net rates of change of the weights of the living roots due to death of the roots(kg ha-1 d-1).
NWrt1           = GWrt1 - DWrt1
NWrt2           = GWrt2 - DWrt2
NWrt3           = GWrt3 - DWrt3

***Growth rates of the different plants 1, 2 and 3.
***Plant 1
GWrt1           =         FrtRED1   * GDM1
GWsh1           = ( 1.0 - FrtRED1 ) * GDM1
FrtRED1         = SWFrt1*prt2(prt_wish,psh_wish,TSUM3I,STGRLV,TSUM1,TSUMflower)
```

```
***Plant 2
GWrt2           =         FrtRED2   * GDM2
GWsh2           = ( 1.0 - FrtRED2 ) * GDM2
FrtRED2         = SWFrt1*prt2(prt_wish,psh_wish,TSUM3I,STGRLV,TSUM2,TSUMflower)

***Plant 3
GWrt3           =         (FrtGR + FrtRED3)   * GDM3
GWsh3           = ( 1.0 - (FrtGR + FrtRED3) ) * GDM3
*The dry matter that is either given to sucker 2 or produced by sucker 2 is also distributed over
*the roots and shoot. This is done by 2 functions: FrtGR and FrtRED3
*Function FrtGR is either increasing or constant between 0 < TSUM3 < 360 Cd (STGRLV)
*Function FrtRED3 decreases from where function FrtGR ends (so at STGRLV), down to zero at
*TSUMflower (2663 C d). For plant 3 function FrtRED3 is read up to TSUM3 = 996 C d, so up to the
*shift. Function FrtGR is only used by plant 3, because of the initialization of this plant 3 as
*zero.

FrtGR           = ( SWemerg3 * (1.0-SWstdm3) ) * ...
                  prt1(TIME,STTIME,prt_wish,psh_wish,Frtmax,STGRLV,TSUM3I,TSUM3)
FrtRED3         =   SWstdm3 * ...
                  prt2(prt_wish,psh_wish,TSUM3I,STGRLV,TSUM3,TSUMflower)

**Death of roots

*Based on experimentation by Moreau et al.1963. Among 110 roots produced during the first 3
*months on a parent banana plant (Gros Michel), 102 roots had dissappeared / died at 7 months,
*therefore maximum lifespan is about 4 months
*Moreau, B., Le Bourdelles, J., 1963. Etude du système racinaire du bananier 'Gros Michel' en
*Equateur. Fruits 18, 71-74.
*After about 4 months (120 days), 7.3% of the original root dry matter will be left
*RDRrt = 1n(0.073)/(-120) =  0.0218 d-1
*RDRrt2 = 0.0218 d-1  (plant 2)
*RDRrt3 = 0.0218 d-1  (plant 3)  - start after 360 C d

*The roots present at flowering remain alive during the reproductive phase, with a moderate
*decrease of about 8% (Blomme, 2000).
*Blomme, G., 2000. The interdependence of root and shoot development in banana (Musa spp) under
*field conditions and the influence of different biophysical factors on this relationship. PhD
*thesis. Katholieke Universiteit Leuven, Leuven, Belgium.
*Duration from flowering to harvest at Ntungamo (150 days)
*RDRrt1 = 1n(0.92)/(-150)  = 0.000556

DWrt1 = RDRrt1 * Wrt1
DWrt2 = RDRrt2 * Wrt2
DWrt3 = RDRrt3 * Wrt3

*Total weight of dead roots for plant 1 (kg DM ha-1)
WrtD1_Tot       = INTGRL(Wrt1DI, dWrt1_plant1)
dWrt1_plant1    = DWrt1

*Total weight of dead roots for plant 2 (kg DM ha-1)
WrtD2_Tot       = INTGRL(Wrt2DI, dWrt2_plant2)
dWrt2_plant2    = DWrt2

*To calculate the total weight of dead roots for plant 3 (kg DM ha-1)
WrtD3_Tot       = INTGRL(Wrt3DI, dWrt3_plant3)
dWrt3_plant3    = DWrt3

TotWrtD         = WrtD1_Tot + WrtD2_Tot + WrtD3_Tot
*Total weight of roots dead for plant 1, 2 and 3 (kg DM ha-1)

RDRrt1 = AFGEN (RDRrt1TB, TSUM1)

FUNCTION RDRrt1TB =  2262.,0.0218, 2663.,0.0218, 2700.,5.56E-4, 3600.,5.56E-4
*Function to cater for reduced root senescence after flowering

Wrt1_After_Harv  = INTGRL(Wrt1_After_HarvI , dWrt1_After_Harv)
*Weight of roots after harvest of plant 1 (kg ha-1)
*The amount in this state "Wrt1_After_Harv" is in fact SOM that decays
*There is a positive flow of material from the Corm1 that is going to the SOM as well, but that
*can perhaps not be added here directly, because of other decay rates
```

```
dWrt1_After_Harv = - RDRrt1_After_Harv * Wrt1_After_Harv
*in HARVEST-event: Wrt1_After_Harv = Wrt1_After_Harv + Wrt1
*Death rate of roots after harvest of plant 1 (kg ha-1 d-1)

***Crop above ground dry matter produced is divided over corm, pseudostem,green leaves and bunch
***The bunch appears on plant 1, so Pbunch2 and Pbunch3 are not meaningful; they are therefore
***named DummyPbunch2 and DummyPbunch3.
***They are calculated to maintain the same calculational structure, but they not used
***Explanation about the dead leaves:
***Weights of dead leaves of the individual plants (WleafDi) increase with the dying of green
***leaves and decrease by pruning (time-event) and harvesting (state-event)

Wcorm1          = INTGRL (Wcorm1I , GWcorm1 )
*Dry matter of corms of plant 1 (kg DM ha-1)
Wpsstm1         = INTGRL (Wpsstm1I, GWpsstm1)
*Dry matter of pseudostem of plant 1 (kg DM ha-1)
Wleaf1          = INTGRL (Wleaf1I , NWleaf1 )
*Dry matter of leaves of plant 1 (kg DM ha-1)
WleafD1         = INTGRL (WleafD1I, DWleaf1 )
*Weight of dry leaves for plant 1 (kg DM ha-1)
Wbunch1         = INTGRL (Wbunch1I, GWbunch1)
*Dry matter of the bunch of plant 1 (kg DM ha-1)

*Further Corm1 dynamics. After harvest "Corm1" decays and partially feeds Wsh1.
*The remainder is going to a state "Corm1_Lost_After_Harv", which is an accumulator only
*(for balances for example, also similar to Wcorm1H)
*The "Corm1_Lost_After_Harv" is in fact soil organic matter

Corm1_After_Harv          = INTGRL( Corm1_After_HarvI , dCorm1_After_Harv )
dCorm1_After_Harv         = - RDRCorm1_After_Harv * Corm1_After_Harv

Corm1_Lost_After_Harv       = INTGRL( Corm1_Lost_After_HarvI , dCorm1_Lost_After_Harv)
dCorm1_Lost_After_Harv      = (1.0 - pcorm1_to_Wsh1) * dCorm1_After_Harv

WshPlnt1Tot     = Wcorm1 + Wpsstm1 + Wleaf1 + WleafD1 +Wbunch1
*Total dry matter of the above ground plant 1 (kg DM ha-1)
LWR1            = Wleaf1/DM1
*LeafWeightRatio as calculated from the program

***Harvests
HarvestWpsstm   = INTGRL(HarvestWpsstm_I, RHarvestWpsstm)
*HarvestWpsstm - "harvested" pseudostems
RHarvestWpsstm  = 0.0

HarvestWLeaf    = INTGRL(HarvestWLeaf_I, RHarvestWLeaf)
*New comment: HarvestWLeaf - "harvested" green leaves in terms of weight.
*These are done only at harvest (and only for the plant 1), not by the prunings, because then
*only dead leaves are taken away (but then for plant 1, 2 and 3) since the accumulation is
*shockwise, the day-to-day continuous inflowrate is taken zero

RHarvestWLeaf   = 0.0

HarvestWLeafD   = INTGRL(HarvestWLeafD_I, RHarvestWLeafD)
*HarvestWLeafD - "harvested" dead leaves in terms of weight. These are done by prunings, so not
*by a daily rate, and by the harvests.
RHarvestWLeafD  = 0.0
*The "RHarvestWLeafD" could represent the decomposition rate of the dead leaves that have just
*been harvested. It obviously NOT only concerns the dead leaves of the harvested plant 1, but
*also the decomposition of the pruned leaves of all three plants (1, 2 and 3)

*DMmulch constitutes leaves and pseudostems. So, THAT state variable will decompose and will
*affect the rain interception and runoff when the model is combined with the water balance
*This "HarvestWLeafD" state variable therefore only accumulates dead leaf weight

HarvestWbunch   = INTGRL(HarvestWbunch_I, RHarvestWbunch)
*HarvestWbunch - harvested bunches.
RHarvestWbunch  = 0.0
*The "RHarvestWbunch" will always be 0.0, because there is no decomposition of the economic yield
*in the model, and the bunches will via the harvest come into the state variable
*In fact, implicitly i assume that there are no harvest losses of the bunches.
```

```
Wcorm2          = INTGRL (Wcorm2I , GWcorm2 )
*Dry matter of corms of plant 2 (kg DM ha-1)
Wpsstm2         = INTGRL (Wpsstm2I, GWpsstm2)
*Dry matter of pseudostem of plant 2 (kg DM ha-1)
Wleaf2          = INTGRL (Wleaf2I , NWleaf2 )
*Dry matter of leaves of plant 2 (kg DM ha-1)
WleafD2         = INTGRL (WleafD2I, DWleaf2 )
*Weight of dry leaves for plant 2 (kg DM ha-1)
WshPlnt2Tot     = Wcorm2 + Wpsstm2 + Wleaf2 + WleafD2
*Total dry matter of the above ground plant 2 (kg DM ha-1)
LWR2            = Wleaf2/DM2
*LeafWeightRatio as calculated from the program

Wcorm3          = INTGRL (Wcorm3I , GWcorm3 )
*Dry matter of corms of plant 3 (kg DM ha-1)
Wpsstm3         = INTGRL (Wpsstm3I, GWpsstm3)
*Dry matter of pseudostem of plant 3 (kg DM ha-1)
Wleaf3          = INTGRL (Wleaf3I , NWleaf3 )
*Dry matter of leaves of plant 3 (kg DM ha-1)
WleafD3         = INTGRL (WleafD3I, DWleaf3 )
*Weight of dry leaves for plant 3 (kg DM ha-1)
WshPlnt3Tot     = Wcorm3 + Wpsstm3 + Wleaf3 + WleafD3
*Total dry matter of the above ground sucker 2 (kg DM ha-1)

LWR3            = Wleaf3/NOTNUL(DM3)
*LeafWeightRatio as calculated from the program

*** The sum of the three plants should equal WshTot, and is used in the
*** Balance
WshTotPlants    = WshPlnt1Tot + WshPlnt2Tot + WshPlnt3Tot

*To calculate the approximate number of green leaves per plant to have an idea whether the number
*is reasonable.

Leafnum_plant1  = (LAI1/MLAH1) / ((100./Plant_distance)**2)
*Number of green leaves for plant 1
Leafnum_plant2  = (LAI2/MLAH2) / ((100./Plant_distance)**2)
*Number of green leaves for plant 2

MLAH1 = AFGEN (MLAHTB, TSUM1)
MLAH2 = AFGEN (MLAHTB, TSUM2)

FUNCTION MLAHTB =  0.,0.        , 360.,0.      , 960.,0.4864E-4, 1500.,0.7652E-4, ...
                   2262.,1.14E-4, 2663.,1.45E-4, 3600.,1.42E-4
*Middle leaf area (MLA) was calculated as a function of the temperature sum

***Total weight of dead leaves of all plants is dynamically calculated (by integrating rate
***DWleafi) and, moreover, this state variable is harvested regularly by pruning (below)
***The states WleafDi and TotWleafD at pruning is then set back to zero, while the harvest state
***for dead leaves, HarvestWleafD, is incremented by the WleafDi with i = 1,2,3
TotWleafD       = INTGRL (TotWleafD_I, DWleafTot)
*Total weight of dry leaves of plant 1, 2 and 3 (kg DM ha-1)
DWleafTot       = DWleaf1 + DWleaf2 + DWleaf3

***Net rates of change of the weights of leaves
NWleaf1         = GWleaf1 - DWleaf1
NWleaf2         = GWleaf2 - DWleaf2
NWleaf3         = GWleaf3 - DWleaf3

***Growth rates of the different plants 1, 2 and 3.
***Plant 1
GWcorm1         = Pcorm1  * GWsh1
GWpsstm1        = Ppsstm1 * GWsh1
GWleaf1         = Pleaf1  * GWsh1
GWbunch1        = Pbunch1 * GWsh1
CALL INTERPOL('PCOTB','PSTTB','PLVTB','PBUTB',...
               PCOTB ,PSTTB  ,PLVTB  ,PBUTB  ,...
               K,TSUM1,  Pcorm1,Ppsstm1,Pleaf1,Pbunch1)

***Plant 2
GWcorm2         = Pcorm2  * GWsh2
```

```
GWpsstm2        = Ppsstm2 * GWsh2
GWleaf2         = Pleaf2  * GWsh2
CALL INTERPOL('PCOTB','PSTTB','PLVTB','PBUTB',...
               PCOTB ,PSTTB  ,PLVTB  ,PBUTB  ,...
               K,TSUM2,  Pcorm2,Ppsstm2,Pleaf2,DummyPbunch2)

***Plant 3
GWcorm3         = Pcorm3  * GWsh3
GWpsstm3        = Ppsstm3 * GWsh3
GWleaf3         = Pleaf3  * GWsh3
CALL INTERPOL('PCOTB','PSTTB','PLVTB','PBUTB',...
               PCOTB ,PSTTB  ,PLVTB  ,PBUTB  ,...
               K,TSUM3,  Pcorm3,Ppsstm3,Pleaf3,DummyPbunch3)

***The summations of the fractions can be taken out as soon as the check on the sum of
***fractions of the partitioning functions has been implemented in the INITIAL

Psum1           = Pcorm1 + Ppsstm1 + Pleaf1 + Pbunch1
Psum2           = Pcorm2 + Ppsstm2 + Pleaf2 + DummyPbunch2
Psum3           = Pcorm3 + Ppsstm3 + Pleaf3 + DummyPbunch3

***Death rates of the leaves of the different plants 1, 2 and 3
DWleaf1         = Wleaf1 * RDR1
*Death of leaves of the plant 1 (kg DM ha-1 d-1)
DWleaf2         = Wleaf2 * RDR2
*Death of leaves of the plant 2 (kg DM ha-1 d-1)
DWleaf3         = Wleaf3 * RDR3
*Death of leaves of the plant 3 (kg DM ha-1 d-1)

EVENT
***Pruning TIME event

*The first pruning should take place at 30 days after the onset of the simulation.
*Since it is an established plantation, DMmulch must have a certain value

***To take care of the pruning of dead leaves
***The dead leaves of plant 1, 2 and 3 (WleafDi, and TotWleafD) are pruned at
***"Days_between_prunings", usually taken as 30 day intervals and is applied as mulch
***Technical remark: because StTime is at least the first day of the year, so StTime=1, the first
***pruning is put to StTime-1. + Days_between_prunings, so that we arrive at prunings at 30, 60,
***90, etc. days, instead of 31, 61, 91, etc.
   FIRSTTIME StTime-1. + Days_between_prunings
***Days_between_prunings affects the pruning of leaves and is a management parameter here set at
***30 days.

   NEXTTIME Time + Days_between_prunings

*In principle dead leaf area for the three separate plants is pruned. However, we did not include
*a state variable for dead leaf area.
*The reason that there are no state variables for the dead leaf area's, is that it is assumed
*that the dead leaves hang along the stem and thus do not take away light.

*Dead leaf weight for the three separate plants is pruned. So, WleafDi must be reset to 0.0, and
*TotWleafD ( = SUM(WleafDi) ) is added to the mulch at prunings.
*Technical remark 1: the "i"'s in the variables HELPWleafD1i are introduced to distinguish these
*variables from the ones in the Harvest section, so just to make them unique

   HELPWleafD1i            = WleafD1
   HELPWleafD2i            = WleafD2
   HELPWleafD3i            = WleafD3
   HELPTotWleafDi          = TotWleafD
   HELPDMmulchi            = DMmulch

   HELPHarvestDM1_Prui     =  HarvestDM1_Pru
   HELPHarvestDM2_Prui     =  HarvestDM2_Pru
   HELPHarvestDM3_Prui     =  HarvestDM3_Pru

   NEWVALUE WleafD1        = 0.0
   NEWVALUE WleafD2        = 0.0
   NEWVALUE WleafD3        = 0.0
   NEWVALUE TotWleafD      = 0.0
```

```
   NEWVALUE DMmulch        = HELPDMmulchi   + HELPTotWleafDi

   NEWVALUE HarvestDM1_Pru =  HELPHarvestDM1_Prui   +   HELPWleafD1i
   NEWVALUE HarvestDM2_Pru =  HELPHarvestDM2_Prui   +   HELPWleafD2i
   NEWVALUE HarvestDM3_Pru =  HELPHarvestDM3_Prui   +   HELPWleafD3i

*The Dry Matter of the plants is affected by the pruned dead leaf weight for the three separate
*plants. So, WleafDi must be subtracted from the DM states as well
   HELPDM1i                = DM1
   HELPDM2i                = DM2
   HELPDM3i                = DM3
   NEWVALUE DM1            = HELPDM1i       - HELPWleafD1i
   NEWVALUE DM2            = HELPDM2i       - HELPWleafD2i
   NEWVALUE DM3            = HELPDM3i       - HELPWleafD3i

*The Shoot Dry Matter of the plants is also affected by the pruned dead leaf weight for the three
*separate plants. So, WleafDi must be subtracted from the Wsh states as well

   HELPWsh1i               = Wsh1
   HELPWsh2i               = Wsh2
   HELPWsh3i               = Wsh3
   NEWVALUE Wsh1           = HELPWsh1i      - HELPWleafD1i
   NEWVALUE Wsh2           = HELPWsh2i      - HELPWleafD2i
   NEWVALUE Wsh3           = HELPWsh3i      - HELPWleafD3i

   HELPHarvestDMi          = HarvestDM
   NEWVALUE HarvestDM      = HELPHarvestDMi + HELPWleafD1i + HELPWleafD2i + ...
                                              HELPWleafD3i
*Here in HarvestDM the dead leaves from the prunings are collected; in the harvest part all
*harvested parts are collected (pseudostem, green leaves, dead leaves and bunch of plant 1

   HELPHarvestWLeafDi      = HarvestWLeafD
   NEWVALUE HarvestWLeafD  = HELPHarvestWLeafDi + HELPWleafD1i + ...
                                                  HELPWleafD2i + HELPWleafD3i
*In HarvestWLeafD the dead leaves from the prunings are collected for the 3 plants, and at
*harvest the dead leaves from plant 1

***END Pruning TIME event
ENDEVENT

*****************************************************************************************************

***If a certain temperature sum has been reached for plant 1, the harvest of bunches takes place,
***plant 2 becomes the plant 1 and plant 3 becomes the new plant 2
***Furthermore, harvested leaves, in terms of weight, and the dry matter of the stems are
***accumulated in a state variable to be used as mulch
***Technically, the parameters TSUMi, LAIi and DMi, with i 1 to 3, have to be reinitialized
***again. TSUM(i) = TSUM(i+1); LAI(i) = LAI(i+1); DM1(i) = DM1(i+1) and i=1 is harvested and i=3
***is reset to its initial values, namely 0.
***Finally the SWitches (SWemerg3 and SWstdm3) should be reset to 0.0.

***TSUMHARV is the temperature sum at harvest
EVENT
   ZEROCONDITION TSUM1 - TSUMHARV
   PARAMETER TSUMHARV      = 3600.0

***Balance section

   HELPBalDmHlp3           = BalDmHlp3
   NEWVALUE BalDmHlp3      = HELPBalDmHlp3       - (HELPDM1 - (HELPWrt1+HELPWcorm1))

***Development section  (Temperature sum)
   HELPTSUM2               = TSUM2
   HELPTSUM3               = TSUM3
   NEWVALUE TSUM1          = HELPTSUM2
   NEWVALUE TSUM2          = HELPTSUM3
   NEWVALUE TSUM3          = 0.0
   NEWVALUE SWemerg3       = 0.0

***State variables section (Leaf area index, dry matter, roots and shoot, shoot parts, corms,
***pseudostems, leaves, bunches, ...)
```

```
*Leaf area for the three separate plants
   HELPLAI1                = LAI1
   HELPLAI2                = LAI2
   HELPLAI3                = LAI3
   NEWVALUE LAI1           = HELPLAI2
   NEWVALUE LAI2           = HELPLAI3
   NEWVALUE LAI3           = LAI3I

*Total dry matter for the three separate plants: the corm and the roots of the plants are not
*harvested, but stay in the soil. Therefore, the new value of DM1 is not only taking over the DM
*of plant 2 but keeps its own roots and corm

   HELPDM1                 = DM1
   HELPDM2                 = DM2
   HELPDM3                 = DM3
***DM adapted because Wrt1 and Wcom1 are apart

   NEWVALUE DM1            = HELPDM2
   NEWVALUE DM2            = HELPDM3
   NEWVALUE DM3            = DM3I

*Total dry matter for the three separate plants is split into roots and shoot
*Root
   HELPWrt1                = Wrt1
   HELPWrt2                = Wrt2
   HELPWrt3                = Wrt3
   HELPWrt1_After_Harv     = Wrt1_After_Harv

*At harvest the plants, including their roots are shifted.
*The roots of plant 1 will decay after the harvest So, NEWVALUE Wrt1 = HELPWrt2, and
*HELPWrt1 goes to a new state, called: "Wrt1_after_Harvest",

   NEWVALUE Wrt1           = HELPWrt2
   NEWVALUE Wrt2           = HELPWrt3
   NEWVALUE Wrt3           = Wrt3I
   NEWVALUE Wrt1_After_Harv= HELPWrt1_After_Harv + HELPWrt1

*  Shoot
   HELPWsh1                = Wsh1
   HELPWsh2                = Wsh2
   HELPWsh3                = Wsh3

   NEWVALUE Wsh1           = HELPWsh2
   NEWVALUE Wsh2           = HELPWsh3
   NEWVALUE Wsh3           = Wsh3I

*Total SHOOT dry matter for the three separate plants is split into corms, pseudostems, green
*leaves and bunches. There is also dead leaves, but these come from the green leaves that died.
*The bunch, of course, only applies to the plant 1.
*First all HELP variables are defined

   HELPWcorm1              = Wcorm1
   HELPWcorm2              = Wcorm2
   HELPWcorm3              = Wcorm3
   HELPWcorm1H             = Wcorm1
   HELPCorm1_After_Harv    = Corm1_After_Harv
   HELPCorm1_to_Wsh1       = Corm1_to_Wsh1

   HELPWpsstm1             = Wpsstm1
   HELPWpsstm2             = Wpsstm2
   HELPWpsstm3             = Wpsstm3

   HELPWleaf1              = Wleaf1
   HELPWleaf2              = Wleaf2
   HELPWleaf3              = Wleaf3

   HELPWleafD1             = WleafD1
   HELPWleafD2             = WleafD2
   HELPWleafD3             = WleafD3
   HELPTotWleafD           = TotWleafD
```

```
   HELPWbunch1             = Wbunch1

   HELPWrtD1_Tot           = WrtD1_Tot
   HELPWrtD2_Tot           = WrtD2_Tot
   HELPWrtD3_Tot           = WrtD3_Tot


   NEWVALUE Corm1_to_Wsh1 =  0.0
   NEWVALUE WrtD1_Tot      = HELPWrtD2_Tot
   NEWVALUE WrtD2_Tot      = HELPWrtD3_Tot
   NEWVALUE WrtD3_Tot      = 0.0

*Then all resettings are arranged. Corm is not harvested.
   NEWVALUE Wcorm1         = HELPWcorm2

**Corm1_After_Harv = Corm1_After_Harv + Wcorm1, via the HELP construction

   NEWVALUE Corm1_After_Harv = HELPCorm1_After_Harv + HELPWcorm1

   NEWVALUE Wcorm2         = HELPWcorm3
   NEWVALUE Wcorm3         = Wcorm3I

   NEWVALUE Wpsstm1        = HELPWpsstm2
   NEWVALUE Wpsstm2        = HELPWpsstm3
   NEWVALUE Wpsstm3        = Wpsstm3I

   NEWVALUE Wleaf1         = HELPWleaf2
   NEWVALUE Wleaf2         = HELPWleaf3
   NEWVALUE Wleaf3         = Wleaf3I

   NEWVALUE WleafD1        = HELPWleafD2
   NEWVALUE WleafD2        = HELPWleafD3
   NEWVALUE WleafD3        = WleafD3I
   NEWVALUE Wcorm1H        = HELPWcorm1H

   NEWVALUE TotWleafD      = HELPWleafD2 + HELPWleafD3 + WleafD3I

   NEWVALUE Wbunch1        = Wbunch1I

*Calculating the Harvest Index at the moment of harvesting
   HI1                     = HELPWbunch1/HELPWsh1
***The harvest index as calculated from only the motherplant
   HIoverall               = HELPWbunch1/WshTot
***The harvest index as calculated from the whole of the mat, so plant 1 + plant 2 + plant 3.

*Harvesting section (for later use as mulch). Also DM1 and Wsh1 will be involved
*The part of DM1 that is no doubt involved is the shoot part (Wsh1). This amount will have to be
*corrected for the the bunch weight

   HELPHarvestDM           = HarvestDM
   HELPDMmulch             = DMmulch

   HELPHarvestWpsstm       = HarvestWpsstm
   HELPHarvestWLeaf        = HarvestWLeaf
   HELPHarvestWLeafD       = HarvestWLeafD
   HELPHarvestWbunch       = HarvestWbunch

   NEWVALUE HarvestDM      = HELPHarvestDM       + (HELPWpsstm1 + HELPWleaf1 + ...
                                                    HELPWleafD1 + HELPWbunch1)

*Prunings shifted to allow proper balancing of individual plant shoots

   HELPHarvestDM1_Pru      =  HarvestDM1_Pru
   HELPHarvestDM2_Pru      =  HarvestDM2_Pru
   HELPHarvestDM3_Pru      =  HarvestDM3_Pru

   NEWVALUE HarvestDM1_Pru =  HELPHarvestDM2_Pru
   NEWVALUE HarvestDM2_Pru =  HELPHarvestDM3_Pru
   NEWVALUE HarvestDM3_Pru =  HarvestDM_pru3I

*In HarvestDM all harvested parts are contained, so pseudostem, green leaves, dead leaves
```

```
*and bunch of plant 1 and the dead leaves from the prunings

   NEWVALUE HarvestWLeaf   = HELPHarvestWLeaf    + HELPWleaf1

*Also HELPWleafD2 and HELPWleafD3 must be added to the HarvestWLeaf, but that should be done
*during the dynamic part of the simulation

   NEWVALUE HarvestWpsstm  = HELPHarvestWpsstm   + HELPWpsstm1
   NEWVALUE HarvestWbunch  = HELPHarvestWbunch   + HELPWbunch1

*Having available these three separate harvested components (psstm, green leaves,dead leaves)
*enables us to introduce their own decomposition rates (if desired), but one rate is used in this
*model

   NEWVALUE HarvestWLeafD  = HELPHarvestWLeafD   + HELPWleafD1


   NEWVALUE DMmulch        = HELPDMmulch         + ...
                             (HELPWpsstm1 + HELPWleaf1 + HELPWleafD1)
*In DMmulch all harvested parts of plant 1 accumulate, so the (chopped) pseudostem1, green
*leaves1 and dead leaves1
*Note that at harvest to the DMmulch is added the Wpsstm1, Wleaf1 and WleafD1, but not the
*WleafD2 and WleafD3. These are only added (together with WleafD1) at the prunings

*The Mulch Area Index (MAI) can be calculated for instance according to the paper of Scopel et *al.
2004 and used in retarding the evaporation of water from the soil.
*Also a certain amount of water will be intercepted by this mulch, thus not reaching the soil
*surface
*Scopel, E., Macena, F., Corbeels, M., Affholder, F., Maraux, F., 2004. Modelling crop residue
*mulching effects on water use and production of maize under semi-arid and humid tropical
*conditions. Agronomie 24, 1-13.

*Resetting the switches
   NEWVALUE SWstdm3        = 0.0
   NEWVALUE SWFSU2         = 1.0
   NEWVALUE SWFrt1         = 1.0

ENDEVENT

END
STOP

* ---------------------------------------------------------------------------------------------*
*  SUBROUTINE GLA                                                                              *
*  Purpose: This subroutine computes daily increase of leaf area index                         *
*           ( ha leaf ha-1 ground d-1 )                                                        *
* ---------------------------------------------------------------------------------------------*

      SUBROUTINE GLA(SLA,Pleaf,GWsh,SWstdm3,TSUM,TSUM3stop_exp,LAI,
     $               LAIstop_exp,RGRL,DTEFF,                GLAI)
      IMPLICIT REAL (A-Z)
      INTEGER  ISWstdm3
      SAVE

*---- Growth during pre-juvenile stage and during maturation stage is given by:
*---- GLAI=SLA*Pleaf*GWsh.
*---- Note that (only)GDM3 can be calculated by two different processes (DM coming from plant
*---- 1(pre-juvenile stage) or due to its own photosynthesis)
*---- The photosynthesis part (in fact only DM production) is taken care of in this subroutine, *-
--- the support from plant 2 is described in the main program.
*---- Below, GLAI is always first calculated from shoot dry matter, and if juvenile conditions
*---- are present this value is over written by the GLAI calculated in the IF condition.

      GLAI     = SLA * Pleaf * GWsh

      ISWstdm3 = NINT(SWstdm3)
*---- ISWstdm3 is introduced to prevent numerical problems in the .EQ.
*---- comparison in the below IF-statement.
*---- Growth during the juvenile stage (at the moment, the value of which is
*---- TSUM3stop_exp = 960.).
*---- Juvenile growth is exponential: dLAI/dt=Rgr x LAI, with Rgr=RGRL x DTEFF.
```

```
*---- Technical remark: the differential equation form is chosen instead of the analytical rate *-
--- equation, because DELT occurs in the analytical formulation.
*---- This might give problems at the TSUM-events where the time step necessarily is adapted. If
*---- this adaptation would not be correctly implemented in the analytical rate equation, this
*---- would give erroneous results.
*---- The time coefficient, 1/Rgr = 1/(RGRL * DTEFF), also allows to use the differential form: *-
--- it is around 1/(0.0077 Cd x 20 C)= 6.5 days, so the time step should be less or equal than *--
-- 6.5/10=0.65 days: it is, however, 1 day, so a little worse that the rule of thumb, but
*---- still acceptable.
*---- A closer investigation, however, yielded that this time step, in combination with Euler,
*---- did not give converging results and it was decided to use the Runge-Kutta method to
*---- integrate the rates, with a time step of 0.25.

      IF ( (ISWstdm3 .EQ. 1) .AND. (TSUM .LT. TSUM3stop_exp) .AND.
     $     (LAI      .LT. LAIstop_exp) )
     $   GLAI  = (RGRL * DTEFF) * LAI

      RETURN
      END

*******************************************************************************************

      FUNCTION Fsu2(FSU2max,TSUMfloinit,TSUMendfulldepe,TSUM)
      IMPLICIT REAL (A-Z)
      SAVE

*---- This function represents a straight line defining the linear decrease of the support of
*---- sucker 2 by sucker 1 during the physiological time period of sucker 1 from TSUM2 = 1662
*---- (corresponds with TSUM3=360 C d) to
*---- TSUM2 = 2298, where harvesting and shifting takes place.
*---- After that physiological moment of 2298 C d, plant 2 is plant 1 and plant 3 has become
*---- plant 2, and the support of (now) plant 2 continues up to flower initiation of (now) the
*---- new plant 1 at 2423 C d.

      Fsu2     = -FSU2max/(TSUMfloinit-TSUMendfulldepe) * (TSUM - TSUMfloinit)

      Return
      END FUNCTION Fsu2

*******************************************************************************************

      FUNCTION prt1(TIME,STTIME,prt_wish,psh_wish,Frtmax,STGRLV,TSUM3I,TSUM3)
      IMPLICIT REAL (A-Z)
      COMMON /SLOPE/ Afixed
      SAVE

      prt_cal  = prt_wish / (psh_wish + prt_wish)
*---- prt_cal is the average amount of the newly grown dry matter that goes to the roots. It is *-
--- calculated from the rt:sh ratio that is given in the main program from prt_wish and
*---- psh_wish. Since the total crop is the sum of the root and shoot, prt_cal is calculated as *-
--- shown.

      IF ( Frtmax .GT. (1.81*prt_cal) ) CALL FATALERR
     &   ('prt1','Frtmax > prt_cal')
*---- The below function, prt1 = A * TSUM3 + B, is a straight line that is calculated "around"
*---- the average value prt_cal. This average value is the root:shoot ratio that is wished to be
*---- reached at the end of the 360 C d period and coincides with measured data. It was found,
*---- however, that during the 0-360 C d period the root:shoot ratio of plant 3 plant increases.
*---- So, if a known average need to be reached at the end of the 360 C d period, the function
*---- should start with a lower value and should end with a higher value than the average.
*---- Therefore, the reference values of the function were taken in the middle of the trajectory
*---- 0-360 C d, so at 180 C d, because in the middle the coordinates (x,y) are known, and at the
*---- end of the period of 360 C d, where the value is called Frtmax.
*---- Obviously, Frtmax should not be larger than 2*prt_cal, because in that case the the start *-
--- of the function would be lower than 0.0. Therefore, the
*---- FATALERR was introduced in this routine and works under the condition:
*---- Frtmax > 2.0*prt_cal. It may be clear that Frtmax may be:
*---- prt_cal <= Frtmax <= (2 * prt_cal).
*---- The value of 2.0* appears to give (very small) negative values (10^-9), due to rounding of.
*---- Therefore, the more practical value of 1.81 is taken, instead of 2.0, as maximum that is
*---- allowed to be reached by prt_cal. The 0.01 in 1.81 was apparently needed for rounding
```

```
*---- purposes, because a Factor of 1.8 gave problems.

      IF ( NINT(TIME) .EQ. NINT(STTIME) ) THEN
         Afixed  = (Frtmax-prt_cal) / (STGRLV-(STGRLV-TSUM3I)/2.0)
      ENDIF
*---- Afixed defines slope A of the line prt1 = A * TSUM3 + B. It is called Afixed because it
*---- should be possible to shift the line parallel to its starting position up and down (but not
*---- beyond its starting position) as a function of water stress. The dynamics of the parallel *-
--- shift is effected via intercept B, that is a linear function of prt_cal:

      B        = prt_cal - (Afixed * (STGRLV-TSUM3I)/2.0)

      prt1     = Afixed * TSUM3 + B

      Return
      END FUNCTION prt1

*******************************************************************************************

      FUNCTION prt2 (prt_wish,psh_wish,TSUM3I,STGRLV,TSUM,TSUMflower)
      IMPLICIT REAL (A-Z)
      COMMON /SLOPE/ Afixed
      SAVE

      prt_cal  = prt_wish / (psh_wish + prt_wish)

      B        = prt_cal - (Afixed * (STGRLV-TSUM3I)/2.0)
*---- The function prt2 should start at the same value as function prt1 ends.
*---- Function prt1 ends at the intercept value B of prt1 plus the slope of prt1 (Afixed) times *-
--- the distance between the start of function prt2 (is the same as the end of function prt1) *---
- and the beginning of prt1, so (STGRLV-TSUM3I).
*---- In prt1 the slope was fixed by calculating Afixed once at time = 0. In function prt2, the *-
--- end point must be fixed (at TSUMflower partitioning to roots is zero), and the slope must *---
- be dynamically adapted by making Frtmax at the end of prt1 equal to { B + Afixed*(STGRLV-
*---- TSUM3I) }, where B is dynamic through prt_cal. The labelled COMMON/SLOPE/ transfers
*---- variable Afixed from function prt1 to prt2.

      prt2     = -1.0*(B + Afixed*(STGRLV-TSUM3I))/(TSUMflower-STGRLV)*
     $                                          (TSUM-TSUMflower)

      Return
      END FUNCTION prt2

*******************************************************************************************

      SUBROUTINE INTERPOL(Name1,Name2,Name3,Name4,
     $                    TABLE1,TABLE2,TABLE3,TABLE4,
     $                    N,TIME,          Y1,Y2,Y3,Y4)
      IMPLICIT NONE
      CHARACTER(LEN=*)    :: Name1,Name2,Name3,Name4
      INTEGER             :: N
      REAL, DIMENSION(N)  :: TABLE1,TABLE2,TABLE3,TABLE4
      REAL                :: TIME, Y1, Y2, Y3, Y4

*     local
      REAL :: LINT2

      Y1 = LINT2 (Name1,TABLE1,N, TIME)
      Y2 = LINT2 (Name2,TABLE2,N, TIME)
      Y3 = LINT2 (Name3,TABLE3,N, TIME)
      Y4 = LINT2 (Name4,TABLE4,N, TIME)

      RETURN
      END

*******************************************************************************************
ENDJOB
```

Appendix 2

List of abbreviations used in LINTUL BANANA 1 model

Abbreviation	Explanation	Unit
Initial		
TSUM*i*I	Initial temperature sum of plant, *i* = 1−3	°C d
LAI*i*I	Initial leaf area index of plant, *i* = 1−3	ha leaf ha^{-1} soil
DM*i*I	Initial dry matter of plant, *i* = 1−3	kg DM ha^{-1}
Wrt*i*I	Initial dry matter of roots of plant, *i* = 1−3	kg DM ha^{-1}
Wsh*i*I	Initial dry matter of shoot of plant, *i* = 1−3. Sucker emerges later (at TSUM2=1302 °C d).	kg DM ha^{-1}
Wcorm*i*I	Initial dry matter of the corm of plant, *i* = 1−3	kg DM ha^{-1}
Wpsstm*i*I	Initial dry matter of the pseudostem of plant, *i* = 1−3	kg DM ha^{-1}
Wleaf*i*I	Initial dry matter of the leaves of plant, *i* = 1−3	kg DM ha^{-1}
Wbunch1I	Initial dry matter of the bunch of plant 1, only plant 1 produces a bunch	kg DM ha^{-1}
WleafD*i*I	Initial dry weight of the dead leaves of plant, *i* = 1−3	kg DM ha^{-1}
Wrt*i*DI	Initial dry weight of the dead roots of plant, *i* = 1−3	kg DM ha^{-1}
TotWleafD_I	Initial total dry weight of dead leaves of plant 1, 2 and 3	kg DM ha^{-1}
Pcorm*i*I	Initial proportion of dry matter in corm for plant, *i* = 1−3	-
Ppsstm*i*I	Initial proportion of dry matter in pseudostem for plant *i* = 1−3	-
Pleaf*i*I	Initial proportion of dry matter in leaves for plant *i* = 1−3	-
Pbunch1I	Initial proportion of dry matter in bunch for plant 1	-
DummyPbunch*i*I	Initial proportion of dry matter in bunch 'dummy' for plant, *i* = 2−3.	-
HarvestWpsstm_I	Initial value of the integral keeping track of harvested pseudostem dry matter	kg DM ha^{-1}
HarvestWleaf_I	Initial value of the integral keeping track of harvested leaves dry matter	kg DM ha^{-1}
HarvestWbunch_I	Initial value of the integral keeping track of harvested bunch dry matter	kg DM ha^{-1}
FrtRED*i*I	Initial fraction of reducing dry matter to the roots of plant, *i* = 1−3.	-
DMmulch_I	Initial amount of mulch on the soil	kg DM ha^{-1}
HarvestDM_I	Initial value of the integral of pruned leaves and non-economic biomass at harvest	kg DM ha^{-1}

Appendix 2 continued

Abbreviation	Explanation	Unit
HarvestDM_Pru*i*I	Initial value of integral keeping track of pruned leaf dry matter of plant, i = 1−2	kg DM ha^{-1}
Corm1_After_HarvI	Initial weight of the corm of plant 1 at harvest	kg DM ha^{-1}
Corm1_Lost_After_HarvI	Initial weight of the corm of plant 1 re-distributed to new plant 1	kg DM ha^{-1}
Corm1_to_Wsh1I	Initial value of the dry matter of the corm of plant 1 after harvest re-distributed to the new plant 1	kg DM ha^{-1}
Wrt1_After_HarvI	Initial value of the roots of plant 1 after harvest	kg DM ha^{-1}
Dry matter partitioning and subroutines		
Prt_wish_0	Dry matter partitioning to the root used to initialize Prt_cal if there is no water stress	-
Prt_wish	Desired dry matter partitioning to the root	-
Psh_wish	Desired dry matter partitioning to the shoot	-
Prt_cal	Average value of the root:shoot ratio that is wished to be reached at 360 °C d	-
Prt1	Function subroutine used to calculate increasing dry matter partitioning to the roots 0−360 °C d for plant 3	-
Prt2	Function subroutine used to calculate decreasing dry matter partitioning to the roots 360−2663 °C d for plants 1, 2 and 3	-
Afixed	Slope of line prt1. Fixed to enable parallel shifts up and down due to water stress	-
FSU2	Function subroutine used to calculate dry matter partitioning to the suckers	-
FSU2RED2_1	Function for the linear decrease of the amount of newly produced DM2, so given by GDM2, that is supplied by sucker 1 to sucker 2 in the period that sucker 2 is not yet shifted to the status of plant 1	-
FSU2RED2_2	Function for the linear decrease of the amount of newly produced DM2, after sucker 1 has become motherplant, and will continue to supply dry matter up to its flower initiation at 2423 °C d	-
FrtGR	Increasing fraction of dry matter allocated to roots of plant 3 for the period 0−360 °Cd	-
FrtRED*i*	Reducing fraction of dry matter allocated to roots of plant, i = 1−2	-

Appendix 2 continued

Abbreviation	Explanation	Unit
'PCOTB'	Character string for partitioning to corm table	-
'PSTTB'	Character string for partitioning to pseudostem table	-
'PLVTB'	Character string for partitioning to leaves table	-
'PBUTB'	Character string for partitioning to bunch table	-
PCOTB	Dry matter partitioning to corm table	-
PSTTB	Dry matter partitioning to pseudostem table	-
PLVTB	Dry matter partitioning to leaves table	-
PBUTB	Dry matter partitioning to bunch table	-
Psum*i*	Sum of the proportions of dry matter in the corm, pseudostem, leaves and bunch for plant, *i* = 1−3	-
Pcorm*i*	Proportion of dry matter in corm for plant, *i* = 1−3	-
Ppsstm*i*	Proportion of dry matter in pseudostem for plant, *i* = 1−3	-
Pleaf*i*	Proportion of dry matter in leaf for plant, *i* = 1−3	-
Pbunch1	Proportion of dry matter in bunch for plant 1	-
DummyPbunch*i*	Proportion of dry matter in bunch for plant, *i* = 2−3	-
Switches		
SWemerg3	Switch to indicate emergence of plant 3 (sucker 2)	-
SWstdm3	Switch to indicate the start of dry matter production through photosynthesis of plant 3 (sucker 2)	-
ISWstdm3	Switch to indicate the start of dry matter production through photosynthesis of plant 3 (sucker 2). Used to prevent numerical problems in the EQ comparison in IF statement	-
SWFSU2	Switch to activate the function-subroutine FSU2 from the moment of harvest of motherplant 1 and shift of sucker 1 to the status of motherplant, until flower initiation (TSUM1 = 2423°C d)	-
SWFrt1	Switch indicating the start of the reducing partitioning to the roots, read between 360−2663 °C d	-

Appendix 2 continued

Abbreviation	Explanation	Unit
Parameters		
SLA*i*	Specific leaf area for plant, *i* = 1−3	ha leaf kg^{-1}
LUE*i*	Light Use Efficiency for plant, *i* = 1−3	kg MJ^{-1} PAR
k*i*	Light extinction coefficient for plant, *i* = 1−3	ha soil ha^{-1} leaf
TBASE	Base temperature	°C
TSUMSUC	Temperature sum for the start of growth for plant 3	°C d
STGRLV	Temperature sum for the start of growth of photosynthetically active leaves plant 3	°C d
TSUM3stop_exp	Temperature sum above which exponential growth of leaf area stops	°C d
LAIstop_exp	Leaf area index above which exponential leaf area growth stops	ha leaf ha^{-1} soil
TSUMendfulldepe	Temperature sum at the end of full dependence of plant 3 (sucker 2) on plant 2 (sucker 1)	°C d
TSUMfloinit	Temperature sum at flower initiation	°C d
TSUMflower	Temperature sum at flowering	°C d
TSUMHARV	Temperature sum at harvest	°C d
RGRL	Relative growth rate of leaves during the juvenile stage	$°Cd^{-1}$
FSU2max	Maximum fraction of dry matter that goes from sucker 1 to sucker 2 in the stage where sucker 2 does not have functional leaves	(kg DM sucker 2) / (kg DM sucker 1)
Fleaf_green*i*	Fraction of green leaves for plant, *i* = 1−3	-
RDRrt*i*	Relative death rate of roots of plant, *i* = 1−3	d^{-1}
RDR*i*	Relative death rate of leaves of plant, *i* = 1−3	d^{-1}
RDcR	Relative decomposition rate of mulch	d^{-1}
RDRrt1_After_Harv	Relative decomposition rate of roots of plant 1 after harvest	d^{-1}
RDRCorm1_After_Harv	Relative decomposition rate of corm of plant 1 after harvest	d^{-1}
pcorm1_to_Wsh1	Proportion of corm dry matter of harvested plant re-distributed to the new plant 1	-
Radiation interception		
PARIN*i*	Total PAR incident for plant, *i* = 1−3	MJ ha^{-1} d^{-1}
PAROUT*i*	Total PAR transmitted by plant, *i* = 1−3	MJ ha^{-1} d^{-1}
PARINT*i*	Total PAR intercepted by plant, *i* = 1−3	MJ ha^{-1} d^{-1}
Weather and simulation control		
CNTR	Country code for weather file	-
DAVTMP	Daily average temperature	°C
DELT	Time step of integration	d

Appendix 2 continued

Abbreviation	Explanation	Unit
RKDRIV	Runge-Kutta DRIVer, with a variable time step	-
TRACE	Used to instruct the driver to produce a detailed integration report including state event iterations (set at 4.0)	-
DELMAX	Upper limit to the time step	d
DTEFF	Daily effective temperature	°C
DTR	Daily total radiation	MJ ha^{-1} d^{-1}
ISTN	Weather station number	-
IYEAR	Year	-
FINTIM	Finish time of simulation run	d
STTIME	Start time of the simulation run	d
PRDEL	Time interval for printing	d
RDD	Daily global radiation (weather file)	KJ m^{-2} d^{-1}
RTSUM12	Rate of increase of temperature sum of plant 1 and 2	°C
RTSUM3	Rate of increase of temperature sum of plant 3	°C d
TMMN	Daily minimum temperature (weather file)	°C
TMMX	Daily maximum temperature (weather file)	°C
WTRDIR	Weather directory	-
State and time events		
EVENT	Used to indicate interruptions in simulation due to events like emergence, start of growth of functional leaves, flowering and harvest	-
HELP	HELP is used to calculate a setting variable (state) during an event e.g. HELPDMi = DM1	-
ZEROCONDITION	Condition that must be reached for an event to take place e.g. sucker emergence, flowering and harvest	-
NEWVALUE	Statement that re-defines the value of the state variable after the event. Enables uses of old values and assignment of new values e.g. NEWVALUE DM1 = HELPDMi	-
END EVENT	Statement that ends the event	-
Rates		
GLAI	Growth rate of leaf area index calculated in the subroutine GLA. Function of temperature in the juvenile stage and GDM and SLA in the maturation stage	ha leaf ha^{-1} soil d^{-1}
NLAI*i*	Net daily increase of leaf area index for plant, *i* = 1−3	ha leaf ha^{-1} soil d^{-1}
DLAI*i*	Death rate of leaf area index for plant, *i* = 1−3	ha leaf ha^{-1} soil d^{-1}

Appendix 2 continued

Abbreviation	Explanation	Unit
NWsh*i*	Net change of the weight of shoot dry matter due to death of leaves for plant, *i* = 1−3	kg DM ha^{-1} d^{-1}
DWsh*i*	Death rate of shoot (leaves) for plant, i = 1−3	kg DM ha^{-1} d^{-1}
NWrt*i*	Net change of the weight of dry matter of roots due to death of plant, *i* = 1−3	kg DM ha^{-1} d^{-1}
GWrt*i*	Growth rate of roots of plant, *i* = 1−3	kg DM ha^{-1} d^{-1}
GWsh*i*	Growth rate of shoot of plant, *i* = 1−3	kg DM ha^{-1} d^{-1}
NWleaf*i*	Net change of the weight of dry matter of leaves for plant, *i* = 1−3	kg DM ha^{-1} d^{-1}
DWleaf*i*	Death rate of leaves of plant, *i* = 1−3	kg DM ha^{-1} d^{-1}
DWleafTot	Total death rate of leaves of plant 1, 2 and 3	kg DM ha^{-1} d^{-1}
GWcorm*i*	Growth rate of corm of plant, *i* = 1−3	kg DM ha^{-1} d^{-1}
GWpsstm*i*	Growth rate of pseudostem of plant , *i* = 1−3	kg DM ha^{-1} d^{-1}
GWleaf*i*	Growth rate of leaves of plant, *i* = 1−3	kg DM ha^{-1} d^{-1}
NDM*i*	Net change of the weight of dry matter due to death of leaves and roots of plant, *i* = 1−3	kg DM ha^{-1} d^{-1}
DWDM*i*	Sum of the death rates of leaves and roots for plant, *i* = 1−3	kg DM ha^{-1} d^{-1}
GWbunch1	Growth rate of bunch of plant 1	kg DM ha^{-1} d^{-1}
GDM*i*	Growth rate of total dry matter of plant, *i* = 1−3	kg DM ha^{-1} d^{-1}
GDMTOT	Sum of the growth of dry matter due to photosynthetically active radiation interception for plants 1, 2 and 3	kg DM ha^{-1} d^{-1}
DWrt*i*	Death rate of roots of plant, *i* = 1−2	kg DM ha^{-1} d^{-1}
GDM*i*HLP	Growth rate of total dry matter of plant, *i* = 1−3 from intercepted PAR	kg DM ha^{-1} d^{-1}
G2from2_1	Dry matter increase of plant 2 during the period when plant 3 has no functional leaves (0−360 °Cd)	kg DM ha^{-1} d^{-1}
G2from2_2	Dry matter increase of plant 2 during the period when plant 3 it is still supported before the shift. Read with TSUM2	kg DM ha^{-1} d^{-1}
G2from1	Dry matter increase of plant 2 due to support from plant 1. Read with TSUM1	kg DM ha^{-1} d^{-1}
G3from2_1	Dry matter partitioning from sucker 1 (plant 2) to sucker 2 (plant 3) during the period when plant 3 has no functional leaves	kg DM ha^{-1} d^{-1}
G3from2_2	Dry matter increase of plant 3 due to a decreasing supply from plant 2 during the period when it is still supported	kg DM ha^{-1} d^{-1}
G3Photos	Dry matter increase of plant 3 due to its own photosynthesis	kg DM ha^{-1} d^{-1}

Appendix 2 continued

Abbreviation	Explanation	Unit
DcRDMmulch	Absolute decomposition rate of mulch	kg DM ha^{-1} d^{-1}
d Corm1_to_Wsh1	Absolute rate of corm dry matter after harvest re-distributed to the new plant 1	kg DM ha^{-1} d^{-1}
dWrt1_After_Harv	Absolute death rate of the roots of plant 1 after harvest	kg DM ha^{-1} d^{-1}
States		
TSUM*i*	Temperature sum of plant, $i = 1-3$	°C d
Wrt*i*	Weight of roots of plant, $i = 1-3$	kg DM ha^{-1}
WrtTot	Total weight of roots of plant 1, 2 and 3	kg DM ha^{-1}
Wsh*i*	Weight of shoot of plant, $i = 1-3$	kg DM ha^{-1}
WshPlnt*i*Tot	Total weight of shoot of plant, $i = 1-3$	kg DM ha^{-1}
WshTotPlants	Total weight of shoot of plant 1, 2 and 3	kg DM ha^{-1}
DMTotRtSh	Total dry matter of the root and shoot of plant 1, 2 and 3	kg DM ha^{-1}
Wcorm*i*	Weight of corm of plant, $i = 1-3$	kg DM ha^{-1}
Wpsstm*i*	Weight of pseudostem of plant, $i = 1-3$	kg DM ha^{-1}
Wleaf*i*	Weight of leaves of plant, $i = 1-3$	kg DM ha^{-1}
TotWleafD	Total weight of dead leaves of plant, $i = 1-3$	kg DM ha^{-1}
DM*i*	Total dry matter of plant, $i = 1-3$	kg DM ha^{-1}
Wrt*i*Tot	Total weight of dead roots for plant, $i = 1-3$	kg DM ha^{-1}
DMTotdm	Total dry matter of plant 1, 2 and 3	kg DM ha^{-1}
Wbunch1	Dry weight of bunch of plant 1	kg DM ha^{-1}
DMmulch	Mulch dry matter of the soil surface	kg DM ha^{-1}
Corm1_After_Harv	Weight of the corm of plant 1 after harvest	kg DM ha^{-1}
Corm1_Lost_After_Harv	Weight of the corm of plant 1 re-distributed to new plant 1	kg DM ha^{-1}
Corm1_to_Wsh1	Weight of the corm of plant 1 after harvest re-distributed to the shoot of new plant 1	kg DM ha^{-1}
HarvestDM*i*_Pru	Integral keeping track of pruned leaf dry matter of plant, $i = 1-3$	kg DM ha^{-1}
HarvestDM	Harvested shoot dry matter (pruned leaves, pseudostem and leaves)	kg DM ha^{-1}
Wrt1_After_Harv	Weight of the roots of plant 1 after harvest	kg DM ha^{-1}
Ratios		
RtShratio*i*	Root shoot ratio of plant, $i = 1-3$	-
LWR*i*	Leaf weight ratio of plant, $i = 1-3$	kg leaf kg^{-1} DM
Balances		
BalDmHlp*i*	Balance for dry matter production of plant, $i = 1-2$.	-
BalDmHlp3	Balance that accumulates all the principal rates of dry matter production, for the three plants	-
BalDmHlp4	Balance that gives the absolute difference	-

Appendix 2 continued

Abbreviation	Explanation	Unit
BalDmHlp5	Balance of the absolute balance relative to the total dry matter production (BalDmHlp3)	-
BalRtShHlp*i*	Root-shoot balance for the plant, i = 1−3.	-
BalRtShHlp4	Overall root-shoot balance with all 3 plants in one calculation relative to the total DM production	-

Summary

The poor yield of East Africa highland bananas (*Musa* spp., AAA-EAHB) on smallholder farms has been attributed to problems of poor soil fertility, soil moisture stress, pests (particularly banana weevil - *Cosmopolites sordidus* and the burrowing nematode *Radopholus similis*), diseases and reduced crop husbandry. In order to improve production, knowledge on highland banana crop physiology, growth patterns and response to fertilization is important. The goal of this thesis was to (i) understand banana crop growth, (ii) quantify potential production of East Africa highland banana, and (iii) explore options for closing the yield gaps between potential and actual yields.

Banana plant morphological characteristics, radiation interception, and biomass (by destructive harvesting) were measured in experimental fields in central and southwest Uganda. The results presented in Chapter 2 show that morphological traits such as height and pseudostem girth can be used to estimate the size of the middle leaf area, which when multiplied by the number of functional leaves can reliably be used to estimate the total plant leaf area. Measurements are easy to perform and are non-destructive. They allow rapid plant growth assessments in the field. However, due to the diversity in highland banana cultivars, these relationships have to be derived and assessed for each cultivar or cloneset. Intercepted photosynthetically active radiation (PAR) data by the banana canopy from measurements over the entire day was used to determine the light extinction coefficient, *k*. The *k* value obtained for highland banana cultivar Kisansa was 0.7. Regular destructive sampling results showed that banana plants partitioned more dry matter (DM) to the leaves during the first phase of development (47% of total DM), with the pseudostem becoming the dominant sink at flowering (58% of total DM), and the bunch being the dominant sink at harvest (53% of total DM). The allometric relationship between above-ground biomass (AGB in kg DM) and girth at base (cm) followed a power function during the vegetative phase ($AGB = 0.0001\ (girth)^{2.35}$). Measurements of girth at base proved to be an accurate estimater of above ground biomass during the vegetative phase. The changes in dry matter partitioning during development resulted in different exponential functions at flowering ($AGB = 0.325e^{0.036\ (girth)}$) and at harvest ($AGB = 0.069e^{0.068(girth)}$). Results showed that girth was an important morphological trait strongly related to the size of the inflorescence at flowering.

Trials were conducted to assess the effects of mineral fertilizers on crop performance at two sites over two to three crop cycles following the application of fertilizers at rates of 0N−50P−600K, 150N−50P−600K, 400N−0P−600K, 400N−50P−0K,

400N−50P−250K and 400N−50P−600K kg ha^{-1} yr^{-1}. All fields, with the exception of the controls, were given the following mix of micro-elements: 60Mg−6Zn−0.5Mo−1B kg ha^{-1} yr^{-1}. Yield increases above the control (5.5 kg $bunch^{-1}$ and 7.9 Mg ha^{-1} yr^{-1}) at Ntungamo (two crop cycles) were larger (ranging 12.4−16.0 kg $bunch^{-1}$, average for all treatments 14.7 kg $bunch^{-1}$; and 7.0−29.5 Mg ha^{-1} yr^{-1}, average for all treatments 17.9 Mg ha^{-1} yr^{-1}) as compared with Kawanda (three crop cycles) (ranging 3.1−6.2 kg $bunch^{-1}$, average for all treatments 11.5 kg $bunch^{-1}$; and 2.2−11.2 Mg ha^{-1} yr^{-1}, average for all treatments 15.8 Mg ha^{-1} yr^{-1}), where the yield for control was 8.8 kg $bunch^{-1}$ and 13.0 Mg ha^{-1} yr^{-1}. The limiting nutrients at both sites were in the order K>P>N. Drought stress seemed to play an important role in the crop response to fertilizer input at Kawanda. It appeared to affect sink filling (weight per finger) more than sink size (number of fingers per bunch). I summarised the results from the Ntungamo site by use of the static nutrient response model QUEFTS. Calibration results were fair (R^2 = 0.57, RMSE = 648 kg ha^{-1}), and the calibrated model predicted yields well (R^2 = 0.68, RMSE = 562 kg ha^{-1}) using data from Mbarara, southwest Uganda. The QUEFTS approach was used to calculate fertilizer recommendations for highland banana, but poor fertilizer recovery rates resulted in high quantities of fertilizers required for a target yield, hence reducing the attractiveness of fertilizer application for smallholder farmers.

A new radiation and temperature-driven growth model, LINTUL BANANA 1 for potential production was developed to developed (Chapter 4). The model considers (i) the physiology of the highland banana crop; (ii) the plant dynamics (i.e. three plant generations, Plant 1, 2 and 3 at different stages of growth constituting a mat), growing over a duration of more than one year; and (iii) three canopy levels formed by the leaves of the three plant generations. Biomass production is modelled as the product of light interception and a constant light use efficiency (kg MJ^{-1} PAR). Partitioning coefficients are defined as a function of the phenological development stage of the banana plant. Dry matter transfers between Plants 1 and 2, and between 2 and 3 are captured in the model. At physiological maturity, harvest of the bunch (Plant 1) takes place, Plant 2 becomes the new Plant 1 and Plant 3 becomes the new Plant 2, with the new sucker (Plant 3) emerging later in the growth process. Average computed potential bunch dry and fresh matter for five harvests was slightly larger at Ntungamo (20 Mg ha^{-1} DW; 111 Mg ha^{-1} FW), compared with Kawanda (18.25 Mg ha^{-1} DW; 100 Mg ha^{-1} FW), and values compared well with banana yields under optimal situations at comparable leaf area index values (20.3 Mg ha^{-1} DW; 113 Mg ha^{-1} FW). Differences between the sites were attributed to a longer growth period (lower temperature due to higher altitude and thus the plant has

more time to accumulate the physiological temperature sum) resulting into more radiation interception and leaf duration. Sensitivity analysis was done to assess the effects of changes in parameters (light use efficiency, *LUE*; the light extinction coefficient, *k*; specific leaf area, *SLA*; relative death rate of leaves, r_d; and initial dry matter values) on bunch dry matter, leaf dry matter and leaf area index (*L*) at flowering. Sensitivity results for Kawanda and Ntungamo sites showed that changes in LUE1 (where 1 refers to Plant 1) resulted in a more than proportional increase in bunch DM (1.30 and 1.36), a higher leaf DM (0.60 and 0.67) and a higher LAI at flowering (0.60 and 0.67). Changes in the photosynthetic capacity of the plant due to death of leaves (r_d1 values) reduced bunch DM, leaf DM and *L* at flowering. Leaf DM and *L* at flowering were reduced by changes in *k*1, but only leaf DM was reduced as a result of changes in SLA1 at both sites. Initial dry matter values had a small effect (sensitivity < 0.0263) on bunch DM, leaf DM and *L* at flowering.

As a contribution of the model to experiment management and crop development, factors affecting light use efficiency (LUE) and relative death rate of leaves (r_d) have to be considered in designing and managing experiments. Sensitivity analysis showed that a higher light extinction coefficient, *k* resulted in increased bunch DM (Chapter 4). Morphological improvements through breeding banana plants with more horizontal and broad leaves could increase radiation interception resulting in higher banana yields. With knowledge on genotypic variation in specific leaf area (SLA) in highland banana cultivars, targeted selection and breeding could focus on plants with higher SLA and reduced r_d. The comparison of the potential and actual yields in the region revealed large yield gaps. In the fertilizer trials, the maximum yield (Mg ha^{-1} yr^{-1}) obtained was about 40% of the calculated potential bunch DM. Fertilizer recovery fractions were low, compared with values reported in banana plantations in south America. It is important to improve the recovery of applied fertilizer, either through the combined use of organic and mineral fertilizers or the use of irrigation.

Samenvatting

De lage opbrengst van Oost-Afrikaanse hooglandbananen (*Musa* spp., AAA-EAHB) op kleinschalige boerenbedrijven wordt toegeschreven aan lage bodemvruchtbaarheid, droogtestress, plagen (de bananensnuitkever - *Cosmopolites sordidus* en wortelnematode *Radopholus Similis*), ziekten en verminderde aandacht voor een goede gewasverzorging. Teneinde de produktie te verbeteren is kennis van de gewasfysiologie, de groeipatronen en de reactie op bemesting van de hooglandbanaan belangrijk. Het doel van dit proefschrift was (i) het begrijpen van de groei van banaan, (ii) het kwantificeren van de potentiële produktie van de Oost-Afrikaanse hooglandbanaan, en (iii) het zoeken naar mogelijkheden om het gat tussen potentiële en actuele opbrengsten te dichten.

Morfologische karakteristieken, lichtonderschepping en biomassa (door middel van oogsten) van de bananenplant werden in veldexperimenten gemeten in centraal en in zuid-west Oeganda. De resultaten die in Hoofdstuk 2 worden gepresenteerd laten zien dat morfologische eigenschappen als hoogte en pseudostamomtrek kunnen worden gebruikt om het bladoppervlak van het middelste blad te schatten. Wanneer deze laatste wordt vermenigvuldigd met het aantal functionele bladeren kan met vertrouwen het totale bladoppervlak van de plant worden geschat. Deze metingen zijn eenvoudig uit te voeren, niet-destruktief en zij geven de mogelijkheid om de groeitoestand van de plant snel vast te stellen. Vanwege de diversiteit van hooglandbanaanvariëteiten dienen deze relaties echter te worden vastgesteld voor elke variëteit. De lichtuitdovingscoëfficient, *k*, voor het fotosynthetisch actieve deel van het lichtspectrum (Engels: photosynthetically active radiation, PAR) werd afgeleid uit de lichtonderschepping door het banaangewas, welke gedurende de gehele dag werd gemeten. De waarde van *k* voor de hooglandbanaan bedroeg 0.7. Resultaten van periodieke destruktieve bemonstering lieten zien dat bananenplanten gedurende de eerste fase van ontwikkeling meer droge stof (DM) toedeelden aan de bladeren (47% van de totale DM), dat de pseudostam bij bloei de belangrijkste put werd (58% van de totale DM), en dat de tros bij de oogst tenslotte 53% van de totale droge stof bevatte. De allometrische relatie tussen bovengrondse biomassa (AGB in kg droge stof) en omtrek aan de basis (cm) volgde een machtsfunctie gedurende de vegetatieve groeifase ($AGB = 0.0001\ (girth)^{2.35}$). De meting van de omtrek aan de basis bleek een nauwkeurige schatter te zijn voor de bovengrondse biomassa gedurende de vegetatieve fase. De verandering in drogestoftoedeling gedurende de plantontwikkeling resulteerde in verschillende exponentiële functies bij bloei ($AGB = 0.325e^{0.036(girth)}$) en bij de oogst ($AGB = 0.069e^{0.068(girth)}$). Resultaten lieten zien dat de bloemkarakteristieken

tijdens de bloei en de tros bij de oogst sterk gerelateerd zijn met de omtrek aan de basis van de plant.

Er werden experimenten opgezet om het effect vast te stellen van minerale meststoffen op het gewas op twee locaties gedurende twee tot drie gewascycli. De mestgiften waren 0N−50P−600K, 150N−50P−600K, 400N−0P−600K, 400N−50P−0K, 400N−50P−250K en 400N−50P−600K kg ha^{-1} yr^{-1}. Met uitzondering van de controlevelden, ontvingen alle velden ook 60Mg−6Zn−0.5Mo−1B kg ha^{-1} yr^{-1} aan spore-elementen. In Ntungamo waren opbrengsttoenames boven de controlewaardes (5.5 kg $tros^{-1}$ en 7.9 Mg ha^{-1} yr^{-1}) groter (varierend van 12.4−16.0 kg $tros^{-1}$, met een gemiddelde voor alle behandelingen van 14.7 kg $tros^{-1}$; en 7.0−29.5 Mg ha^{-1} yr^{-1}, met een gemiddelde voor alle behandelingen van 17.9 Mg ha^{-1} yr^{-1}) dan in Kawanda (varierend van 3.1−6.2 kg $tros^{-1}$, met een gemiddelde voor alle behandelingen van 11.5 kg $tros^{-1}$; en 2.2−11.2 Mg ha^{-1} yr^{-1}, met een gemiddelde voor alle behandelingen van 15.8 Mg ha^{-1} yr^{-1}), waar de opbrengsten van de controlewaardes 8.8 kg $tros^{-1}$ en 13.0 Mg ha^{-1} yr^{-1} bedroegen. De beperking van voedingsstoffen op beide lokaties liep van K (meest beperkend) via P naar N (minst beperkend). Droogtestress leek een belangrijke rol te spelen in de gewasreactie op meststoffen in Kawanda. Het bleek vooral putvulling te beïnvloeden (gewicht per individuele banaan) en niet zozeer de omvang van de put (aantal individuele bananen per tros). De resultaten van de lokatie in Ntungamo zijn met behulp van het statische nutriëntenresponsmodel QUEFTS samengevat. Kalibratieresultaten waren redelijk (R^2 = 0.57, RMSE = 648 kg ha^{-1}), en het gekalibreerde model voorspelde opbrengsten goed (R^2 = 0.68, RMSE = 562 kg ha^{-1}) waarbij onafhankelijke gegevens werden gebruikt uit Mbarara, in zuid-west Oeganda. De QUEFTS benadering werd gebruikt om bemestingsadviezen voor hooglandbanaan te berekenen, maar de lage verhouding van meststofopname ten opzichte van de meststofgift resulteerde in hoge aanbevelingen van de hoeveelheid meststoffen welke benodigd zouden zijn voor een bepaalde gewenste opbrengst. Hierdoor wordt het minder aantrekkelijk voor kleine boeren om meststoffen toe te dienen.

De opgedane kennis werd vervolgens gebruikt om een nieuw groeimodel (LINTUL BANANA 1) te ontwikkelen voor banaan op basis van lichtonderschepping en temperatuur gestuurde ontwikkeling voor potentiële produktie (Hoofdstuk 4). Het model omvat (i) de fysiologie van de hooglandbanaan; (ii) de groei van de plant (d.w.z. drie plant generaties, de onderling verbonden Plant 1, 2 en 3, in verschillende groeistadia die samen een plantcluster vormen) gedurende meer dan een jaar, en (iii) drie bladerdekniveaus van de drie generaties van de plant. Biomassaproduktie wordt

gemodelleerd als het product van lichtinterceptie en een constante lichtbenuttingsefficiëntie (kg MJ^{-1} PAR). Toedelingscoëfficiënten van droge stof hangen af van het fenologische ontwikkelingsstadium van de bananenplant. Drogestofoverdracht van Plant 1 naar 2 en van Plant 2 naar 3 zijn in het model opgenomen. De tros (Plant 1) wordt geoogst als deze fysiologisch rijp is. Op het moment van oogsten wordt Plant 2 de nieuwe Plant 1 en Plant 3 de nieuwe Plant 2, terwijl de nieuwe scheut (Plant 3) later in het groeiproces verschijnt. Berekende gemiddelde potentiële droog- en versgewichten van de tros over 5 oogsten waren een beetje hoger in Ntungamo (20 Mg ha^{-1} drooggewicht; 111 Mg ha^{-1} versgewicht) vergeleken met Kawanda (18.25 Mg ha^{-1} drooggewicht; 100 Mg ha^{-1} versgewicht), en deze waardes kwamen goed overeen met banaanopbrengsten onder optimale omstandigheden bij vergelijkbare bladoppervlakindexwaardes (20.3 Mg ha^{-1} drooggewicht or 113 Mg ha^{-1} versgewicht). Verschillen tussen de lokaties werden toegeschreven aan een langere groeiperiode (een lagere temperatuur door grotere hoogteligging verlengt de periode voordat de geaccumuleerde fysiologische temperatuursom is bereikt) en bladlevensduur, die beide meer lichtonderschepping tot gevolg hebben. Een gevoeligheidsanalyse werd uitgevoerd om de effecten van veranderingen in parameters (lichtbenuttingsefficiëntie, *LUE*; de lichtuitdovingscoëfficiënt, *k*; specifiek bladoppervlak, *SLA*; relatieve sterftesnelheid van de bladeren, r_d; initiële waardes van de droge stof) op de droge stof van de tros, het blad en de bladoppervlakindex (*L*) bij bloei vast te stellen. Resultaten van de gevoeligheidsanalyse voor de locaties bij Kawanda en Ntungamo lieten zien dat veranderingen in *LUE*1 (waarbij 1 refereert aan Plant 1) een meer dan proportionele toename in drogestofgewicht van de tros (1.30 en 1.36) tot gevolg had, en tevens een hoger drooggewicht van blad (0.60 en 0.67) en bladoppervlakindex (0.60 en 0.67) bij bloei veroorzaakte. Een vermindering van de fotosynthesecapaciteit van de plant door het afsterven van bladeren (r_d1 waardes) verminderde de hoeveelheid droge stof van de tros, bladeren, en bladoppervlakindex bij bloei. Het drogestofgewicht van het blad en de bladoppervlakindex bij bloei verminderden door veranderingen in *k*1, maar alleen bladdrooggewicht verminderde als gevolg van een verandering in specifiek bladoppervlak van Plant 1 op beide lokaties. Initiële drogestofwaardes hadden een klein effect (gevoeligheid < 0.0263) op het drogestofgewicht van de tros, het blad en *L* tijdens de bloei.

Het model maakt duidelijk dat factoren welke de lichtbenuttingsefficientie (LUE) en de relatieve sterftesnelheid van de bladeren (r_d) beïnvloeden beschouwd dienen te worden bij het opzetten en uitvoeren van experimenten. De gevoeligheidsanalyse liet zien

dat een hogere lichtuitdovingscoëfficiënt, *k*, resulteerde in een toename van het drogestofgewicht van de tros (Hoofdstuk 4). Morfologische verbeteringen door middel van het veredelen van bananenplanten teneinde meer horizontale en grotere bladeren te verkrijgen zouden de lichtonderschepping kunnen verhogen en daarmee tot hogere opbrengsten kunnen leiden. Met behulp van kennis omtrent genotypische variatie in het specifiek bladopppervlak (SLA) in hooglandbanaanvariëteiten, zouden doelgerichte selectie en veredeling gericht moeten zijn op planten met hogere SLA en gereduceerde r_d. De vergelijking van de potentiële en actuele opbrengsten in de regio lieten grote opbrengstverschillen zien (yield gaps). Uit de bemestingsexperimenten bleek dat de maximale opbrengsten van de drogestofgewichten van de tros (in Mg ha^{-1} yr^{-1}) ongeveer 40% bedroegen van de berekende potentiële opbrengst. Dit betekent dat het van belang is om de verhouding van meststofopname ten opzichte van de meststofgift te verhogen, ofwel door gecombineerd gebruik van organische en minerale meststoffen, ofwel door middel van irrigatie.

Acknowledgements

This study was carried out within the framework of the AfricaNUANCES project, implemented by the Plant Production Systems (PPS) Group, Wageningen University. I am deeply grateful to Prof. Dr. Ken E. Giller for selecting me to pursue a PhD. I am grateful for the stimulating discussions, the guidance and encouragement throughout the study. In the same vein, I am thankful to my co-promoter Dr. ir. Peter A. Leffelaar for the guidance, discussions and exhaustive comments on the reports and papers. Model development is never an easy task, you often encouraged me to think deeply about the modules, the small programs and their testing before incorporating them into the main program.

A vote of thanks goes to Dr. Crammer Kaizzi (National Agricultural Research Laboratories Institute, Kawanda – Soils and Soil fertility management program) for selecting me to pursue a PhD, for local supervision and guidance. Dr. Piet Van Asten (International Institute of Tropical Agriculture, IITA) is thanked for the invaluable support and willingness to discuss issues any time. My appreciation also goes to Dr. Marc Corbeels (CIRAD) for the supervision, guidance and fruitful discussions especially during the field visits to Uganda.

At Kawanda, the scientific, technical and support staff provided a warm working environment during my 2½ year research period. Am particularly grateful to Dr. Drake Mubiru (the Head), Dr. Onesmus Semalulu, Dr. John Byalebeka and Dr. Moses Isabirye for the facilities and discussions. Mr Stewart Kibirango and Mr Moses Mubiru are thanked for the help in the laboratory analyses. Modelling crop growth is never possible without good weather data, Mr Moses Ojara is thanked for all the assistance with the weather data. Am deeply grateful to Mr Godfrey Taulya (IITA) for the help in running the trials and Mr. Xavier Hamon for the help with the initial allometric relationships. My gratitude goes to all field assistants for the help in collecting data, maintaining the trials and handling the plant samples. Mr Simei Turyaija, Kikoni parish, Ntungamo district provided land for the trial and was so kind to allow me to collect data from his banana plantation.

I am deeply grateful to Makerere University, my employer for granting a study leave to complete this study. My sincere gratitude to staff of the Faculty of Forestry and Nature Conservation for the support. Am particularly grateful to the former Dean, Assoc. Prof. John Kaboggoza, the new Dean Dr. Gorettie Nabanoga and Prof. William Gombya-Ssembajjwe, the head Forest Management department, for all support and guidance.

I thank Prof. Ken Giller for the good working environment and facilities. Eelco Meuter, Marcel Lubbers and Antonio Valente provided valuable help with computers and software. To Ria van Dijk, Charlotte Schilt and Gijsbertje Berkhout, I appreciate all the assistance and most especially the professionalism and urgency in dealing with issues. Ken, thanks for regular invitations to your house for dinner. I enjoyed and will miss the dinners at Nico's place, where PhD students prepare dishes from their home countries. Nico and Rita, my appreciation for your hospitality. I did get chance to visit some Dutch farms and the water works, many thanks to Nico and Bert Rijk for organising the trips.

Wageningen is a vibrant place, with new people from different countries coming and others leaving. I shared the Attic with Dr. Assefa Abegaz, Dr. Shibu Ebrahim Muhammed and colleagues on the AfricaNUANCES project, Ousmane Mama Sanogo, Amos Mwijage and Christine Chizana. In the former library, I shared jokes with Dr. Peter Ebanyat, Bui Tan Yen, Chrispen Murungweni, Wilson Leonardo and Leonard Rusinamhodzi. I often interacted with other colleagues; Sander de Vries, Dr. Glaciela Kaschuk, Charles Bucagu, Myriam Adam, Lenny van Bussel, Michiel de Vries, Maryia Mandryk, Sheida Sattari, Andre Monteiro Novo, Jairos Rurinda and Joao Dal Belo Leite. Away from home, country mates Enoch Kikulwe, Denis Ochieno, Ahebwa Wilber, Suubi Godfrey and Odong Thomas made academic life more enjoyable.

Lastly, I would not have reached the end without the unyielding support of my best friend for the last 11 years, wife and mother of our two sons. Lydia, thanks for the love, support and patience during the study period and for the morale boosting visit to Wageningen. I now hand over the baton stick to you. I appreciate the support from my entire family. Mum, I am deeply grateful for laying the foundation that has enabled me to get this far. I am deeply grateful to my mother-in-law who accepted to take care of the children while we both pursue further studies. To Mr Mohamed Bukenya, thanks for the friendship, support and the time to keep all my projects in Uganda running well.

Curriculum vitae

Kenneth Nyombi was born at Nkumba, Wakiso district, Uganda on March 4th 1976, the last child in a large Ugandan family. He attended Nkumba primary school (1982–1988), Entebbe secondary school (1989–1992) for ordinary level and St Henry's college Kitovu (1993–1995) for the advanced secondary school. He joined Makerere University on a government scholarship in September 1995 and graduated in October 1999 with a BSc Agriculture (Hons) degree majoring in Crop Science with a final year project on the manufacture and use of Bio-earth organic fertilizers. He worked with Banga Multipurpose Cooperative Society under the DANIDA funded Bio-earth fertilizer project as an Agronomist from July 1999 to October 2000. He joined the International Food Policy Research Institute, IFPRI as a Research assistant on the Land Management project in Uganda in November, 2000. In August 2001, he started a Masters degree in Natural Resources Management and Sustainable Agriculture (MNRSA) at the Norwegian University of Life Sciences (UMB) under NORAD sponsorship, which was completed in May 2003. IFPRI offered him a job in July 2003 as a Research assistant under the Strategic Criteria for Rural Investments in Productivity (SCRIP) project funded by USAID, and he later worked for the East Africa 2020 research network under Dr. Steven Were Omamo. On January 3rd 2005, he started a Sandwich PhD programme on the AfricaNUANCES project with the Plant Production Systems Group, Wageningen University. During the research period (July 2005−December 2007), he was based at the National Agricultural Research Laboratories Institute, Kawanda. He is currently working with the Faculty of Forestry and Nature Conservation, Makerere University as an Assistant Lecturer with teaching, research and outreach roles. Kenneth is married to Lydia, and they are already blessed with two sons, Elvis James Ssemanda (5 yrs) and Ernest Elijah Muyanja (3 yrs). Contacts: email knyombi@yahoo.co.uk or nyombi@forest.mak.ac.ug and Tel: +256−772−399838.

PE&RC Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of Literature (5.6 ECTS)

- Principles of production ecology; Department of Theoretical Production Ecology and Centre for Agrobiological Research (2005)

Writing of Project Proposal (7 ECTS)

- Understanding and improving East Africa Highland banana (AAA-EAHB) cultivation in Uganda (2005)

Laboratory Training and Working Visits (2.8 ECTS)

- Soil and plant chemical analysis; Kawanda Agricultural, Research Institute (2007)
- Soil moisture release; Makerere University Soil Science Department (2007)

Post-Graduate Courses (3 ECTS)

- The art of modelling; PE&RC (2008)

Deficiency, Refresh, Brush-up Courses (2.8 ECTS)

- Systems analysis, simulation and systems management; PPS/BIOB (2005)

Competence Strengthening / Skills Courses (5.4 ECTS)

- Quantitative analysis of land use systems (QUALUS); PPS/BIOB (2005)
- Techniques for writing and presenting a scientific paper; PE&RC (2008)

Discussion Groups / Local Seminars and Other Scientific Meetings (5.6 ECTS)

- Thursday seminars, Faculty of Forestry and Nature Conservation; Makerere University (2007)
- Statistics, maths and modelling (2008)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (1.8 ECTS)

- Perennial rye grass for dairy cows (2005)
- PE&RC Days (2005 and 2008)
- PE&RC Weekend (2008)

International Symposia, Workshops and Conferences (5.7 ECTS)

- AfricaNUANCES Workshop (2005)
- AfricaNUANCES Workshop (2007)
- Banana2008 Conference (2008)

The research described in this thesis was financially supported by:
European Union (AfricaNUANCES project - Contract no. INCO-CT-2004-003729) and the **IITA** (International Institute for Tropical Agriculture, Uganda).
I thank the **Dr. Judith Zwartz Foundation** and the **LEB fonds** for their contributions to the costs of printing the thesis.