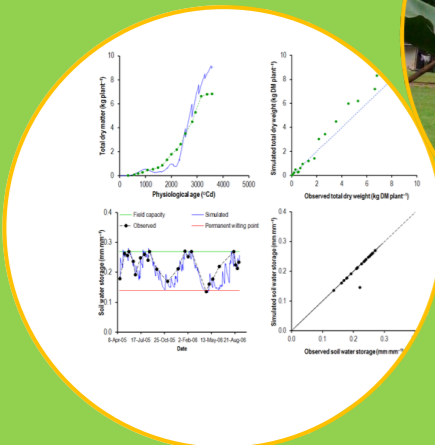**Ky'osimba onaanya**

Understanding productivity of East African highland banana

Godfrey Taulya

Ky'osimba onaanya: Understanding productivity of East African highland banana   **Godfrey Taulya**   2015

KY'OSIMBA ONAANYA:

UNDERSTANDING PRODUCTIVITY OF EAST AFRICAN HIGHLAND BANANA

Godfrey Taulya

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UNDERSTANDING PRODUCTIVITY OF EAST AFRICAN HIGHLAND
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Godfrey Taulya

Thesis

submitted in fulfilment of the requirements for the degree of doctor

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ABSTRACT

Drought stress, potassium (K) and nitrogen (N) deficiencies are major constraints to East African highland banana (*Musa* spp. AAA-EA; hereafter referred to as 'highland banana'), a primary staple food crop for over 30 million people in East Africa. This study explored the main and interactive effects of water, K and N on growth and yield of highland banana. The aim was to build a crop growth model geared towards a decision support tool for managing the crop water and nutrient requirements across agro-ecological zones. Individual plant data from three on-station fertilizer response trials in central and south-western Uganda were used to quantify the effect of drought stress on banana production and explore possible interactions with nutrient availability. Cumulative rainfall within 12 months to the date of harvest (CRF_{12_H}) was computed from daily rainfall records for each plant harvested at maturity. Average bunch weight ranged from 8.0 to 21.9 kg between trials and cycles and was 8–28% less in dry ($CRF_{12\_H} \leq 905$ mm) than in normal ($905 < CRF_{12\_H} \leq 1365$ mm) rainfall periods. Linear relations were observed between CRF_{12_H} and maximum bunch weight over the whole range of observed CRF_{12_H} ($500 - 1750$ mm), whereby every 100 mm decline in rainfall caused maximum bunch weight losses of $1.5 - 3.1$ kg or $8 - 10\%$. The drought-induced yield losses in areas with annual rainfall < 1100 mm are perhaps as high as $20 - 65\%$. To evaluate the highland banana dry matter allocation in response to drought stress and deficiency of K and N, individual plant measurements at harvest from two fertilizer response field trials in central and south western Uganda and the cumulative rainfall received 365 days from sucker emergence (CRF_{12_E}) were analysed. Plants that received $CRF_{12\_E} < 1100$ mm were considered to have grown under dry conditions; otherwise they were considered to have grown under wet conditions. The impact of drought stress on dry matter accumulation and its partitioning between above- and below-ground biomass at harvest stage was evaluated. The main findings were verified through allometric analysis of pre-harvest stage plants sampled from farms of known K and N nutritional status and plants from a screenhouse drought stress pot trial in Uganda. Fresh bunch weight for plants that received K was about 15 kg plant^{-1} irrespective of whether the plant grew under dry or wet conditions. Dry conditions without K application reduced fresh bunch weight by 50% compared to when the plant grew under wet conditions. Drought stress had no effect on DM allocation but enhanced DM allocation to below-ground biomass due to K deficiency. The phenology of highland banana was evaluated to test whether highland bananas' flowering is independent of site (Kawanda vs. Ntungamo in central and south-western Uganda, respectively) effects. A growth analysis was also done to evaluate the relative contribution of morphological (specific leaf area and leaf mass ratio) *vis-à-vis* physiological (net assimilation rate) components of growth rate (RGR) to mitigation of growth reduction in response to limiting supply of water, K or N. Physiological age at flowering was delayed by 739 °C d at Kawanda compared with that at Ntungamo whose chronological age at flowering was in turn 51 d older. At both sites a threshold total dry mass of 1.5 kg per plant was required for flowering. Net assimilation rate contributed at least 90% to RGR increase due to wet conditions at both sites. A soil water balance

model was adapted to the highland banana cropping system from an annual cropping system simulation framework. A sensitivity analysis was done on the adapted model to identify input parameters for calibration. The model output variables were most sensitive to the rooting depth and soil water contents at field capacity and permanent wilting point. The adapted soil water balance model was linked to the model for potential highland banana production (LINTUL-BANANA1) to explore the water-limited growth and yield of highland bananas in central and south-western Uganda. The model accurately predicted total dry weight (RMSE <0.09; R^2 > 0.85). The drought stress yield gap across sites was 55% and was higher (74%) at Kawanda than at Ntungamo (41%). Self-mulch reduced drought stress yield gap by 10% at Kawanda, but had no effect at Ntungamo. The model needs further calibration of the soil water balance parameters defining available water capacity and crop parameters defining dry matter partitioning between the plant structures for accurate simulation of yield components. Adding nutrient limitations, especially potassium, to the model is also recommended for comprehensive evaluation of the contribution of mulch to drought stress mitigation and sustaining highland productivity in the low-input production systems of Uganda.

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CHAPTER ONE

1.0.   General Introduction

1.1.   Importance of East African highland bananas

East African highland bananas (*Musa* spp. AAA-EA; hereafter referred to as 'highland bananas'), constitute over 80% of the banana cultivars in the Great Lakes region of Africa (Karamura et al., 1998). The region straddles Uganda, Kenya, Tanzania, Rwanda, Burundi and the eastern part of Democratic Republic of Congo (DR Congo). Highland bananas are cultivated on deep, well-drained loamy soils in areas with at least 1000 mm yr^{-1} of well distributed rainfall in the African Great Lakes region. By the late 1990s, an estimated 30 million people in Uganda, Kenya and Tanzania, were dependent on highland bananas as their main staple food crop (Karamura et al., 1998).

Per capita consumption of bananas in the region exceeds 200 kg fresh weight per year (Smale and Tushemereirwe, 2007), which is the highest globally. Highland bananas therefore constitute a major source of calories and vitamins A, B6 and C (Robinson 1996) in the African Great Lakes region. The number of malnourished inhabitants in the region is on the rise due to low agricultural productivity and poverty (FAO, IFAD and WFP, 2014), highlighting the need for improving banana productivity, the primary staple food crop. Highland bananas' year-long harvest period makes them an important source of income for the rural farmers (Davies, 1995; Komarek, 2010). Bananas therefore contribute to poverty alleviation, especially with the increasing demand, which is driven by urbanisation in the region.

Highland bananas' permanent canopy cover and self-mulch render it more effective in controlling soil erosion than any other staple food crop in the region (Lufafa et al., 2003). Soil erosion is a major land degradation process in the region due to long steep slopes, intensive rainstorms and high population pressure-induced deforestation (Drake et al., 2004). The highland banana agro-ecologies are characterised by population densities as high as 230 to 300 people km^{-2} (Kanyamibwa, 1998; Lumumba-Kasongo, 2005) due to high (>3.0% yr^{-1}) population growth rates (Ogutu-Ohwayo et al., 1997). Highland banana agroecologies' location on the fringes of tropical rain forests, with multitudes of endemic plant and animal species, dictates that intensive approaches be used for matching production with the escalating demand for highland bananas.

1.2.   Production constraints of East African highland bananas

Cultivated by resource-poor smallholder farmers (Gold et al., 2002) on 38% of Uganda's arable land area (Smale and Tushemereirwe, 2007), Uganda is the leading producer of highland banana regionally and globally (FAO, 2010). The mean on-farm fresh bunch yields in Uganda range from 10 to 20 t ha^{-1} yr^{-1} (Wairegi et al., 2010); less than half of the crop's attainable yield of over 60 t ha^{-1} yr^{-1} (Smithson et al., 2001; van Asten et al., 2005). The observed yield gap in Uganda has been attributed to the abiotic stresses drought (Okech et al., 2004) and nutrient deficiencies, notably, potassium (K) and nitrogen (N), which cause 28 to 68% yield loss (Nyombi et al., 2010; Wairegi and van Asten, 2010). The biotic stresses, *i.e.* pests (Rukazambuga et al., 1998; Barekye et al., 2000; Kashaija et al., 2004) and diseases (Tushemereirwe et al., 1993; Tripathi et al., 2009), have also been implicated. Prominent among the biotic stresses are banana weevils, causing 6 to 60% yield loss (Gold et al., 2004; Wairegi et al., 2010), and nematodes, causing 10 to 50% yield loss (Speijer et al., 1999; Wairegi et al., 2010). Whether the principle causes of the yield gap are weevil and nematode damage resulting in inadequate water and nutrient uptake is a point of contention.

A decline in highland banana production in central Uganda and a concomitant rise in production in south-western Uganda has been documented (Gold et al. 1999). However, researchers have alluded to a banana yield decline in the country as a whole, without any time series data to support this claim. Several authors (Bekunda and Woomer, 1996; Woomer et al., 1998a; Gold et al., 1999; Sseguya et al. 1999; Tenywa et al., 1999) cited soil fertility depletion and soil degradation among the causative factors for the alleged yield decline in Uganda. Smithson et al. (2001) concluded from historical soil analysis results that there was no evidence supporting soil fertility depletion as a cause for the alleged yield decline. However, it is not clear whether their conclusion was based on time series soil sampling from the same banana fields in central Uganda or not. Smithson et al. (2001) showed foliar nutrient concentrations of N and K to be sub-optimal, despite adequate concentrations of the nutrients in soils sampled from the banana fields. Smithson et al. (2001) accordingly hypothesised that pest damage, mainly by banana weevils (Rukazambuga et al., 1998) and nematodes (Barekye et al., 2000) hampered water and nutrient uptake causing the observed discrepancy between soil and foliar nutrient concentrations. Ssali et al. (2003) reiterated this hypothesis.

McIntyre et al. (2003) reported that mulched highland banana produced heavier bunches yet they suffered more extensive weevil damage than those that were not mulched in an

on-station trial in central Uganda. They attributed the greater productivity of mulched treatments to greater water and nutrient uptake compared with no-mulch treatments. McIntyre et al. (2003) recorded significantly higher foliar K concentration from mulched highland banana than that from non-mulched highland banana. Similar findings were reported from an on-station mulch × nematode inoculation trial (McIntyre et al., 2000) at another location in central Uganda. This was corroborated by Wairegi et al. (2010), who concluded that abiotic factors were more important than the biotic factors in driving highland banana yields in Uganda, from on-farm monitoring studies in eastern, central, southern and south-western Uganda. Apparently, initial research efforts towards improving highland banana productivity in Uganda were premised on anecdotal evidence. Little attention was paid towards systematic understanding of the highland banana cropping system, which can guide development of suitable management interventions. The findings by McIntyre et al. (2000; 2003) demonstrate that water and nutrient availability are the drivers of attainable growth and yield, while pests are its reducing factors as conceptualised in Wageningen University crop growth models (van Ittersum et al., 2003).

Positive, albeit variable highland banana response to mineral K and N inputs have been reported in Uganda (Smithson et al., 2001; Nyombi et al., 2010; Wairegi and van Asten, 2010). Variation in crop response to the inputs may be due to spatial and/or temporal variations in the relative importance of drought stress, K and N deficiencies in driving highland banana growth and yield. On the other hand, drought, K and N stress effects on plant growth are so interlinked (Marschner, 1995) that interactions between soil water supply, mineral N and K inputs are plausible. These interactions may also account for the observed variations in crop response to the ameliorative inputs. Studies on highland banana (e.g. McIntyre et al., 2000; McIntyre et al., 2003; Ssali et al., 2003; Nyombi et al., 2010) neither attempted to explicitly separate the main from interactive effects of water, K and N supply on the highland banana growth and yield response, nor probe the underlying physiological processes. For example, soil moisture and exchangeable soil K increased with application of external mulch in highland banana cropping systems (McIntyre et al., 2000; Ssali et al., 2003). However, it is not clear from these studies to what extent each of the two factors contributed to the observed crop growth and yield in response to external mulch use. Understanding the physiological responses of highland banana to drought stress and nutrient deficiencies or their ameliorative inputs is necessary for designing a growth model for the crop.

1.3.   Modelling banana cropping systems

Insights gained from crop growth modelling improve efficiency in development of management practices across heterogeneous pedo-climatic zones compared with sole field experimentation. The heuristic potential of a generic crop growth model permits delineation of gaps in the body of knowledge on the crop's eco-physiology and hence guide orientation of field and laboratory experiments towards better understanding of the cropping system (Seligman, 1990; Sinclair and Seligman, 1996; Mathews et al., 2001). Ultimately this can lead to design of robust decision support tools and more effective management interventions. Crop growth models applied on banana cropping systems were based on the CENTURY (Woomer et al., 1998b), STICS (Brisson et al., 1998) and SIMBA (Tixier et al., 2004) models. They differ in terms of purpose, level of integration of the underlying processes and/or their temporal/spatial scale of simulation.

Woomer et al. (1998b) used assumed assimilate allocation patterns between banana roots, shoots and bunch to adapt the CENTURY model for simulating highland banana growth with the aim of understanding the soil-plant interactions influencing and being influenced by the system. CENTURY is a biogeochemistry model that simulates plant productivity and soil organic carbon pools and flows in response to climate variables, management factors and soil properties (Parton et al., 1987; 1988). The plant production sub-model in CENTURY estimates potential aboveground biomass production from empirical functional relationships with soil temperature, available soil moisture and level of plant self-shading. The potential aboveground biomass is then reduced by the most limiting of N, phosphorus (P) or sulphur (S) deficiency (Parton et al., 1993). The model is more suited for exploring crop impacts on soil biogeochemistry than understanding growth and yield formation in response to eco-physiological and management factors.

Brisson et al. (1998a) simulated banana growth using an adapted generic model, STICS, which was originally developed as a general model for temperate annual crops (Brisson et al., 1998b). Growth is driven by solar radiation interception according to de Wit (1978), adjusted for limitations due to simulated drought stress and N deficiency. Crop development is regulated by a thermal index adjusted for photoperiodic and vernalisation effects depending on the crop specie's inherent biology (Brisson et al., 1998b). Brisson et al. (1998a) adapted the original STICS model to simulate banana growth by calibrating model parameters describing leaf and root growth dynamics as well as those for phenological transitions against observations in a Tillage × Irrigation experimental banana crop under the tropical conditions of the French West Indies. They also modified

the dynamics of N leaching to match those observed under the tropical soils. However, the adapted STICS model does not simulate the self-ratooning nature and phenological heterogeneity of established highland banana cropping systems.

Tixier et al. (2004) developed the SIMBA-POP model, which simulates the self-ratooning nature and phenological heterogeneity of banana. Simulated at field level, the model stratifies the banana plant population into two chains of interlinked cohorts. One cohort chain is for pre-flowered and another for flowered plants in a given simulation time step. Development is driven by thermal time up to a certain threshold heat sum beyond which stochastic laws governed by a log-normal function determine which plants within a cohort advance to flowering and harvest stages (Tixier et al., 2004). The stochastic laws are also used to estimate the number of suckers selected to repeat the development cycle besides those that fail to advance to the next cohort in each time step. The primary output from SIMBA-POP is number of plants at each phenological stage. From this output, frequencies of flowering and harvest can be estimated, and hence the number of bunches harvested per week over time in a simulation run can be predicted (Tixier et al., 2004). SIMBA-POP is a robust bio-economic decision support tool in market-oriented banana production. However, the unit of analysis in SIMBA-POP is a cohort, rather than an average plant. This restricts the amount of information that can be deduced from heuristic exploration of plant level growth and yield formation processes in response to eco-physiological and management factors.

1.4.   Goal and research questions

This thesis focuses on highland banana crop response to drought stress, K and N deficiencies with a long-term aim of contributing to a decision support tool for crop water, K and N management across pedo-climatic zones of the Great Lakes region of Africa. It addresses the following Research Questions:

1. To what extent does drought stress contribute to the yield gap in highland bananas?

2. Are the effects of drought stress, K and N deficiency in highland bananas on dry matter accumulation and yield formation over a crop cycle additive?

3. Do highland bananas shift dry matter allocation between above- and below-ground biomass structures in response to drought stress, K and N deficiency in an additive manner?

4. What is the relative contribution of highland banana physiological *vis-à-vis* morphological components towards mitigation of relative growth rate decline in response to drought stress, K and N deficiency?

5. Do highland bananas flower at the same physiological age regardless of site or growing conditions in terms of water, K and N supply?

6. To what extent does mulch mitigate highland banana yield gap due to drought stress, assuming no limitation from K and N deficiency?

1.5.   Thesis outline and overview of study approaches

A survey of individual plants from existing farmers' fields, on-farm field experiments and on-station field/screen house experiments, were used to address Research Questions 1 to 5, which informed development of a model that was used to address Research Question 6. Chapter 2 addresses Research Question 1, placing the drought stress constraint into perspective. Boundary line analysis was used to quantify the reduction in relative bunch weight per unit decrease in cumulative rainfall received within 12 months to harvest. Cumulative rainfall received 12 months to harvest was chosen to cover the period just before flowering, which was assumed to be crucial for yield formation. However, this excluded the early phenological stages, which may also be crucial for plant development and yield formation. This omission was catered for in the approach used for addressing Research Questions 2 and 3 in Chapter 3.

The cumulative rainfall received in 365 days from sucker emergence was used to group the plants into two categories *viz.* those that experienced 'Wet' and those that experienced 'Dry' conditions within the first year of growth. These categories were factored into the analysis for answering Research Questions 2 and 3 in Chapter 3. However, the one-year duration chosen for summing up rainfall in Chapters 2 and 3 may have been too long to detect short term drought stress effects on growth. Chapter 4 was thus based on individual plant growth monitoring, with observations taken at approximately 4 week-intervals. Therefore, the cumulative rainfall received in the 28-day period preceding a growth parameter data collection event was used to group the plants into 'Wet' and 'Dry' categories for a given growth interval, which was then factored into the analysis for answering Research Question 4 in Chapter 4. Research Question 5 was also addressed in Chapter 4, based on site-specific boundary line analysis of physiological age at flowering as a function of total dry matter per plant at flowering.

Drought stress, as a very important overriding constraint, was the starting point for the modelling work in this thesis. A soil water balance module, whose parameterisation and sensitivity analysis are described in Chapter 5, was built. The soil water balance module was linked to a light interception and utilisation-based (LINTUL) potential growth model for highland banana (Nyombi, 2010) as described in Chapter 6 where the water-limited highland banana growth and yield are simulated. The linked model was then used to address Research Question 6 in Chapter 6. Improvements to the model to include the effects of K and N limitation as a decision support system tool for water, K and N management in highland banana cropping system are discussed in Chapter 7.

CHAPTER TWO

2.0.   Drought is a major yield loss factor for rain-fed East African highland banana

Abstract

Drought stress has been identified among the production constraints of East African highland bananas (*Musa* spp., AAA-EA genome) without any supportive quantitative data. This study uses data from three on-station fertilizer trials (5–6 crop cycles) in central and south-western Uganda to quantify the effect of drought stress on banana production and explore possible interactions with nutrient availability. Production data were collected on individual plant basis from 1996 to 2002 in one trial and from 2004 to 2009 in two trials. Cumulative rainfall in the 12 months before harvest (CRF_{12}) was computed per plant from daily rainfall measurements. Average bunch weight ranged from 8.0 to 21.9 kg between trials and cycles and was 8–28% less in dry ($CRF_{12} \leq 905$ mm) than in normal ($905 < CRF_{12} \leq 1365$ mm) rainfall periods. Linear relations were observed between CRF_{12} and maximum bunch weight over the whole range of observed CRF_{12} (500 – 1750 mm), whereby every 100 mm decline in rainfall caused maximum bunch weight losses of 1.5 – 3.1 kg or 8 – 10%. Optimum annual rainfall for East African highland bananas may thus be well above 1200 – 1300 mm yr^{-1}. Relative drought-induced yield losses were independent of soil fertility. Absolute losses on fertile/fertilized soils were similar to those recorded in well fertilized irrigation studies in Latin America. Our study suggests that drought-induced yield losses in areas of the East African highlands with annual rainfall < 1100 mm are perhaps as high as 20 – 65% compared with the wetter areas in this region. To improve productivity of smallholder banana farmers in Africa, more attention should be given to research geared towards improved water/drought stress management.

Keywords: *Banana, Boundary line analysis, Drought stress, Physiology, Soil fertility, Uganda*

2.1.   Introduction

East African highland bananas (*Musa* spp., AAA-EA genome; hereafter referred to as highland banana) are an important food and cash crop for more than 30 million people in East Africa (Karamura et al., 1998), where bananas contribute, on average, 16 to 31% of total calorie intake (Abele et al., 2007). With average observed farmer yields ranging between 10 and 20 t ha^{-1} yr^{-1} and maximum observed farmer yields exceeding 60 t ha^{-1} yr^{-1}, the gap between attainable and actual yields is often large (Bouwmeester et al., 2009; Wairegi et al., 2010). Scientists and farmers variously attribute the observed gap to low soil fertility, pests and diseases, poor crop management and drought stress (e.g. Bekunda and Woomer, 1996; Gold et al., 1999; Bagamba, 2007). It is essential to understand the importance of the various production constraints to guide research efforts and development programmes towards banana production improvement. Several studies (e.g., Bananuka et al., 1999; Speijer et al., 1999; Zake et al., 2000; Gold et al., 2004; Murekezi, 2005) attempted to quantify individual production constraints, but due to their limitations (few fields, single visits) only present a snapshot picture of reality, whereas production constraints may vary considerably in space and time and may interact (Fermont et al., 2009; Wairegi et al., 2010).

Having a shallow rooting system and a permanent green canopy, bananas are thought to require an abundant and constant supply of water for optimal production (Robinson, 1996). Consequently, it is estimated that more than two-thirds of the bananas grown world-wide for export are irrigated (Carr, 2009). On the contrary, highland banana production is completely rain-fed. Rainfall in the major banana producing areas of this region has a bimodal pattern and averages 900 – 1100 mm yr^{-1} in much of south-western Uganda, eastern Rwanda and the western Kagera region in Tanzania. The rainfall increases to above 1400 mm yr^{-1} in the high altitude areas close to the Albertine rift, Mt. Elgon, and some patches bordering Lake Victoria in Uganda (Fig. 2.1). However, with a reported annual rainfall span of 600 – 2700 mm yr^{-1}, variation between years and sites is considerable (Bouwmeester et al., 2009). Hegde and Srinivas (1989) report estimates of evapotranspiration rates for banana ranging from 1200 to 2690 mm yr^{-1}, depending on climatic conditions and management. Purseglove (1985) and Robinson (1996) report similar values; a consumptive water use of 1300 mm yr^{-1} or 3 – 6 mm d^{-1} for optimal production. This is an indication that drought stress may limit banana production in large parts of East Africa. Wairegi et al. (2010) found that drought stress was the primary yield constraint in a quarter of studied farmer fields in Southwest Uganda. Farmers in Rwanda,

Burundi and Eastern DRC identified drought stress as the second most important constraint to production, following declining soil fertility (Murekezi and van Asten, 2008; Bouwmeester et al., 2009). Climate change, which is predicted to affect rainfall distribution patterns with possibly more intense dry spells in East Africa (Hulme et al., 2001), may further increase the impact of drought stress on banana production.

Drought triggers signals from the roots to the leaves, which induce closure of stomata, allowing the banana to remain highly hydrated, but reducing carbon assimilation and therefore yield (Turner et al., 2007). Expanding tissues such as emerging leaves and growing fruits are among the first to be affected. Considerable research has been conducted in the broad field of banana irrigation (Robinson and Alberts, 1986). Little to no attention has been given to quantifying the effects of drought stress in rain-fed highland banana systems. Highland bananas are generally cultivated on Ferralsols, Acrisols and Nitisols, though pockets of Andosols are found along the Albertine Rift (Zake et al., 2000). Foliar nutrient concentrations differ considerably between sites (CIALCA, 2008), indicating that nutrient stresses may be highly variable. Metcalfe and Elkins (1984) report that for most grain crops optimal fertilization decreases crop water requirements by 20%. Studies on the interactions between water and nutrient stresses for banana are scarce. Baiyeri (1996) suggests that the use of N fertilization enhanced water use efficiency of bananas. However, Hegde and Srinivas (1989) found no significant interaction between N application rate and water use efficiency in bananas. They explained that dry matter increased in the same proportion with N input as with increase in water uptake, thus keeping water use efficiency constant across N input rates. Lahav and Kalmar (1988) also reported that water use increased upon N application. Bhattacharyyaa and Madhava Raoa (1985) found that banana plants that received 10 t ha^{-1} of banana trash mulch had an external water use efficiency of $30 - 40\%$ higher than plants without soil cover under different irrigation regimes. This may suggest a higher water use efficiency for fertilized plants that produce more self-mulch resulting in a better soil cover. Cooper et al. (1987) showed that fertilizer application in barley under rain-fed conditions resulted in large increases in water use efficiency, but that this was only partially due to improved transpiration efficiency and largely due to reduced soil evaporation arising from increased soil shading by the canopy.

We hypothesize that drought is an important production constraint to rain-fed highland banana production. To investigate this hypothesis we analysed data from three on-station trials (5–6 crop cycles) from central and south-western Uganda. Our specific objectives

were (i) to quantify drought-induced yield losses of highland banana and (ii) to explore whether drought-induced yield losses are influenced by soil fertility status and fertilizer input.

2.2. Materials and Methods

2.2.1. Experimental site characterisation

Data from three medium-term fertilizer experiments (5 − 6 crop cycles) were used to quantify the effect of cumulative rainfall on banana production in Uganda. The trials were installed on research farms in Mbarara (0°33′ S, 30°36′ E, 1380 masl) and Ntungamo (0°54′ S, 30°15′ E, 1405 masl) in south-western Uganda, and in Kawanda (0°25′ N, 32°31′ E, 1156 masl) in central Uganda (Fig. 2.1). The climate at the three sites is typical for much of the banana growing areas in the mid-altitude East African highlands; mean daily minimum and maximum values range from 13 to 17 °C and 26 to 27 °C, respectively and temperatures are fairly constant throughout the year (Okech et al., 2004; Nyombi et al., 2010). Rainfall patterns are bimodal with dry spells from June to August and December to February (Fig. 2.2). Reference evapotranspiration at Kawanda for the period 1997–1999 averaged 3410 mm as compared with a total rainfall of 2930 mm during this period (Ssali et al., 2003). Average annual rainfall during the trials was considerably lower in Mbarara and Ntungamo (1018 and 1019 mm, respectively) than in Kawanda (1310 mm; Table 2.1). Nonetheless, annual rainfall varied strongly between years in all sites. It ranged from 678 mm (1999) to 1230 mm (2000) in Mbarara, from 818 mm (2007) to 1319 mm (2006) in Ntungamo and from 1014 mm (2005) to 1460 mm (2007) in Kawanda. The CRF_{12} values varied significantly (P < 0.001) between cycles in all sites and ranged from 767 mm for cycle 3 in Mbarara to 1538 mm for cycle 3 in Kawanda (Table 2.2). In all sites, less than 10 extreme rainfall events (>50 mm in 24 h) were recorded over the duration of the trials. The Mbarara trial experienced more pronounced drought periods than the Ntungamo and Kawanda trials: 31% of the trial duration could be considered as dry ($693 \leq CRF_{12} < 905$ mm), whereas 19% could be considered as very dry ($CRF_{12} < 693$ mm). The lowest CRF_{12} values during the trial in Ntungamo and Kawanda were 770 and 920 mm, respectively.
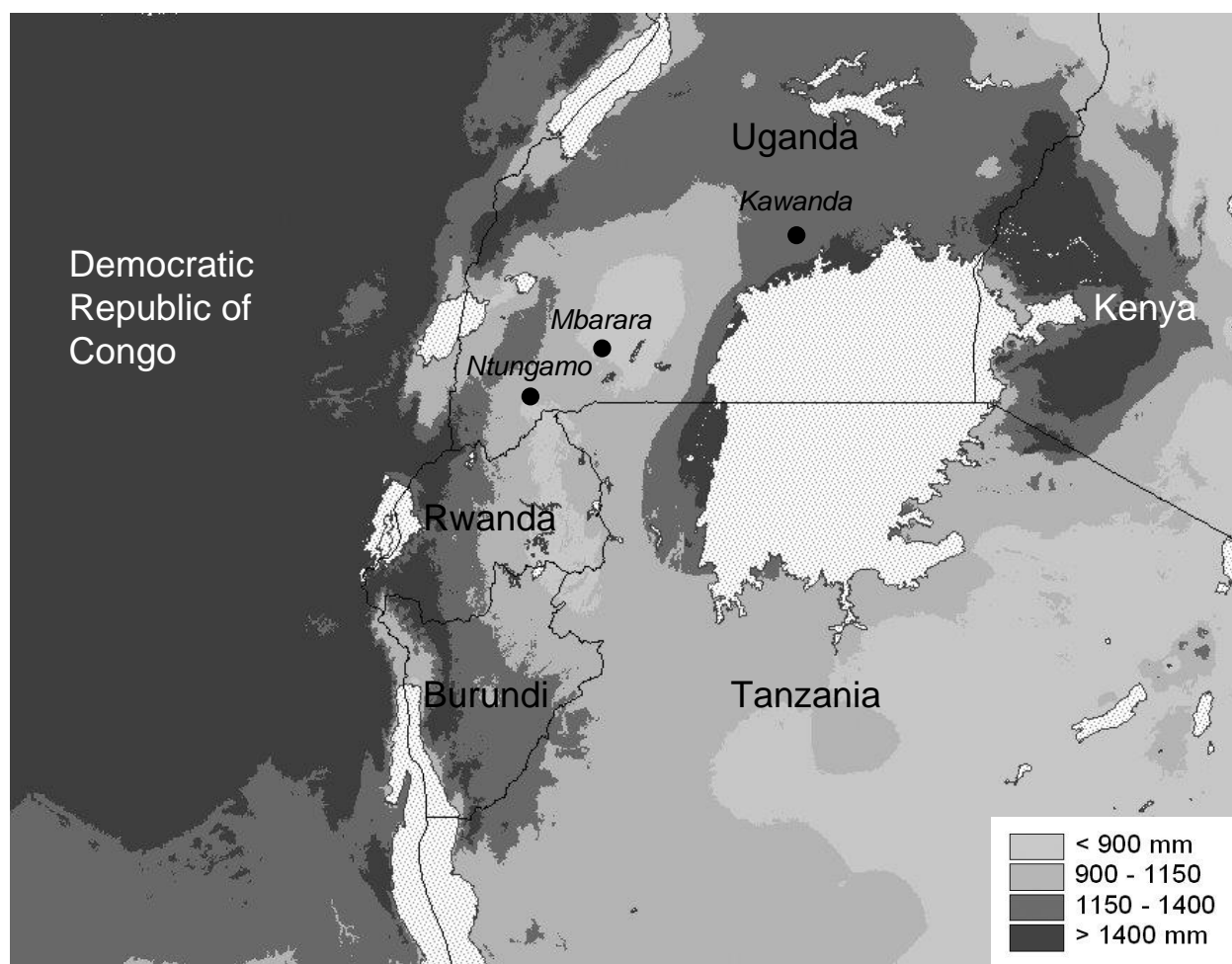
Fig. 2.1. Annual rainfall (mm) in the East African highlands.

Circles indicate the location of the three research sites (Mbarara, Ntungamo and Kawanda); Data adapted from Hijmans et al. (2005).

Table 2.1: Main soil characteristics and annual rainfall for the 1997–2002 Mbarara trial, the 2005–2009 Ntungamo trial and 2005–2009 Kawanda trial.

	Soil characteristic						
	pH water (1:2.5)	OM (%)	Total N (g kg^{-1})	Extractable P mg kg^{-1}	Exchangeable K (cmol$_+$ kg^{-1})	Clay (%)	Rainfall (mm yr^{-1})
Mbarara	4.3	2.5	0.14	5.2	0.50	19	1019
Ntungamo	4.9	0.6	0.09	2.5	0.14	23	1018
Kawanda	5.6	3.3	0.13	2.3	0.53	36	1310
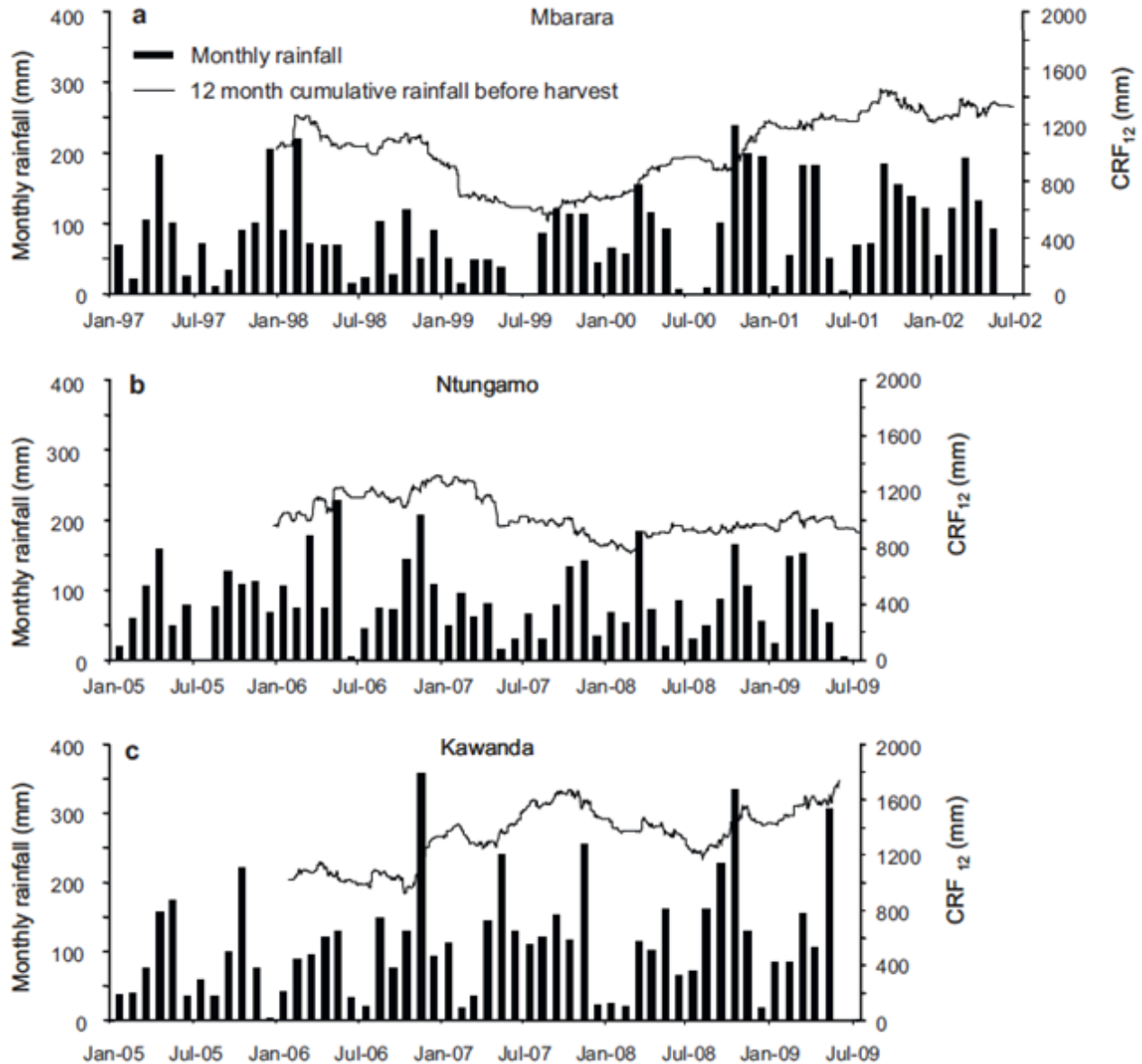
Fig. 2.2. Monthly rainfall and cumulative rainfall 12 months before harvest (CRF$_{12}$) in the Mbarara, Ntungamo and Kawanda trial.

Slopes at all sites are gentle to moderate (4 – 15%) and soils are classified as Ferralsols (Okech et al., 2004; Nyombi et al., 2010). Composite soil samples were taken at planting; 4 sub-samples per plot at 0–15 cm depth in the Mbarara trial and 5 sub-samples per plot at 0–16 cm depth in the Ntungamo and Kawanda trials. Samples were oven-dried at 40–50 °C, ground to pass through a 2 mm sieve and analysed for pH, organic matter, total N (Kjeldahl method), Available P (Mehlich-3) and Exchangeable K (ammonium acetate extraction) following Okalebo et al. (2002). Soil texture was determined using the

hydrometer method. Soil fertility varied between trials, with those at Kawanda and Ntungamo being the most and least fertile, respectively (Table 2.1). All trials showed strong variation in soil fertility parameters between blocks and plots, often (but not always) following the slope. This was most apparent from the exchangeable K values that ranged between blocks from 0.33 to 0.63 $cmol_+$ kg^{-1} in Mbarara, from 0.12 to 0.18 $cmol_+$ kg^{-1} in Ntungamo, and from 0.39 to 0.68 $cmol_+$ kg^{-1} in Kawanda (data not shown). Additional information on the trials and their sites can be found in Nyombi et al. (2010) and Okech et al. (2004).

2.2.2. Trial set up and management

In all sites, pest-free tissue-cultured plants of popular highland cooking banana cultivars were used. The cultivar 'Enyeru' was used in Mbarara, while 'Kisansa' was used in Ntungamo and Kawanda. Both trials were planted at a spacing of 3m × 3m, resulting in a plant density of 1111 mats ha^{-1}. Excess suckers were removed to maintain mat densities over time. Dead leaves and crop residues were chopped and spread as surface mulch. The Mbarara trial (Trial 1) was planted on fallow land in October 1996. The first bunches were harvested in January 1998 and data collection lasted up to June 2002, spanning 6 crop cycles. The trial was installed to study the effect of inorganic fertilizer and weevil (*Cosmopolites sordidus* Germar) control on crop performance (Okech et al., 2004). Weevil damage was low and control measures had no significant effect. We therefore only consider fertilizer application in this paper; a control without fertilizer versus 100, 50, and 100 kg $ha^{-1}yr^{-1}$ of N, P and K, respectively. A randomised complete block design (RCBD) with four replications was used, whereby blocks followed the contour lines. Each plot consisted of 7 × 7 mats and plots were separated by 20-m wide grass strips to minimise fertilizer run-off/run-on effects. Nitrogen was applied as Urea in 4 splits per year. Potassium was applied as muriate of potash (MOP) in 2 splits per year, whereas P was applied as triple superphosphate (TSP) once a year.

The Ntungamo and Kawanda trials (Trials 2 and 3, respectively) were planted in October to December 2004 on fields with no recent banana history. The first bunches were harvested in February and March 2006; data collection lasted up to May and July 2009 for Kawanda and Ntungamo, respectively, covering 3–5 crop cycles. The trials were installed to study the effect of N, P, K, micro-nutrients and weevil control on crop performance. Crop response for the Ntungamo and Kawanda trials to fertilizer inputs were reported in Nyombi et al. (2010). In both Kawanda and Ntungamo, K had by far the largest impact on fresh bunch weight while weevil control had no effect (data not shown).

For this paper, we therefore used six treatments with contrasting K fertilizer use in the data analysis. The three treatments without K included: (T1) 0-0-0 kg ha^{-1} yr^{-1} N-P-K, no micronutrients, no weevil control; (T2) as T1 but with weevil control and (T3) 400-50-0 kg ha^{-1} yr^{-1} N-P-K, with micronutrients and weevil control. The three treatments with full K rate (600 kg ha^{-1} yr^{-1}) included (T4) 150-50-600 kg ha^{-1} yr^{-1} N-P-K, with micronutrients and weevil control; (T5) as T4 but with 400 kg ha^{-1} yr^{-1} N and (T6) as T5 but without weevil control. Plots with weevil control were included to increase the number of observations available for further analysis. Magnesium was applied at a rate of 60 kg ha^{-1} yr^{-1}. Micronutrients were applied at rates of 6, 0.6 and 1 kg ha^{-1} yr^{-1} of Zn, Mo and B, respectively. Weevil control was done with Dursban (active ingredient chlorpyrifos). A RCBD design with four repetitions was used, whereby blocks followed the contour lines and each plot consisted of 5×7 mats. Nitrogen was applied as Urea, K as MOP, P as TSP, Mg as magnesium sulphate and micro-nutrients as sodium molybdate, borax and zinc sulphate. The N and K were applied in 8 splits (4 times per rainy season), while P, Mg and the micro-nutrients were applied twice a year (at the start of each rainy season). Microbunds were installed between plots to prevent runoff/run-on. Details on management can be found in Nyombi et al. (2010).

2.2.3. Data collection

The inner twenty-five mats in each plot of the Mbarara trial and inner fifteen mats in each plot of the Ntungamo and Kawanda trials were monitored on an individual plant basis. Flowering and harvesting dates were recorded for each plant. Banana bunches were completely removed at horticultural maturity (i.e. just before ripening). In all trials, fresh bunch weight (fingers plus peduncle, with peduncle cut-off at the point where it crosses the petiole bases of the two last fully emerged leaves) was recorded in the field. In the Ntungamo and Kawanda trials, fresh finger weight and the number of fingers per bunch were also recorded at harvest time. Broken, toppled, or stunted plants, plants without a bunch, and plants with incomplete yield data records were excluded from the analysis. Complete yield data were available for 59, 34 and 63% of the observed plants in Mbarara, Ntungamo and Kawanda trial, respectively. Strong winds caused considerable toppling of plants in all trials, while many mats had not yet completed cycle 6 in Mbarara, cycle 5 in Kawanda and cycle 4 and 5 in Ntungamo by the end of data collection.

The absolute fresh bunch weight (ABW) was used to calculate the relative bunch weight (RBW) as the ratio of the ABW to the 95 percentile ABW. The RBW was calculated to

study the relative yield decrease as a function of drought and nutrient stresses. Rainfall data were collected daily using a rain gauge in each site. The cumulative rainfall in the 6, 9, 12 and 15 months prior to the date of harvest (CRF_6, CRF_9, CRF_{12} and CRF_{15}) and in the 3, 6 and 9 months prior to the date of flowering ($CRFF_3$, $CRFF_6$ and $CRFF_9$) were computed for each bunch harvested. Very dry, dry, normal and wet periods were determined on the basis of the combined rainfall records, using 10, 20 and 80 percentile rainfall values (i.e. 693, 905 and 1365 mm) as lower cut-off points.

2.2.4. Analytical approach

Analysis of variance (ANOVA) was performed to test for the effect of cycle, K fertilization and/or rainfall on the ABW, time between two consecutive harvests, number of fingers per bunch and average finger weight. Non-parametric tests for two or more independent samples using the Mann–Whitney U or Kruskal Wallis test, respectively, were performed if variables could not be normalized by transformation. Statistical analyses were carried out using SPSS for Windows (version 10.0).

The boundary line approach (Webb, 1972) was used to further detail the effect of cumulative rainfall on ABW and RBW for each trial. This approach has been used to determine yield functions in order to establish optimum soil and plant nutrient levels (e.g., Evanylo and Summer, 1987) or to rank crop growth constraints (e.g., Casanova et al., 1999; Fermont et al., 2009; Wairegi et al., 2010). Boundary lines were fitted regression lines through the upper points of a data cloud whereby ABW or RBW was the dependent variable and cumulative rainfall the independent variable. It is assumed that the upper boundary points subsequently represent the maximum value of the dependent variable that can be achieved at a given level of the independent variable. Boundary points were selected using the algorithm (BOLIDES) developed by Schnug et al. (1996). Pearson correlations of ABW with CRF_6, CRF_9, CRF_{12} and CRF_{15} were calculated for all trials. Absolute bunch weight was most consistently and positively associated with CRF_{12}. Therefore, for each block and K fertilizer level (without vs. with K) in the three trials, boundary lines were defined that described the relation between CRF_{12} and maximum ABW and RBW. Maximum bunch weights did not approach a clear plateau value within the range of rainfall observations in the large majority of cases; i.e. it could normally be expected that bunch weights no longer increase once a certain rainfall threshold is achieved. Hence, linear functions and not sigmoid curves (e.g., Fermont et al., 2009) were fitted through the boundary points. Bunch weight observations below the boundary line suggest that constraints other than rainfall (i.e. CRF_{12}) contribute to

limiting plant production. Within each trial, we tested for each block whether K fertilization affected the gradients of the boundary lines using simple linear regression with groups function in GenStat Discovery.

For each trial, the mean relation between CRF_{12} and maximum dependent variable (either ABW or RBW) was determined by averaging all available boundary points for each step of 20-mm CRF_{12}. Separate relations were determined for the two K fertilizer treatments (with and without K). Two-way ANOVA was applied using GenStat (Payne et al., 2003) to compare if ABW and RBW boundary line gradients varied between trial sites and fertilizer treatments. In newly planted banana fields in the East African highlands, production generally increases during the first few cycles due to the build-up of biomass and subsequent transfer of resources from mother plant to follower suckers (e.g., Nyombi et al., 2010), which gives the suckers a better start during early growth. As cycle 1 bunch weights were significantly ($P < 0.001$) lower than the overall average, cycle 1 data were omitted from the analyses of the effect of rainfall on banana production.

2.3. Results

2.3.1. Effect of rainfall and K fertilisation on banana production

The average fresh bunch weight between sites ranged from 12.1 kg in Kawanda to 14.9 kg in Ntungamo and from 8.4 for Cycle 3 in Mbarara to 21.9 kg for Cycle 5 in Ntungamo ($P < 0.001$; Table 2.2). In all sites, ABW was significantly ($P < 0.01$) influenced by crop cycle. The number of fingers per bunch varied from 96 in Kawanda to 109 in Ntungamo ($P < 0.001$), whereas average finger weight ranged from 113 g in Ntungamo to 115 g in Kawanda (data not shown). The average time between two consecutive harvests on a given mat varied from 292 d in Mbarara to 263 and 257 d in Ntungamo and Kawanda, respectively ($P < 0.001$) and also varied significantly between cycles ($P < 0.001$) in all sites (Table 2.2). With 1.5 bunches ha^{-1} d^{-1} being harvested during dry periods versus 2.8 bunches ha^{-1} d^{-1} during normal rainfall periods ($905 \leq CRF_{12} < 1365$ mm), the Mbarara trial produced 46% less bunches in dry than in normal rainfall periods (Table 2.3). In very dry periods bunch production was further reduced to 0.7 ha^{-1} d^{-1}, or a loss of 71% compared with normal rainfall periods. In Ntungamo, dry weather conditions did not affect the number of bunches harvested, but absence of K fertilizer resulted in 61% less bunches (Table 2.2).

Table 2.2: Cumulative rainfall 12 months before harvest (CRF$_{12}$), absolute fresh bunch weight (ABW) and time between two consecutive harvests (H-H) for highland banana in the 1997–2002 Mbarara trial, 2005-2009 Ntungamo trial and 2005-2009 Kawanda trial by cycle and K fertilization.

Factor	Level	Mbarara				Ntungamo				Kawanda			
		n	CRF$_{12}$ (mm)	ABW (kg)	H-H (days)	n	CRF$_{12}$ (mm)	ABW (kg)	H-H (days)	n	CRF$_{12}$ (mm)	ABW (kg)	H-H (days)
Cycle	2	257	998	14.4	285	213	986	16.6	242	264	1189	10.5	229
	3	140	767	8.4	323	150	900	19.3	284	271	1538	13.2	275
	4	247	1066	11.4	334	46	962	20.9	281	251	1351	13.1	259
	5	313	1289	15.2	290	23	987	21.9	275	119	1476	11.6	268
	6	161	1292	21.1	264	-	-	-	-	-	-	-	-
K Fertilizer	No K	526	1104	12.0	300	122	951	7.2	262	425	1365	10.6	259
	With K	593	1098	16.0	286	310	954	22.6	264	480	1387	13.6	255
Source of variation													
Cycle			<0.001	<0.001	<0.001		<0.001	<0.001	<0.001		<0.001	<0.001	<0.001
K Fertilizer			ns	<0.001	<0.010		ns	<0.001	ns		ns	<0.001	ns

No K = 0-0-0 kg ha^{-1} NPK in the Mbarara trial and 0-0-0 or 400-50-0 kg ha^{-1} NPK in the Ntungamo and Kawanda trials; K Fertilization consisted of 100-50-100 kg ha^{-1} NPK in the Mbarara trial and 150-50-600 or 400-50-600 kg ha^{-1} NPK in the Ntungamo and Kawanda trials.

Table 2.3: Effect of rainfall and potassium fertilizer on absolute fresh bunch weight (ABW), number of fingers per bunch and weight per finger for cycles 2 to 6 of East African highland banana in the 1997-2002 Mbarara trial, 2005-2009 Ntungamo trial and the 2005-2009 Kawanda trial.

Rainfall class	K fertilizer	†Mbarara n	Prod. (t ha⁻¹)	ABW (kg)	Ntungamo n	Prod. (t ha⁻¹)	ABW (kg)	Fingers	Finger weight (g finger⁻¹)	Kawanda n	Prod. (t ha⁻¹)	ABW (kg)	Fingers	Finger weight (g finger⁻¹)
Very dry	No K	37	0.7	9.3 ± 4.5	-	-	-	-	-	-	-	-	-	-
	With K	54	1.0	11.5 ± 3.2	-	-	-	-	-	-	-	-	-	-
Dry	No K	54	1.5	9.4 ± 4.5	22	0.8	4.4 ± 2.7	57 ± 19	111 ± 06	-	-	-	-	-
	With K	55	1.5	11.6 ± 4.3	60	2.2	21.4 ± 8.4	115 ± 27	113 ± 08	-	-	-	-	-
Normal	No K	413	2.7	12.4 ± 6.3	100	0.8	7.8 ± 4.5	76 ± 28	110 ± 06	206	3.2	9.8 ± 3.5	85 ± 22	107 ± 28
	With K	455	2.9	16.9 ± 6.9	250	2.2	22.9 ± 7.1	125 ± 28	114 ± 15	195	3.0	12.6 ± 4.2	93 ± 25	124 ± 32
Wet	No K	22	2.1	16.2 ± 7.8	-	-	-	-	-	219	2.2	11.3 ± 4.9	95 ± 27	106 ± 29
	With K	29	2.8	19.2 ± 7.3	-	-	-	-	-	285	2.9	14.2 ± 5.2	107 ± 29	121 ± 40
Source of variation														
Rainfall class (R)			<0.001			<0.001	<0.001	<0.001	ns		<0.001	<0.001	<0.001	ns
K Fertilizer (K)			<0.001			<0.001	<0.001	<0.001	<0.05		<0.001	<0.001	<0.001	<0.001
R × K			ns			ns	ns	ns	ns		ns	ns	ns	ns

Rainfall classes are defined using 10, 20 and 80 percentile values of cumulative rainfall received 12 months to harvest (CRF_{12}) in the pooled dataset as follows: 'Very dry' ($CRF_{12} < 693$ mm); 'Dry' ($693 \leq CRF_{12} < 905$ mm); 'Normal' ($905 \leq CRF_{12} < 1365$ mm), and; 'Wet' ($CRF_{12} \geq 1365$ mm). 'No K' fertilizer = 0-0-0 kg ha⁻¹ NPK in the Mbarara trial and 0-0-0 or 400-50-0 kg ha⁻¹ NPK in the Ntungamo and Kawanda trials; With K Fertilizer consisted of 100-50-100 kg ha⁻¹ NPK in the Mbarara trial and 150-50-600 or 400-50-600 kg ha⁻¹ NPK in the Ntungamo and Kawanda trials. †No records on number of fingers per bunch and fresh weight per finger taken. Prod. = number of bunches harvested

Table 2.4: Effect of K Fertilizer[a] and K availability in the soil (0–16 cm) on the boundary line gradients[b] for absolute and relative bunch weight[c] versus 12 months' cumulative rainfall before harvest (CRF[12]) of AAA-EA banana for cycles 2–6 in the 1997–2002 Mbarara trial, the 2005–2009 Ntungamo trial and the 2005–2009 Kawanda trial.

Block	K-fertilizer	Mbarara K soil (cmol+ kg^{-1})	n	ABW slope	RBW slope	Ntungamo[d] K soil (cmol+ kg^{-1})	n	ABW slope	RBW slope	Kawanda K soil (cmol+ kg^{-1})	n	ABW slope	RBW slope
1	No K	0.66	142	0.029a	0.0010a					0.62	111	0.021a	0.0011a
	With K	0.61	159	0.030a	0.0010a	0.19	88	0.021	0.0006	0.75	110	0.017a	0.0007b
2	No K	0.47	134	0.020a	0.0011a					0.59	105	0.015a	0.0009a
	With K	0.57	161	0.032b	0.0009a	0.05	80	0.026	0.0008	0.70	126	0.016a	0.0007a
3	No K	0.31	132	0.014a	0.0009a					0.35	96	0.011a	0.0007a
	With K	0.40	149	0.026b	0.0009a	0.13	60	0.035	0.0013	0.50	116	0.017b	0.0010b
4	No K	0.41	118	0.015a	0.0008a					0.32	113	0.013a	0.0009a
	With K	0.25	124	0.019b	0.0009a	0.13	82	0.029	0.0008	0.45	128	0.019b	0.0009a

[a] No K fertilization consisted of 0-0-0 kg ha^{-1} yr^{-1} NPK in the Mbarara trial and 0-0-0 or 400-50-0 kg ha^{-1} yr^{-1} NPK in the Ntungamo and Kawanda trials; With K Fertilization consisted of 100-50-100 kg ha^{-1} yr^{-1} NPK in the Mbarara trial and 150-50-600 or 400-50-600 kg ha^{-1} yr^{-1} NPK in the Ntungamo and Kawanda trials.

[b] See text for more details.

[c] Relative bunch weight was defined for each observation as absolute bunch weight over 95% percentile value.

[d] Too few observations (14–49) were available for unfertilized conditions in Ntungamo to determine boundary lines.

Means within same column for a given Block followed by different letters are significantly different at P < 0.05.

Drought stress significantly (P < 0.001) affected ABW and the number of fingers per bunch, but not finger weight (Table 2.3). In dry periods banana bunches harvested in Ntungamo were on average 8% (1.5 kg) lighter and contained 10% fewer fingers than in periods with normal rainfall. Bunch weights in Mbarara decreased on average by 17% (3.1 kg) from wet ($CRF_{12} \geq 1365$ mm) to normal rainfall periods, and by 28% (4.2 kg) from normal to dry periods, but did not decrease any further in very dry periods. Bunch weights in Kawanda decreased on average by 13% (1.7 kg) from wet to normal rainfall periods and contained 13% more fingers in a wet period. The number of fingers was positively associated with $CRFF_6$ in both the Ntungamo and the Kawanda trials (r = 0.24–0.36; P < 0.01; Fig. 2.3).
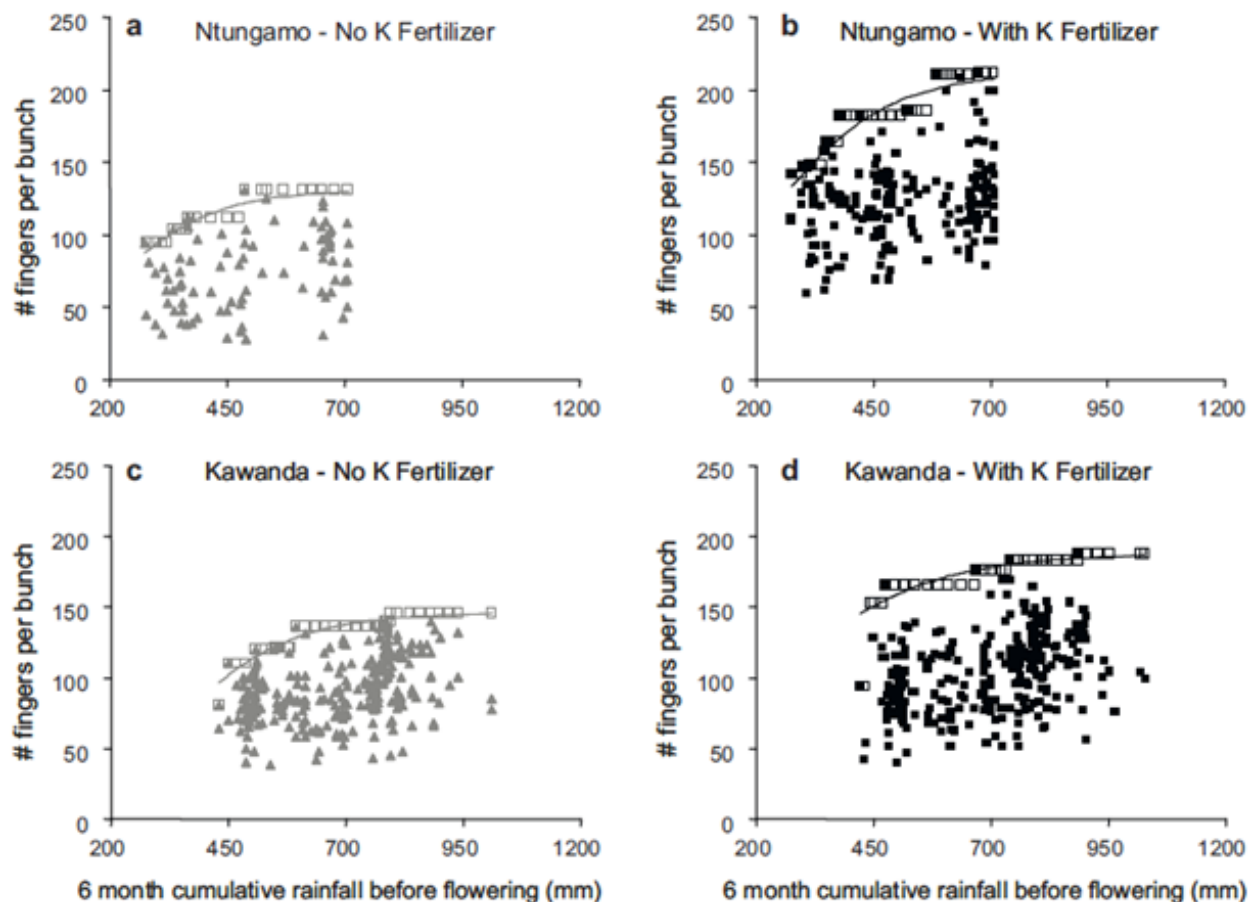

Fig. 2.3. Effect of cumulative rainfall 6 months before flowering ($CRFF_6$) on number of fingers per bunch of East African highland banana at Ntungamo and Kawanda without and with potassium fertilizer.

Lines indicate boundary lines while open squares symbolise boundary points. See text for details.

Sigmoid boundary lines, with plateaus starting between 650 and 800 mm, best described the maximum number of fingers obtained as a function of $CRFF_6$. No consistent trends were found for the effect of drought stress on time from planting/emergence to flowering, time from planting/emergence to harvest and time between two consecutive harvests (data not shown).

Application of K fertilizer significantly ($P < 0.001$) increased average bunch weight by 214% (15.4 kg) in Ntungamo, 33% (4.0 kg) in Mbarara and 28% (3.0 kg) in Kawanda (Table 2.2). It also increased the number of fingers per bunch by 71% in Ntungamo and by 12% in Kawanda ($P < 0.001$) and individual finger weight by 4% in Ntungamo and by 15% in Kawanda ($P < 0.05$; Table 2.3). In Ntungamo, K fertilisation reduced the time from planting/emergence to flowering and the time from planting/emergence to harvest by 44 and 34 days, respectively ($P < 0.01$; data not shown), but had no effect on time between two consecutive harvests (Table 2.2). In 20 out of 24 block $\times$ K fertilizer combinations, CRF_{12} was positively and significantly ($P < 0.05$ in 12 cases) correlated with ABW. Pearson correlations ranged from 0.11 to 0.58 in the Mbarara trial, from -0.06 to 0.43 in the Ntungamo trial and from -0.04 to 0.26 in the Kawanda trial.

The boundary lines that describe the relation between maximum ABW and RBW were linear and positively related to CRF_{12} over the entire cumulative rainfall range (500–1750 mm) for all blocks and K treatments (Fig. 2.4). Gradients of the boundary lines describing the relation between maximum ABW and CRF_{12} varied from 0.011 to 0.029 kg mm^{-1} between blocks and trials if no K fertilizer was applied, and from 0.017 to 0.035 kg mm^{-1} with K fertilizer application (Table 2.4). Gradients of the boundary lines describing the relation between maximum RBW and CRF_{12} varied from 0.07 to 0.11% mm^{-1} between blocks and trials if no K fertilizer was applied, and from 0.07 to 0.13% mm^{-1} with K fertilizer application (Table 2.4). Potassium fertilizer application significantly ($P < 0.05$) increased the gradients of the boundary lines for ABW observations in 5 out of 8 blocks, but did not affect the boundary lines for RBW observations in 6 out of 8 blocks (Table 2.4). Soil K test values were positively associated with the gradients of the boundary lines for ABW in the Mbarara trial ($P < 0.05$), but not in the Ntungamo and Kawanda trials (data not shown).
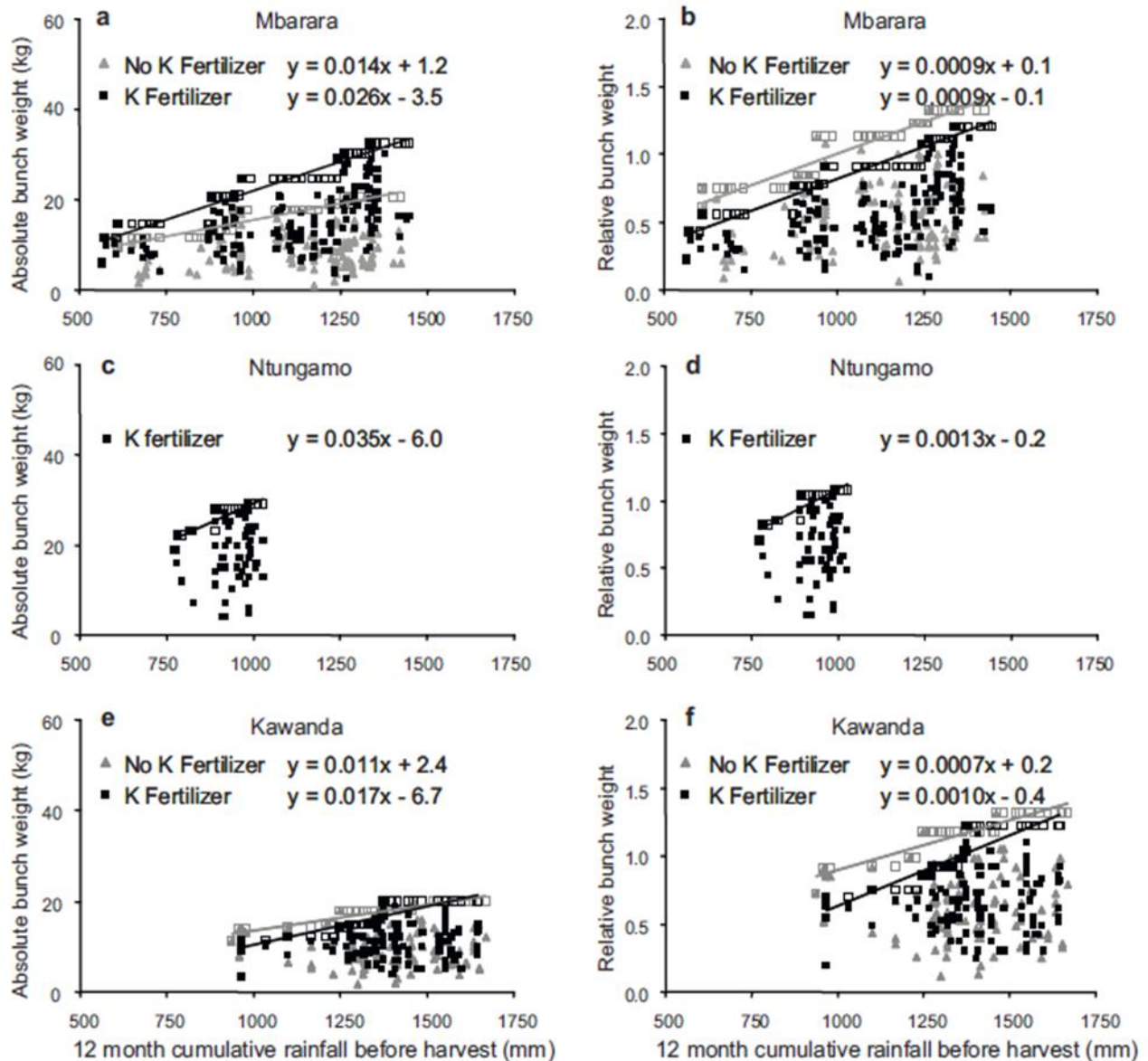
Fig. 2.4. Effect of cumulative rainfall 12 months before harvest (CRF_{12}) and potassium fertilisation on absolute and relative bunch weight of East African highland banana for cycles 2 to 6 in block 3 of the at Ntungamo and Kawanda without and with potassium fertilizer in the 1997-2002 Mbarara trial, the 2005-2009 Ntungamo trial and the 2005-2009 Kawanda trial.

Lines indicate boundary lines while open squares symbolise boundary points. See text for details.
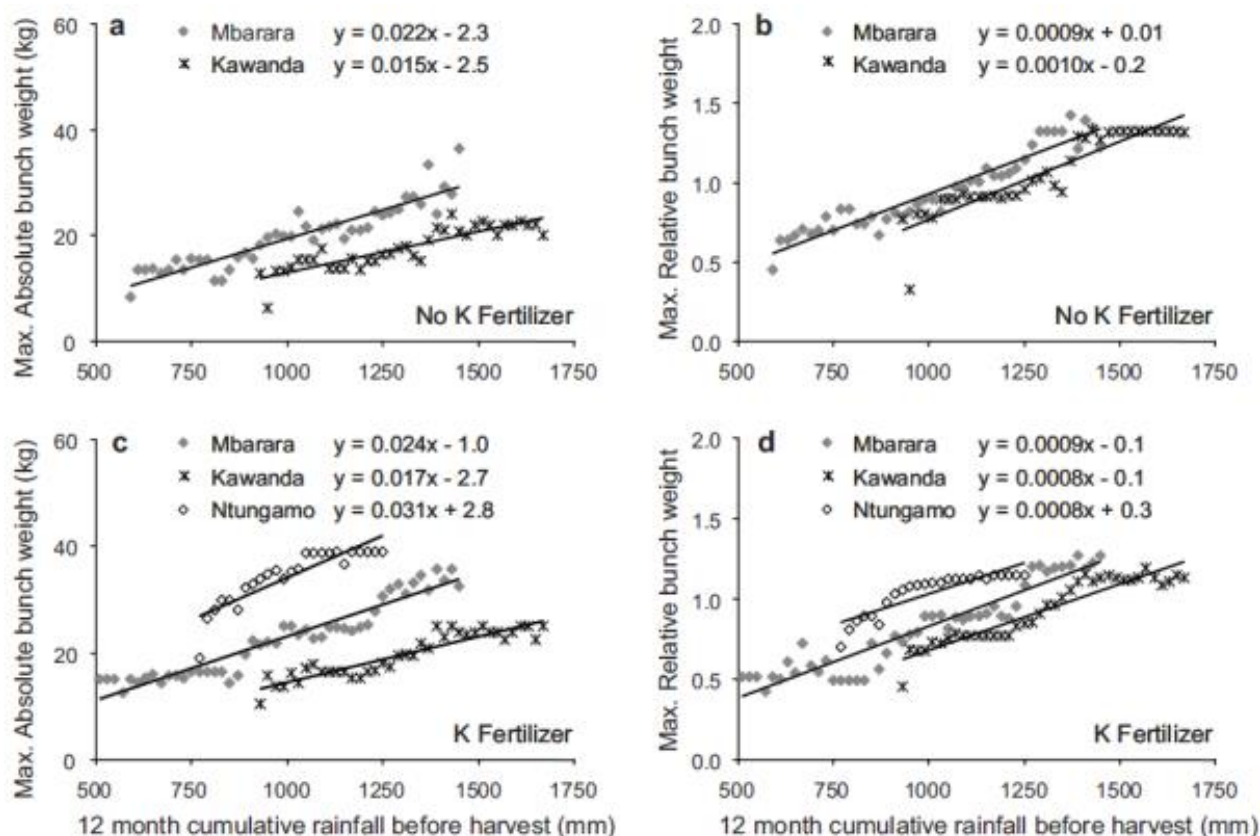
Fig. 2.5. Average relation between cumulative rainfall 12 months before harvest (CRF$_{12}$) and maximum absolute and relative bunch weight of East African highland banana without and with potassium fertilizer in the 1997-2002 Mbarara trial, the 2005-2009 Ntungamo trial and the 2005-2009 Kawanda trial.

Refer to text for details

Averaging the boundary lines per trial resulted in gradients of 0.015–0.022 kg mm^{-1} and 0.09–0.10% mm^{-1} between trials if no K fertilizer was applied, and gradients of 0.017–0.031 kg mm^{-1} and 0.08–0.09% mm^{-1} between trials with K fertilizer application for ABW and RBW, respectively (Fig. 2.5). Within locations, K fertilization affected neither the average gradients of the ABW nor the average gradients of the RBW boundary lines. The gradients of the average ABW boundary lines varied between locations (P < 0.05) unlike the average gradients of the RBW boundary. The average gradient of the RBW boundary lines was 0.09% mm^{-1} for the entire data set. The factors site, fertilizer, and site × fertilizer had no significant (P < 0.05) impact on this gradient.

2.4. Discussion

2.4.1. Variability in production

The observed range of average absolute bunch weights (8.4–21.9 kg; Table 2.2) would translate to average yields of 9–24 t ha^{-1} cycle^{-1}, if all mats had produced a bunch. These fall within the range of average farmer yields commonly reported in Uganda (Bagamba,

2007; Wairegi et al., 2010), but are lower than average farmer yields (18–63 t ha^{-1} cycle^{-1}) reported for other banana producing areas in the East African highlands (Bouwmeester et al., 2009), and are far below simulated potential yields of 100 t ha^{-1} cycle^{-1} for Uganda (Nyombi, 2010). Though annual rainfall was much higher in Kawanda than in Mbarara and Ntungamo (Table 2.1), absolute bunch weights in this site were lowest (Table 2.2). This may be related to a combination of relatively higher incidence of the fungal disease 'black sigatoka' and of high bulk densities (>1.5 g cm^{-3}) in the B-horizon (Nyombi, 2010). The latter would likely point to a limited exploration of the soil volume and restricted water and nutrient uptake, as banana roots are extremely sensitive to soil physical constraints (Delvaux, 1995).

2.4.2. Drought as a production constraint

The observed range in rainfall (Table 2.1) is representative for the banana producing areas in the central and eastern parts of the East African highlands and for dry to average years in areas located west of the Albertine Rift (Fig. 2.1). We used cumulative rainfall in the 12 months before harvest as an indicator of drought stress due to lack of data on available soil water storage. Runoff in our trials was low due to the use of contour bunds and retention ditches between plots. Leaching, however, may have been important after (rare) extreme rainfall events. Inherent to the bimodal rainfall distribution, banana production in our trials experienced two periods (1–3 months) of seasonal drought stress per year. Moreover, there is considerable variation in drought stress between years as shown from the large variation in CRF$_{12}$ over time. As plantations in the East African highlands often persist for long periods of time (5–100 years; Wairegi et al., 2010), drought stress will affect all growth stages across all plantations.

Drought stress consistently reduced both average bunch weight and maximum (or water-limited) bunch weight in all trials (Table 2.3 and Fig. 2.5). Average bunch weight in dry periods was 8–28% less than in normal rainfall periods. Within the observed cumulative rainfall range (500–1750 mm), we found linear relations between rainfall and maximum bunch weights in all trials, whereby every 100-mm decline in rainfall resulted in an average 8–10% loss in relative maximum bunch weight or an average 1.5–3.1 kg loss in absolute maximum bunch weight (Fig. 2.5). Similar linear relationships between production and water use were found in irrigation experiments by Young et al. (1985) in Hawaii and by Goenaga and Irizarry (1995, 2000) in two contrasting conditions in Puerto Rico. Production in these trials was likely only water limited, as NPK fertilizer and chemical weed control were judiciously applied and pressure from pests and diseases was

minimal. Young et al. (1985) observed that every 100-mm decline in evapotranspiration resulted in a yield loss of 3.1 t ha^{-1} for the plant crop (*Musa* spp. AAA genome, cv. Cavendish) and a yield loss of 2.6 t ha^{-1} for the first ratoon. Data from Goenaga and Irizarry (1995, 2000) were used to calculate that every 100-mm decrease in irrigation water resulted in a 2.5–2.7 kg and a 2.4–3.1 kg loss in absolute bunch weight in their two trials using Cavendish cultivars as well. The similarity between these findings and absolute maximum bunch weight losses in our fertilized plots, suggest that the observed relation may be valid for fertile/well fertilised plots in a wider range of agro-ecologies and banana types. Although the drought studies on Cavendish and highland bananas are all on triploid acuminata cultivars, caution has to be taken when extrapolating results within the AAA genome group given the diversity that exists within this group. Ude et al. (2002) suggested that more than one *M*. *acuminata* subspecies may be involved in the origin of different triploid AAA bananas. There is some evidence that *Musa* cultivars containing a balbisiana genome are more drought tolerant (Thomas et al., 1998).

The observed linearity between cumulative rainfall and water-limited production within the observed cumulative rainfall range (500–1750mm) suggests that, under the prevailing climatic conditions, East African highland bananas may have higher rainfall requirements than the 1200 mm yr^{-1} proposed by Doorenbos and Kassam (1979) for the humid tropics and the 1300 mm yr^{-1} proposed by Purseglove (1985) for bananas in general. This is confirmed by an irrigation experiment in central Uganda, where maintaining soil moisture around field capacity through daily irrigation increased yields from 28 to 40 t ha in the plant crop and from 29 to 59 t ha in the first ratoon (Bananuka, 2001). Annual rainfall in this experiment ranged from 1490 to 1540 mm and evapotranspiration was larger than rainfall in 4–6 months per year. Indirect evidence that drought stress affects banana production in Uganda is provided by several mulch trials. Mulching is a common management strategy to increase water availability to the plant by promoting infiltration of rainwater and reducing evaporation (McIntyre et al., 2000). A mulching trial (4.5 years) in central Uganda with an average rainfall of 1250 mm showed that a maize stover mulch plus a base fertilisation of 0-50-60 kg ha^{-1} yr^{-1} N-P-K resulted in 20–50% higher banana yields than fertilisation with 100-100-200 kg ha^{-1} yr^{-1} N-P-K only. This suggests that water availability limited production more than nutrients (Zake et al., 2000). A 13-months long mulching trial with 1620 mm rainfall showed that a maize stover plus grass mulch increased banana yields from 5.2 to 14.1 t ha^{-1} yr^{-1} as a combined result of improved water uptake and higher nutrient availability (McIntyre et al., 2000).

2.4.3. Physiological effects of drought

Drought stress in our trials resulted in a reduction in finger numbers within a bunch, but had no effect on finger weight (Table 2.3). Drought stress may both negatively impact on fruit initiation (e.g., the number of hands and fingers) and on the fruit filling process (Robinson and Alberts, 1986). Its effect depends on the timing of the stress. Drought stress during flower initiation translates in a reduction in the number of hands per bunch and fingers per hand (Holder and Gumbs, 1982, 1983), whereas drought stress after flower/bunch emergence translates in poor fruit filling (Mahouachi, 2007). If drought stress occurs during the whole growth cycle, then both the number of hands/fingers and fruit filling may be affected (Goenaga and Irizarry, 1995). In our trials, individual bunches were harvested throughout the year. It is therefore unlikely that drought stress occurred predominantly during flower initiation. Instead, the observed reduction in finger number, and not finger weight, may be explained by a possibly larger sensitivity of highland bananas to water stress at flower initiation than during fruit filling stage. Consequently, similar stress levels will reduce the number of fingers more than it will affect fruit weight (Holder and Gumbs, 1983; Robinson and Alberts, 1986). In our trials, the attainable number of fingers per bunch was reduced when cumulative rainfall in the 6 months before flowering was less than 550–700 mm (Fig. 2.3). During our trials, this was most likely for plants that flowered from September to November in south-western Uganda, while in central Uganda this was most likely for plants that flowered from May to August. Drought stress did not consistently affect time from planting/emergence to flowering or to harvesting nor did it consistently affect the time between two consecutive harvests in our trials. Many authors (Robinson and Alberts, 1986; Hedge and Srinivas, 1989; Goenaga and Irizarry, 1995, 2000) observed that irrigation advanced flowering and/or harvesting. The lack of consistent trends in our trials may be related to other factors (e.g., 'Sigatoka' and dense subsoil in Kawanda, K effects in Ntungamo) confounding possible effects of drought stress on banana development. It is unlikely that drought stress induced heat stress as average daily temperature was only 0.5 °C higher on non-rain days compared with rain days.

In long-term exploited plantations, annual production is determined by time between two consecutive harvests from the same mat, bunch weight and the number of productive mats. Drought-induced yield losses in rain-fed East African highland banana production were the result of lower bunch weight (both average and maximum) as a result of less

fingers per bunch in all sites, and through a loss in productive mats in one site (Tables 2.3 and 2.4).

2.4.4. Influence of soil fertility status and fertilizer

In Ntungamo and Kawanda, K was the main limiting nutrient for banana production (Nyombi et al., 2010). Application of K fertilizer roughly increased banana yields by 30% in Mbarara and Kawanda and by more than 200% in Ntungamo (Table 2.2), where soil K was one-third of that in the other two sites (Table 2.1) and far below the critical value of 0.32–0.74 $cmol_+$ kg^{-1} reported by Landon (1991). Lack of K decreased finger number as much as or even more than drought (Table 2.3) and in Ntungamo resulted in delayed flowering and harvesting. Bananas require large amounts of K as a harvest of 50 t ha^{-1} may remove 700–800 kg of K (Lahav, 1995). Soils in the central and eastern part of the East African highlands consist mainly of highly weathered Ferralsols, Acrisols and Nitisols that have low inherent soil fertility (Sanchez et al., 1997). Potassium limitations are therefore common in this region (Smithson et al., 2004).

The gradients of the boundary line functions that described the relation between maximum (or water-limited) ABW and CRF_{12} were generally steeper for K-fertilised plots than for non-K fertilised plots (Table 2.4). In the Mbarara trial, boundary line gradients for ABW were positively associated with K availability in the soil. Hence, absolute maximum drought-induced yield losses are larger in sites with good soil fertility status or good soil fertility management than in areas with poor soil fertility status or no addition of nutrient inputs. Radersma et al. (2005) showed that low soil water content decreases nutrient diffusion and transport to the roots and thus hampers nutrient uptake. Consequently, root growth rates are slowed down, which further reduces nutrient uptake over time. Drought stress in the Ntungamo and Kawanda trials is therefore perhaps the main reason for the low apparent fertilizer recovery rates (<10% for N, <5% for P and 14–49% for K) as observed by Nyombi et al. (2010) during the first three cycles in these trials, compared with 15% N recovery observed by Prasertsak et al. (2001) and 75% K recovery observed by Lopez and Espinosa (2000) in irrigated banana production. Haefele et al. (2006) also reported decreasing fertilizer use efficiencies with increasing drought stress in rain-fed rice production. If, on the other hand, the impact of production constraints (e.g., nutrients, water) is reduced, this will result in more above-ground growth, increased evapotranspiration demands and consequently promote water absorption from the soil. Thus, the application of a mulch in central Uganda resulted in greater water utilization at 0–30 and 30–50cm depth (McIntyre et al., 2000).

In contrast to ABW, the relation between maximum or water-limited RBW and CRF_{12} was remarkably stable across a wide range of soil conditions and K fertilizer treatments; site, fertilizer, and site $\times$ fertilizer did not have any significant effect on these gradients. We observed an average relative bunch weight loss of 9% for every 100-mm decrease in rainfall across all sites (Table 2.4 and Fig. 2.5). This is an indication that relative drought induced yield losses are independent of plant nutritional status and suggests that the observed relation between CRF_{12} and maximum RBW may be extrapolated to areas with a similar ecology, but with a different soil fertility status or soil fertility management. Potential bunch weights in the drier parts (900–1100 mm yr^{-1}) of the East African highlands (e.g., Southwest Uganda, eastern Rwanda and Burundi and much of the Kagera region in north-western Tanzania) are therefore likely 20–65% lower than those in wetter parts (1350–1550 mm yr^{-1}), such as eastern DRC. This estimation is lower than the actual yield decline observed in farmers' fields along the geographical gradient from Uganda to Rwanda/Burundi to eastern DRC: 9–24 t ha^{-1} $cycle^{-1}$ with 1000-1300 mm rainfall in Uganda, 18–45 t ha^{-1} $cycle^{-1}$ with 1000–1400 mm in Rwanda and Burundi, and 35–63 t ha^{-1} $cycle^{-1}$ with 1350–1550mm in eastern DRC (Bouwmeester et al., 2009; Wairegi et al., 2010). Actual yield differences between the regions may be larger due to (1) a loss in productive mats due to drought stress (Table 2.3); (2) reduced nutrient uptake under drought stress; (3) higher inherent levels of soil fertility in parts of eastern DRC and Rwanda (areas with soils on volcanic and relatively young metamorphic rock); and (4) different mat densities (CIALCA, 2008). Though irrigation, without doubt, has the potential to considerably increase banana production in the drier regions of the East African highlands, farm-gate prices for banana bunches in areas that are located far (>150 km) from the major markets may be too low to justify such investments (e.g., Van Asten et al., 2008).

2.5.   Conclusions

This study shows that drought-induced yield losses are important in rain-fed East African highland banana production. Within the observed rainfall range (500–1750 mm) we found linear relations between CRF_{12} and maximum absolute and relative bunch weight in three trials across central and south-western Uganda, whereby a 100-mm decline in rainfall caused maximum (water-limited) bunch weight losses of 1.5–3.1 kg or 8–10%. Annual rainfall requirements for AAA-EA banana production may thus be well above 1200–1300 mm yr^{-1} as suggested earlier, though our results require confirmation in the form of irrigation experiments. Drought-induced yield losses in areas with a rainfall of

less than 1100 mm yr^{-1} are estimated to be around 20–65% due to loss in bunch weight. Loss of productive mats due to drought stress will increase yield losses in many plantations. Relative bunch weight losses were independent of soil fertility and absolute losses on fertile/fertilised soils were similar to those recorded in well fertilised irrigation studies with Cavendish banana in Latin America. Although the results of our study correspond well with those found in other areas, further validation may be needed before our findings can be extrapolated across sites and cultivars.

Smallholder banana farmers in the East African highlands are unlikely to introduce irrigation practices on the short to medium term. Overcoming drought stress in these banana systems will therefore have to be attained through increasing rainwater use efficiencies. This may practically be achieved through a combination of mulching and fertilizer use, in combination with rainwater harvesting on steeper slopes and more drought tolerant genotypes. In addition, farmers may be able to reduce the impact of drought stress by carefully managing sucker selection such that the period 6 months to flowering does not coincide with a dry spell. Little to no research has been done on these themes in Africa. To overcome drought-induced yield losses and improve productivity of smallholder banana production in Africa, national and international agricultural research institutes will have to emphasise drought stress/water management on their research agenda.

Acknowledgements

CHAPTER THREE

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

Abstract

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

Keywords: Allocation plasticity, Functional equilibrium model, *Musa* spp., Osmotic adjustment, Shoot:root ratio.

3.1.   Introduction

Among the factors constraining East African highland banana (*Musa acuminata* genome group AAA-EA; hereafter referred to as highland banana) production in Uganda are drought stress (van Asten et al., 2011), nitrogen (N) and potassium (K) deficiencies (Nyombi et al., 2010). Spatial heterogeneity in crop N and K deficiencies (Smithson et al., 2001; Wairegi and van Asten, 2010) in Uganda calls for a decision support tool that takes into account interactions between the stress factors or their ameliorative inputs. This would guide efficient agronomic management decisions for improving highland banana productivity. Models that can predict crop growth response to water and nutrient supply present an opportunity to develop such a decision support tool. Dry matter (DM) allocation between aerial and subterranean biomass structures of plants is a critical parameter in most eco-physiological crop growth models. Resource-limiting conditions often induce adjustments in plant DM allocation between aerial and subterranean biomass structures due to DM allocation plasticity. This is different from the normal shifts in DM allocation between biomass structures due to phenological development, also called ontogenetic drift (Wright and McConnaughay, 2002) and hence it should be taken into account when simulating resource-limited crop growth. Wilson (1988) reviewed the models used to describe DM allocation plasticity in plants, namely, the allometric models, hormone models, Thornley's model and functional equilibrium models. True DM allocation plasticity is however poorly understood (Wardlaw, 1990) and hence the mechanisms underlying DM allocation models are still under debate (Franklin et al., 2012). Consequently, 'explanatory' models like Thornley's Model (Thornley, 1972), are frequently substituted by empirical ones (Evans, 1990), such as the functional equilibrium models.

The functional equilibrium models predict preferential allocation of fresh DM to biomass structures involved in acquisition of the limiting resource. If water or nutrients are limiting, then plastic DM allocation favours roots against the shoots; the reverse is true if light or carbon dioxide is limiting (Brouwer, 1962; Davidson,1969; McCarthy and Enquist, 2007). The zero sum or trade-off principle implied in the functional equilibrium models tends to maximise use efficiency of the limiting growth resources (Bloomet al., 1985; Chapin, 1991), hence their relatively frequent application in plant growth simulation (e.g. Maire et al., 2012). Several authors report findings that support the functional equilibrium models (e.g. Poorter et al., 2012; Slot et al., 2012). Although some drought stressed plant species exhibit DM allocation plasticity in favour of the roots

(Chartzoulakis et al., 1993; Slot et al., 2012), others do not (Bhattachan et al., 2012; McConnaughay and Coleman,1999; Poorter and Nagel, 2000). Low K supply induces increased DM allocation to the roots in some plant species (Hafsi et al., 2011) while in other species, it reduces DM allocation to roots (Ericsson and Kähr, 1993). Such variations within the functional equilibrium models' predictions depend not only on the specific growth resource but also on plant genotype (McMichael and Quisenberry,1991) and species (McCarthy and Enquist, 2007). Prior knowledge on the crop's DM allocation plasticity with respect to a given growth resource is thus required in order to rely on functional equilibrium models for describing DM allocation plasticity.

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

Allometric analysis is based on the linear regression of logarithm-transformed root DM on logarithm-transformed shoot DM. The regression slope or allometric coefficient is the mean root DM to shoot DM ratio over ontogeny or experimental plant size range. When roots and shoots exhibit isometric growth (i.e. receive DM in equal proportions), the slope is 1 and hence any observed changes in DM allocation between them are only due to normal ontogenetic drift. When root growth supersedes shoot growth, then the slope is significantly greater than 1. The slope is significantly less than 1 when shoot growth supersedes root growth (Hunt and Nicholls, 1986). Significant departures of the slope from unity indicate that the observed change in DM partitioning between roots and shoots is due to true plasticity in DM allocation. However, phenological development, e.g. flowering may also induce a significant deviation of the slope from 1 (Troughton, 1956). Allometric analysis for correcting size-dependency is thus best done with young plants,

which is not true for studies reporting DM allocation in bananas. Furthermore, valid interpretation of the fitted regression parameters assumes all root biomass can be recovered and the DM content accurately quantified. This is a major challenge for field-grown plants (Poorter et al., 2012), especially large ones like bananas. Studies involving DM distribution between banana biomass structures report corm DM but not root DM (e.g. Hegde,1988; McIntyre et al., 2000) for subterranean biomass structures. Poorter and Nagel (2000) suggested a more flexible approach for allometric analysis that does not necessitate quantification of root DM *per se* but relies on quantification of biomass fractions relative to any plant size parameter.

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

3.2. Materials and Methods

3.2.1. Study approach

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

3.2.2. Fertilizer response trials

These were planted in October, 2004 and individual plant data spanning three crop cycles collected. One trial was conducted on-station on a Haplic Ferralsol at Kawanda (0°25ˈN or 0.0073 rad, 32°31ˈE or 0.5675 rad; 1156 m above sea level or m.a.s.l) in central Uganda. The second trial was conducted on-farm (0°54ˈS or −0.0157 rad, 30°15ˈE or 0.5280 rad; 1405 m.a.s.l) on a Lixic Ferralsol in Ntungamo district, south western Uganda. The annual rainfall at Kawanda was 1034, 1334 and 1663 mm in 2005, 2006 and

2007, respectively, while values at Ntungamo were 1206, 1380 and 935 mm, respectively. Both sites experience a bimodal rainfall distribution with rainy seasons from March to June and September to November.

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

Highland banana cultivar 'Kisansa' tissue culture plantlets were planted spaced 3 m × 3 m in plots with 35 plants (5 × 7 matrix) per plot, of which 15 plants (i.e. inner 3 × 5 matrix) were used as net plot for data collection. The trials were set up in a randomized complete block design with 5 nutrient treatments and an un-amended control (T1 in Table 3.1) replicated 4 times. Between blocks, which were in general oriented along contour lines, retention ditches, bordered with soil bunds on the up-slope edge, were dug alongside each plot's length to minimise transfer of treatment nutrients between plots through runoff/soil erosion processes.

Potassium (as muriate of potash, 52% K) and N (as urea, 46% N) were applied 4 times per rainy season. The micronutrients, including boron (as borax), molybdenum (as sodium molybdate) and zinc (as zinc sulphate) were applied twice a year along with magnesium (as magnesium sulphate) and phosphorus (P) (as Triple Superphosphate or TSP) at the start of each rainy season. All the fertilizers were applied as aqueous solutions in a 60-cm radius ring around the base of each banana mat, with the exception of TSP, whose granules were broadcasted on the soil surface and lightly covered with soil around the banana mat. Herbicides were used to control weeds whenever need arose. Pesticides were blanket-applied monthly to control banana weevils and nematodes.

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Table 3.1: Description of treatments in banana field trials conducted in Uganda.

Nutrient rate	Treatment					
	T1	T2	T3	T4	T5	T6
Nitrogen (kg N ha^{-1} yr^{-1})	0	400	0	150	400	400
Phosphorus (kg P ha^{-1} yr^{-1})	0	50	50	50	50	50
Potassium (kg K ha^{-1} yr^{-1})	0	600	600	600	0	250
Magnesium (kg Mg ha^{-1} yr^{-1})	0	60	60	60	60	60
Zinc (kg Zn ha^{-1} yr^{-1})	0	6	6	6	6	6
Boron (kg B ha^{-1} yr^{-1})	0	1	1	1	1	1
Molybdenum (kg Mo ha^{-1}yr^{-1})	0	0.5	0.5	0.5	0.5	0.5

The date of planting of the mother plant (cycle 1) was recorded, as well as the date of sucker emergence for the follower suckers (constituting cycle 2 and cycle 3 or the first ratoon and second ratoon, respectively). A maximum of 3 plants of different generations were maintained per mat. Excess suckers were periodically removed. The dates of flowering (i.e. appearance of the flower bud out of the pseudostem) and harvest were recorded. Cycle duration was computed as the number of days from emergence to harvest, vegetative duration as the days from sucker emergence to flowering, and the bunch-filling duration as the days from flowering to harvest.

Bunches were harvested at horticultural maturity, just before ripening of the banana fingers. The fresh mass of bunches, functional leaves (<50% chlorotic/necrotic surface) and pseudostem were recorded per plant. Hands and fingers were detached from the bunch and their number recorded, as well as the separate fresh mass of peduncle and fingers. The corm of the harvested plant was excavated and any attached roots pared off before taking its total fresh mass. Subsamples from each biomass structure (banana fingers, peduncle, leaves, pseudostem and corm) were taken to determine DM content. The midribs and petioles were sampled as part of the pseudostem. Other than the bunch, all plant residues were chopped up and spread in the plot as mulch after harvest.

At each site, an automatic weather station (HOBO®; Onset Computer Corporation) was installed to record daily rainfall. The cumulative rainfall received by each plant 365 days after sucker emergence (CRF) was computed. Plants at both trial sites that received less than the first quartile CRF value from the Ntungamo dataset (used as the reference site because it was generally drier than Kawanda) were considered to have grown under 'dry' conditions; otherwise, they were considered to have grown under 'wet' conditions. The first quartile CRF was 1100 mm. This is less than the consumptive water use for optimal

banana production, which was estimated at 1300 mm yr^{-1} (Robinson, 1996) though recent work in Uganda suggests it is above 1500 mm yr^{-1} (van Asten et al., 2011).

In a preliminary analysis of the data, contrasts between150 kg N ha^{-1} yr^{-1} (Table 3.1, treatment T4) and 400 kg N ha^{-1} yr^{-1} (Table 3.1, treatments T2, T5 and T6) for bunch mass and biomass DM contents were not significant. Likewise, contrasts between 250 kg K ha^{-1} yr^{-1} (Table 3.1, treatment T6) and 600 kg K ha^{-1} yr^{-1} (Table 3.1, treatments T2, T3 and T4) for bunch mass and biomass DM contents were also not significant. Variances for bunch mass and biomass structure DM contents from T2, T3, T4 and T6 (Table 3.1) were homogenous but different from those for the control (T1), and T5, which in turn had homogenous variances. For purposes of this study therefore, plants from T5 were isolated as the 'Sole N' group since they received N but not K, while those from T3 were isolated as the 'Sole K' group since they received K but not N. Plants from T1were isolated as the 'Control' group (no external nutrient inputs) while those from T2, T4 andT6, which received both K and N, were pooled as the 'K + N' group.

3.2.3. Farmers' field surveys

Twenty banana fields belonging to four N and K nutritional status groups based on CND indices according to Wairegi and van Asten (2011) were selected for destructive sampling. The nutritional groups were (1) deficient in both N and K, equivalent to 'Control' described in Section 3.2.2; (2) sufficient in K but not N, equivalent to 'Sole K'; (3) sufficient in N but not K, equivalent to 'Sole N', and; (4) sufficient in both K and N, equivalent to 'K + N'. The selected farmers' fields received no mineral fertilizer inputs. They were located in Mbale district in eastern Uganda; Mukono, Mpigi and Luwero district in central Uganda; Masaka and Rakai district in southern Uganda, and; Mbarara and Bushenyi district in southwestern Uganda. The soils are mainly Acrisols and Ferralsols and rainfall is received in bimodal distribution as described for the fertilizer response trials in Section 3.2.2.

A total of 82 pre-harvest stage plants were selected from the farmers' fields spread across the phenological stages of 'small sucker', 'pre-flowerers' and 'early-flowerers'. Small suckers were young plants but with fully expanded leaves. Pre-flowerers were plants that had attained adult stature but had neither a flag leaf nor a bulbous swelling at the distal end of the pseudostem indicative of an impending flower bud emergence. Early-flowerers were adult plants with either signs of an impending flower bud emergence or already had an emerged inflorescence but whose fingers had not yet started swelling and curling

upwards. The selected plants were sampled to provide data for allometric analysis in relation to K and N nutrition status. Sampling and DM data collection was done as described for the fertilizer response trials in Section 3.2.2.

3.2.4. Screen house pot trial

This was conducted at the International Institute of Tropical Agriculture (IITA) research station in Sendusu (Wakiso district, Central Uganda) in two phases. The first phase was a preliminary trial for determining functional relationships used for guiding watering regimes so as to maintain target pF in the second phase. The second phase was a drought stress pot trial with differential watering regimes designed to maintain the plants within pre-determined pF ranges.

3.2.4.1. Preliminary pot trial

Pots of 22.5-dm^3 capacity were filled with 30 kg of soil (oven-dry basis) and planted with highland banana cultivar 'Mpologoma' plantlets from macro-propagation. The soil was 61% sand, 24% clay and 15% silt and the same as that used in the drought stress pot trial. Six pots each were assigned to 'low', 'moderate' and 'high' moisture stress watering regimes established by adding, respectively, 1.0, 0.5 and 0.3 dm^3 of water daily up to harvesting at 8 weeks after planting. Data on the growth parameters plant height, pseudostem girth at the base and at the top, and number of functional leaves (less than 25% necrotic) were recorded at harvest. The total fresh mass of the leaves, petioles, pseudostem, corm and roots were taken on a digital scale (± 0.1 g). The resulting data were subjected to regression analysis to determine allometric functions (Eqs. 3.01 and 3.02) for estimating the fresh mass of the plants from the growth parameters in the drought stress pot trial.

$$M_T = \left(0.03873H + 0.281L + 3.169 \times 10^{-6} P_V\right) - 2.905 \quad \text{..Eq. 3.01}$$

where M_T (kg) is the total fresh mass per plant; H (cm) is the plant height; L is the number of functional leaves; P_V (cm^3) is the mean pseudostem volume.

$$P_V = \pi H \left[\frac{G_B + G_T}{4\pi}\right]^2 \quad \text{...Eq. 3.02}$$

where G_B (cm) and G_T (cm) is the pseudostem girth at base and girth at top, respectively and H (cm) is plant height.

The preliminary study included pots without banana plantlets but had the same mass of soil added as the rest of the pots. The soil was allowed to settle to the same degree as in the pots containing plants through repeated cycles of watering before taking five soil core samples using a 100-cm³ pF ring. The samples were used to determine the relationship between pF and volumetric water content using the pressure plate method set to pF values within the same range (1.5–2.8) as that targeted in the drought stress pot trial. The resulting data were fitted to a polynomial function (Eq. 3.03) through regression.

$$pF = 28.41\theta^2 - 24.755\theta + 6.8422 \dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\text{Eq. 3.03}$$

where θ is the volumetric water content.

From Eq. 3.03, the volumetric water content required to attain the upper and lower limit of the pF ranges targeted for each moisture stress level in the drought stress pot trial was computed. These were converted to gravimetric water content, assuming a uniform dry bulk density of 1.4 g cm^{-3} (from soil dry mass of 30000 g and soil volume of 21500 cm³).

3.2.4.2. Drought stress pot trial

Pots were prepared and planted with highland banana cultivar Mpologoma as described in Section 3.2.4.1. The growth parameter data described in Section 3.2.4.1 were collected from each plant at 2-week intervals throughout the 6-month-long drought stress pot trial. A randomized complete block design was used with 4 replicates. The plantlets were allowed a 4-week establishment period after planting prior to imposing the controlled watering treatments, namely, 'low stress' (pF 2.0–2.1), 'moderate stress' (pF 2.5–2.7) and 'high stress' (pF 2.8–2.9). The pF values for 'low stress' correspond to gravitational water potentials, closer to field capacity (pF = 2.5) than saturation (pF = 0). The pF values for 'moderate' and 'high' stress are within the range of capillary water potentials but far below the permanent wilting point (pF = 4.2). Three pots per moisture stress level were randomly selected and fitted with a tensiometer (Tensior 5, Eijelkamp) at 15-cm depth. On each day, the pF value from the tensiometer was recorded before adding water to maintain the target pF value for the treatment to which a given pot was assigned.

Each pot was weighed (±0.1 g) to record its gross weight on a given day. Then the fresh mass of the plant and total mass of empty pot, dry soil and tensiometer (where applicable) subtracted from the gross weight recorded to obtain the gravimetric water content on that day. The fresh plant mass was estimated using Eqs. 3.01 and 3.02 and this was maintained for up to 2 weeks when it was updated using the current growth monitoring

data collected. The amount of water to be added per pot on a given day was then computed as the difference between the gravimetric water content required to attain the lower limit of the moisture stress level to which the pot belongs, and the gravimetric water content measured on that day. Two months after imposing the controlled watering treatments, 4 plants per treatment (i.e. 12 plants in total) were randomly selected for destructive sampling to validate the allometric function used for estimating the fresh plant mass. This was repeated two months later using 8 plants per treatment (i.e. 24 plants in total). On both occasions, the allometric function was found to estimate the fresh plant mass per pot satisfactorily. The final harvest was done 6 months after planting. Data on corm, pseudostem and leaf DM were collected from 57 suckers at final harvest as described in Section 3.2.2.

3.2.5. Data analysis

Bunch yield and biomass DM parameter data taken at harvest stage in the fertilizer response trials were subjected to ANOVA using unbalanced treatment structure in GenStat15.0, adjusting for site, crop cycle and block effects as confounding variables (Payne et al., 2003). Dry matter partitioning between aerial shoot and subterranean biomass structures was evaluated as the ratio of aerial shoot (leaves and pseudostem) DM to corm DM contents. The aerial shoot:corm DM data were log-transformed prior to ANOVA. Allometric analysis was applied to the farmers' field survey and screen house pot trial datasets in order to compare the effects of nutrient deficiency and drought stress, respectively, on DM partitioning between aerial shoots and corms. For allometric analysis, mass fractions were computed for each biomass structure (corm, pseudostem and leaves) as the ratio of the DM in the biomass structure to the total plant DM according to Poorter and Nagel (2000). Log-transformed mass fractions were then subjected to linear regression with groups against log-transformed total DM in GenStat15.0 with plant nutrition status (K + N, Sole K, Sole N and Control) or moisture stress level (low, moderate or high) as the grouping factor (Payne et al., 2003) in the farmers' field survey and screen house pot trial datasets, respectively. The slopes corresponding to the different levels of a grouping factor of a given dataset were compared using standard t-tests. For all the analyses performed, significance is reported at $P < 0.05$.

3.3. Results

3.3.1. Potassium, rainfall and nitrogen effects on fresh bunch yield

Fresh bunch mass response reduced in the order K > CRF > N, with the N effect being insignificant. Application of K increased bunch mass by over 65% (Table 3.2). On its own however, K had no effect on the cycle duration and length of the vegetative period though it increased the bunch filling period by 3 days (Table 3.2). Wet conditions produced similar responses in bunch yield components as K, with the exception of the bunch-filling duration where wet conditions had no significant effect. Wet conditions increased bunch mass by 12% and slightly increased the number of hands and fingers per bunch compared with dry conditions (Table 3.2).

The K × CRF interaction effects on bunch mass were highly significant (Table 3.2). Without K, bunch mass averaged about 6 kg in dry conditions and was greater by 80% in wet conditions (Fig. 3.1.A). Bunch mass in dry and wet conditions with K was >160% of that in dry conditions without K (Fig. 3.1A). Similar trends were observed in the number of hands and number of fingers per bunch (data not shown). Dry conditions without K input resulted in a cycle duration of about 595 days (Fig. 3.1B). Wet conditions and/or K input reduced the cycle duration by between 30 and 45days compared with that for dry conditions without K (Fig. 3.1B). The vegetative and bunch-filling durations followed similar trends as those described for the cycle duration with respect to K × CRF interactions.

Initially (February 2006), K × CRF interactions on bunch yields were not significant (Fig. 3.2). Regardless of whether they experienced dry or wet conditions, plants that received K had an initial mean bunch yield of about 8 Mg ha^{-1} yr^{-1}. This was significantly greater than the initial mean bunch yield of 6 Mg ha^{-1} yr^{-1} for plants that received no K and experienced either dry or wet conditions (Fig. 3.2). A year later however, K × CRF interaction effects on bunch yield were significant. The mean bunch yield from plants that received K, regardless of whether they experienced dry or wet conditions, increased to about 15 Mg ha^{-1} yr^{-1} while that from plants that experienced wet conditions but received no K rose to 8 Mg ha^{-1} yr^{-1}. The mean bunch yield from plants that experienced dry conditions but received no K input reduced to about 4 Mg ha^{-1} yr^{-1} (Fig.3.2).

Table 3.2: Effects of potassium, rainfall and nitrogen supply on East African highland banana fresh bunch yield and its components in Uganda.

Factor	Level	n	Bunch mass (kg plant⁻¹) ˣMean ± se	Number of hands per bunch ˣMean ± se	Number of fingers per bunch ˣMean ± se	Crop cycle duration (d) ˣMean ± se	Vegetative duration (d) ˣMean ± se	Bunch filling duration (d) ˣMean ± se
Potassium	−K	207	9.7 ± 0.54 a	6.0 ± 0.10 a	82.1 ± 2.30 a	567 ± 7.3 a	437 ± 7.2 a	123 ± 1.1 a
	+K	604	16.3 ± 0.36 b	6.9 ± 0.07 b	101.2 ± 1.54 b	564 ± 4.9 a	433 ± 4.8 a	126 ± 0.8 b
CRF	Dry	242	13.5 ± 0.50 a	6.4 ± 0.09 a	90.2 ± 2.11 a	566 ± 6.7 a	437 ± 6.6 a	124 ± 1.0 a
	Wet	569	15.1 ± 0.42 b	6.8 ± 0.08 b	98.9 ± 1.76 b	564 ± 5.6 a	432 ± 5.6 a	125 ± 0.9 a
Nitrogen	−N	266	14.6 ± 0.48 a	6.7 ± 0.09 a	96.4 ± 2.03 a	569 ± 6.4 a	440 ± 6.4 a	124 ± 1.0 a
	+N	545	14.6 ± 0.38 a	6.7 ± 0.07 a	96.3 ± 1.59 a	563 ± 5.0 a	431 ± 5.0 a	125 ± 0.8 a

Source of variation								
Site (S)			***	***	***	***	***	***
Cycle (C)			***	***	***	***	***	***
Replication (Rep)			***	***	***	***	***	ns
S × C			ns	ns	**	***	***	ns
S × Rep			***	***	***	***	***	ns
C × Rep			ns	ns	ns	ns	ns	ns
S × C × Rep			ns	ns	*	ns	ns	ns
Potassium (K)			***	***	***	ns	ns	**
CRF			***	***	***	ns	ns	ns
Nitrogen (N)			ns	ns	ns	ns	ns	ns
K × CRF			***	**	**	***	***	*

ˣAdjusted for site, cycle and replication effects; se = Standard error of mean; Means in the same column for a given factor followed by the same letter are not significantly different; −K = 0 kg K ha⁻¹ applied, +K = 250 to 600 kg K ha⁻¹ yr⁻¹ applied; −N = 0 kg N ha⁻¹ yr⁻¹ applied; +N = 150 to 400 kg N ha⁻¹ yr⁻¹ applied; CRF = cumulative rainfall received in 365 days from emergence; 'Dry' is CRF < 1100 mm; 'Wet' is CRF ≥ 1100 mm; ns = not significant (P > 0.05), *, ** and *** = significant at 95.0, 99.0 and 99.9% confidence levels, respectively; K × N, CRF × N and K × CRF × N interactions (not shown) are not significant.
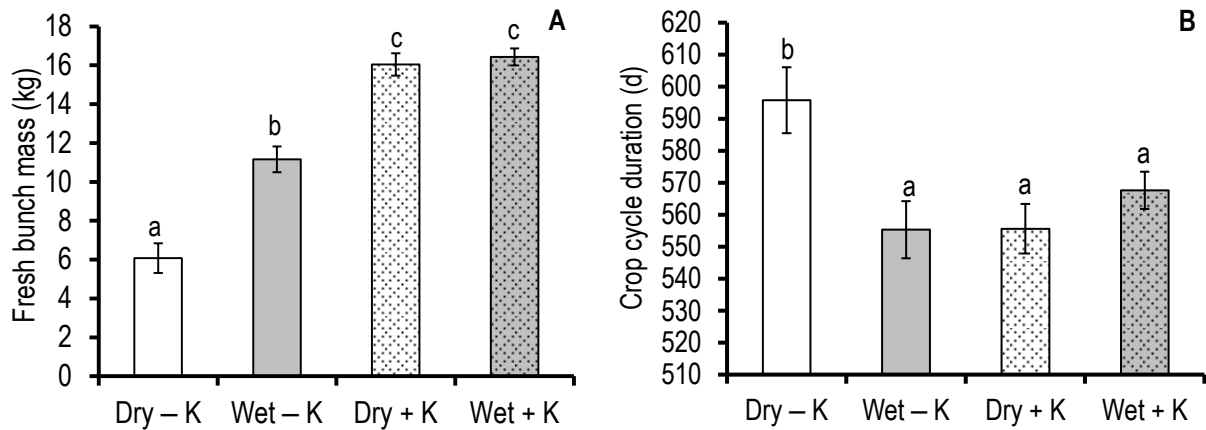
Fig. 3.1: Interaction effects of potassium (K) input and rainfall adequacy on the East African highland banana yield components fresh bunch mass (**A**) and cycle duration (**B**) over 3 crop cycles in central and south western Uganda.

−K = 0 kg K ha⁻¹ yr⁻¹ applied; +K = 250 to 600 kg K ha⁻¹ yr⁻¹ applied; Dry = cumulative rainfall received over 365 days from emergence (CRF) < 1100 mm; Wet = CRF ≥ 1100 mm; Bars are standard errors of means; Means for a given banana yield component crowned with the same lower case letter are not significantly (P>0.05) different.
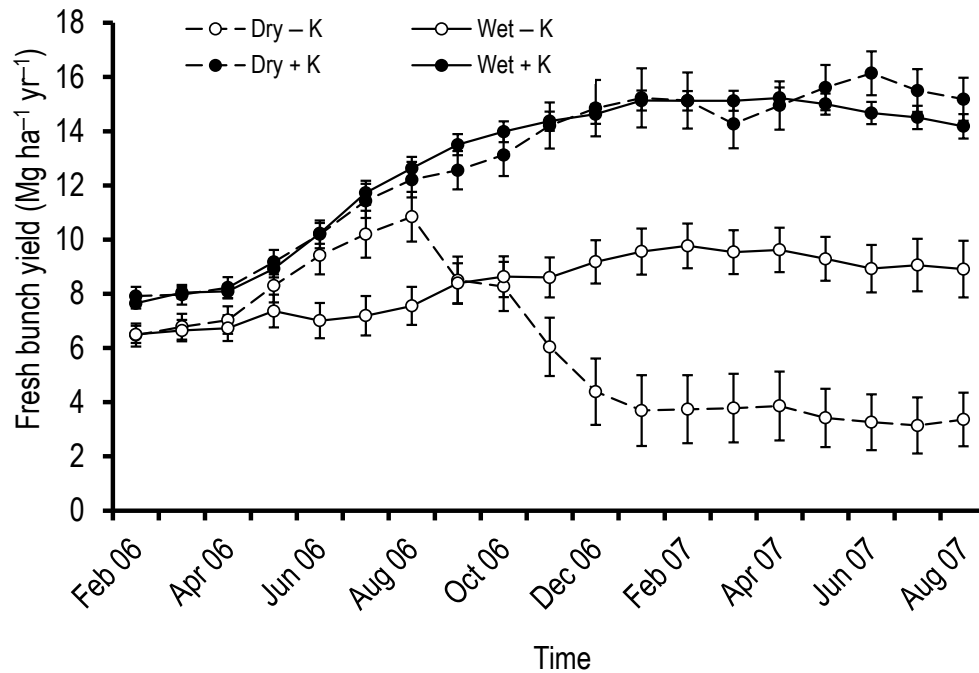
Fig. 3.2: Interaction effects of potassium (K) and rainfall on twelve-month rolling average fresh bunch yield of East African highland banana in Uganda.

−K = 0 kg K ha⁻¹ yr⁻¹ applied; +K = 250 to 600 kg K ha⁻¹ yr⁻¹ applied; Dry = cumulative rainfall received in 365 days after emergence (CRF) < 1100 mm; Wet = CRF ≥ 1100 mm; Bars are standard errors of means; Each mean is the average yield recorded 12 months forwards starting from the date at which the mean is plotted.

3.3.2. Potassium, rainfall and nitrogen effects on dry matter allocation plasticity

Application of K increased total DM by 31% and increased DM allocation to the bunch, leaves pseudostem and corm at harvest stage by 51%, 38%, 34% and 13%, respectively (Table 3.3). At pre-harvest stage from the farmers' field survey dataset, DM content in response to K sufficiency increased by 154%, 50% and 30% for the leaves, pseudostem and corm, respectively (Table 3.4). Allocation of DM to the corm was least responsive to K of all the biomass structures at both the harvest stage and pre-harvest stage. The aerial shoot to corm DM ratio observed at harvest stage was significantly reduced from 5.6 with K to 4.7 without K (Table 3.3) while the corresponding values observed at pre-harvest stage were 3.9 and 3.1, respectively (Table 3.4). Lack of N input had no effect on the aerial shoot to corm DM ratio at harvest stage (Table 3.3) but N deficiency at pre-harvest stage significantly reduced the ratio from 3.8 to 3.1 (Table 3.4).

Wet conditions significantly increased total DM and leaf DM by 6% and 3%, respectively, but affected neither DM allocation to the rest of the biomass structures nor the aerial shoot to corm DM ratio at harvest stage. The K $\times$ CRF interaction effects on total DM and its distribution to all the biomass structures except corm at harvest was significant (Table 3.3). In plants that received K, there was no significant difference in total DM at harvest between dry and wet conditions (Fig. 3.3A). The aerial shoot to corm DM ratio was largest among plants that received K irrespective of whether they experienced wet or dry conditions, followed by those that received no K but experienced wet conditions, while those that received no K but experienced dry conditions had the smallest ratio (Fig. 3.3B).

Among the pre-harvest stage banana plants from the farmers' field survey, corm mass fractions per unit increase in total DM (linear regression slope) decreased linearly by between 9% and 31% across nutritional groups. The slope was significantly steeper for K + N plants (sufficient in both K and N) than for those that were deficient in either (Sole K and Sole N) or both (Control) K and N (Fig. 3.4A). However, the slopes for corm mass fraction did not differ significantly between moisture stress groups (Fig. 3.4B) from the screen house pot trial dataset. Between nutrition status groups from the farmers' field survey dataset, there was no significant difference in slopes for the pseudostem mass fraction (Fig. 3.4C) and leaf mass fraction (Fig. 3.4E). Likewise, there was no significant difference in slopes for the pseudostem mass fraction (Fig. 3.4D) and leaf mass fraction (Fig. 3.4F) between moisture stress groups from the screen house pot trial dataset.

Table 3.3: Effects of potassium, rainfall and nitrogen on East African highland banana total dry matter and its distribution in biomass structures at harvest in Uganda.

Factor	Level	n	Total DM (kg plant⁻¹) [x]Mean ± se	Bunch DM (kg plant⁻¹) [x]Mean ± se	Leaf DM (kg plant⁻¹) [x]Mean ± se	Pseud. DM (kg plant⁻¹) [x]Mean ± se	Corm DM (kg plant⁻¹) [x]Mean ± se	AS: Corm DM ratio [x,y]Mean
Potassium	−K	174	3.8 ± 0.15 a	1.5 ± 0.08 a	0.27 ± 0.010 a	1.5 ± 0.06 a	0.38 ± 0.012 a	4.7a
	+K	467	5.0 ± 0.09 b	2.3 ± 0.05 b	0.37 ± 0.006 b	2.1 ± 0.03 b	0.43 ± 0.007 b	5.6b
CRF	Dry	159	4.5 ± 0.15 a	2.0 ± 0.08 a	0.33 ± 0.010 a	1.9 ± 0.06 a	0.45 ± 0.012 a	5.5a
	Wet	482	4.7 ± 0.07 b	2.1 ± 0.05 a	0.34 ± 0.006 b	1.9 ± 0.03 a	0.41 ± 0.007 a	5.5a
N	−N	212	4.9 ± 0.13 a	2.2 ± 0.07 a	0.35 ± 0.009 a	2.0 ± 0.05 a	0.44 ± 0.011 a	5.5a
	+N	429	4.5 ± 0.09 a	2.1 ± 0.05 a	0.34 ± 0.006 a	1.9 ± 0.03 a	0.41 ± 0.007 a	5.3a
Source of variation								
Site (S)			***	***	***	***	***	***
Cycle (C)			***	***	***	***	***	***
Replication (Rep)			***	***	***	***	***	***
S × C			ns	ns	**	ns	***	***
S × Rep			***	***	***	***	***	ns
C × Rep			ns	ns	ns	ns	*	ns
S × C × Rep			**	ns	ns	ns	ns	ns
Potassium (K)			***	***	***	***	***	***
CRF			***	ns	*	ns	ns	ns
Nitrogen (N)			ns	ns	ns	ns	ns	ns
K × CRF			*	***	*	*	ns	**

[y]*Means are back-transformed log_{10} values; se = Standard error of mean; Means in the same column for a given factor followed the same letter are not significantly (P>0.05) different; DM = Dry matter; Pseud. = Pseudostem; AS = Aerial shoot (pseudostem + leaves); −K = 0 kg K ha⁻¹ yr⁻¹ applied; +K = 250 to 600 kg K ha⁻¹ yr⁻¹ applied; −N = 0 kg N ha⁻¹ yr⁻¹ applied; +N = 150 to 400 kg N ha⁻¹ yr⁻¹ applied; CRF = cumulative rainfall received in 365 days from emergence; 'Dry' is CRF < 1100 mm; 'Wet' is CRF ≥ 1100 mm; ns = not significant (P > 0.05); *, ** and *** = significant at 95.0, 99.0 and 99.9% confidence levels, respectively; K × N, CRF × N and K × CRF × N interactions (not shown) not significant.*
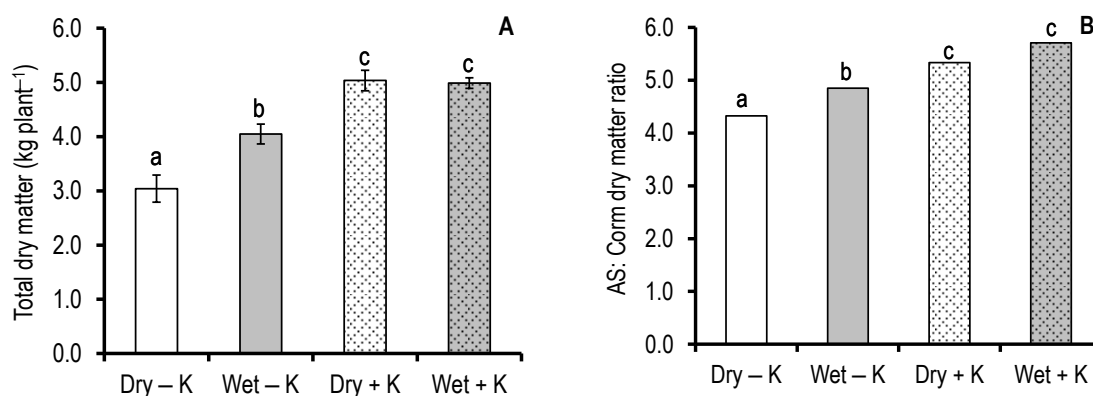
Fig. 3.3: Interaction effects of potassium (K) and rainfall on East African highland banana total dry matter (**A**) and aerial shoot to corm dry matter ratio (**B**) at harvest in central and south-western Uganda.

AS = Aerial shoot (leaves + pseudostem); Bars are standard errors of means; Means crowned with the same letter are not significantly (P>0.05) different.

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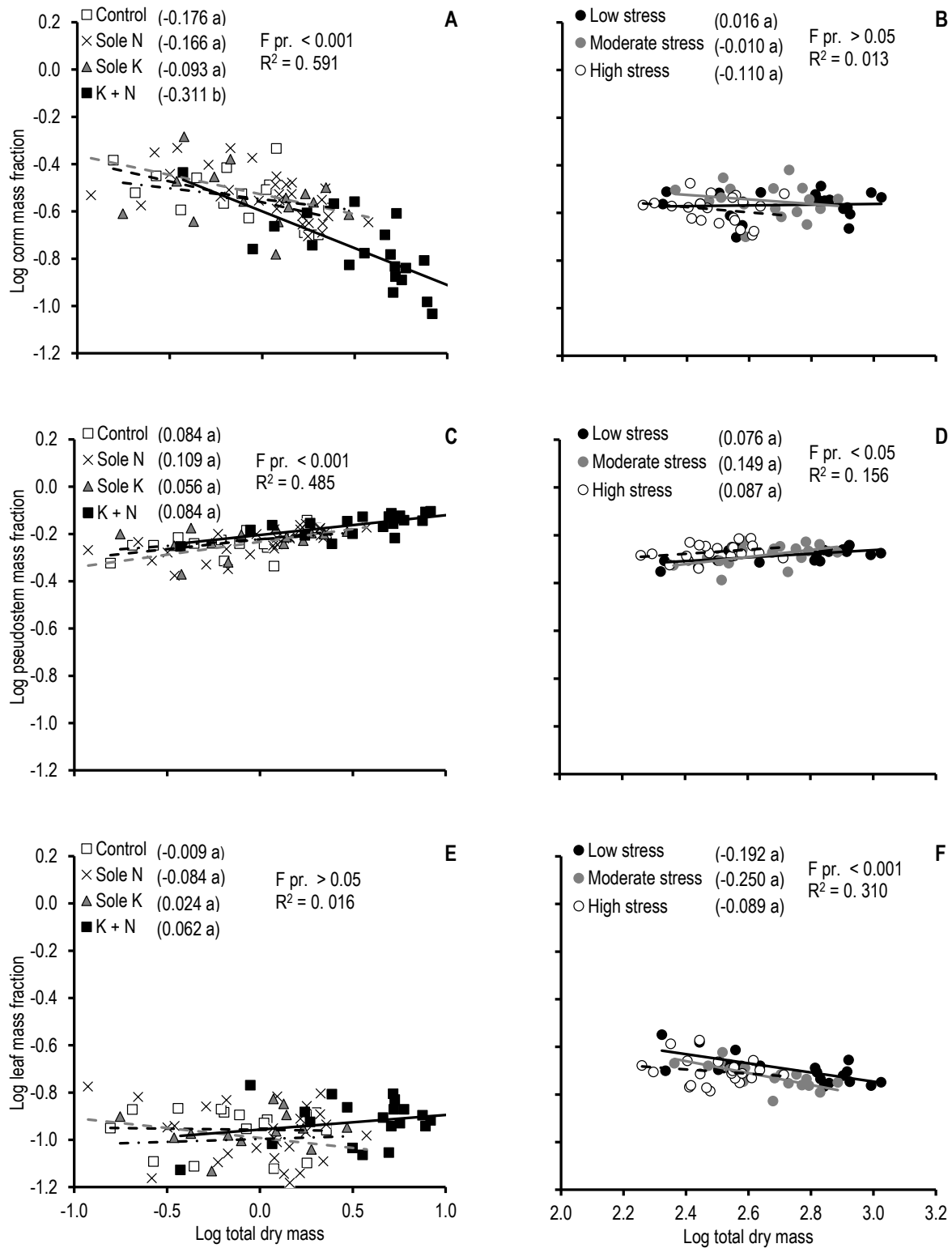
Fig. 3.4: Fitted vs. observed plots for linear regression of banana corm (**A**, **B**) pseudostem (**C**, **D**) and leaf (**E**, **F**) mass fractions on total dry matter with nutrient (**A**, **C** and **E**) and water stress (**B**, **D** and **F**).

Log = log₁₀; Control = deficient in both N and K; Sole N = sufficient in N; Sole K = sufficient in K; K+N = sufficient in both N and K; Low, Moderate and High stress correspond to pF ranges 2.0-2.1, 2.5-2.7 and 2.8-2.9; n = 17, 29, 15, and 21 for Control, Sole N, Sole K and K + N, respectively; n = 19, 17 and 21 for Low, Moderate and High stress, respectively; Values in parentheses against legends are slope estimates; Slope estimates for a given plot followed by the same lower case letter are not significantly (P>0.05) different based on a t-test.

Table 3.4: Effect of potassium and nitrogen nutritional status on East African highland banana total dry matter and its distribution in biomass structures at pre-harvest phenological stages across the major banana-growing districts of Uganda.

[x]Nutrient status	n	Total DM (kg plant^{-1}) [y]Mean	Leaf DM (kg plant^{-1}) [y]Mean	Pseud. DM (kg plant^{-1}) [y]Mean	Corm DM (kg plant^{-1}) [y]Mean	AS: Corm DM ratio [y]Mean
K-deficient	47	1.32 a	0.11 a	0.82 a	0.34 a	3.1 a
K-sufficient	36	1.93 b	0.28 b	1.23 b	0.46 b	3.9 b
N-deficient	33	1.41 a	0.18 a	0.83 a	0.38 a	3.1 a
N-sufficient	50	1.68 a	0.16 a	1.10 b	0.39 a	3.8 b
Source of variation						
District		***	***	***	***	***
Farm		***	***	***	***	***
Phenological stage		***	***	***	***	***
Potassium (K)		***	***	***	**	***
Nitrogen (N)		ns	ns	*	ns	*
K × N		ns	ns	ns	ns	ns

[x]*Determined using compositional nutrient diagnosis and diagnosis and recommendation integrated systems indices by Wairegi and van Asten (2011); [y]Back-transformed values from log$_{10}$ means that were adjusted for District, Farm and Phenological stage effects; Means in the same column for a given factor followed by the same letter are not significantly (P>0.05) different; DM = Dry matter; Pseud. = Pseudostem; AS = Aerial shoot (Pseudostem + leaves); –K = K-deficient; +K = K-sufficient; –N = N-deficient; +N = N-sufficient; ns = not significant at 95.0% confidence level; *, ** and *** = significant at 95.0, 99.0 and 99.9% confidence levels, respectively.*

3.4. Discussion

3.4.1. Potassium, rainfall and nitrogen effects on fresh bunch yield

The mean bunch yields ranged from 6 to 15 Mg ha^{-1} yr^{-1} (Fig. 3.2) and are similar to those from previous mineral fertilizer/organic mulch studies on highland banana in Uganda. Smithson et al.(2004) reported mean yields ranging from 4.9 to 18.2 Mg ha^{-1} yr^{-1} in response to mineral K and Mg fertilizers in central and south-western Uganda, while Ssali et al. (2003) reported mean yields of 6.4–8.4 Mg ha^{-1} yr^{-1} in response to mineral N, P, K and Mg fertilizers combined with mulch in central Uganda. Unlike in the past studies however, the main and interactive effects of experimental factors (rainfall, K and N) on bunch yield, its components and underlying DM allocation are explicitly separated and quantified in the current study. The results show that K, interacting with rainfall, was the main driver of bunch yield and its components. Nitrogen had no effect on the yield parameters (Table 3.2) although the antecedent soil analysis results suggested possible N deficiency at both sites where the trials were conducted. These

results are in line with reports that K deficiency (Nyombi et al., 2010) and drought stress (van Asten et al., 2011) are the key factors limiting banana production in Uganda.

Bananas take up K in much larger quantities than all other essential plant nutrients combined (Turner et al., 1989). Potassium is involved in translocation of assimilates from the sources (i.e. leaves) to the sinks (Pettigrew, 2008). The sinks include the bunch soon after the end of vegetative growth, the growing points during the vegetative stages and the follower suckers. This perhaps explains why K supply strongly influenced bunch mass (Table 3.2) and yields (Fig. 3.2), besides total DM (Table 3.3). Soil moisture on the other hand is required for the movement of K and N to the roots for uptake. Nutrient availability and uptake are impaired under drought stress (Duman, 2012). This however, does not explain why in the current study K increased bunch yields regardless of whether wet or dry conditions prevailed within 365 days from emergence (Fig. 3.2). Weerasinghe and Premalal (2002) reported strong yield response to K from irrigated Embul bananas in Sri Lanka with a more pronounced effect in ratoon crops than in the mother plants due to K depletion from the surface soil layer after the third crop cycle. This may also explain the decline in bunch yields under dry conditions without K input observed in the current study (Fig. 3.2).

Adequate soil water supply is required to keep the stomata open and hence ensure the supply of carbon dioxide for photosynthesis to proceed. Photosynthesis in plants, however, also requires optimal foliar N concentration (Marschner, 1995), which in turn is dependent on an adequate N supply to banana plants from soil or fertilizers (Weerasinghe et al., 2004; Damour et al., 2012). It is thus surprising that N had no effect on banana yields in the current study, even in interaction with K, whose deficiency was reported to strongly affect enzymes involved in N assimilation (Armengaud et al., 2009). Damour et al. (2012), Weerasinghe et al. (2004) and Baiyeri (2002) reported lack of response to N in bananas in Guadeloupe (French West Indies), Sri Lanka and Nigeria, respectively, in line with the results from the current study. However, significant yield increases in response to N have been reported on Robusta bananas in India (Hegde, 1988; Singh, 2004). Wairegi and van Asten (2010) reported highland banana yield increases in response to NPK mineral fertilizer application in southern Uganda, which they attributed to N deficiency as deduced from the negative CND indices for N, unlike for P and K at the responsive sites. This supports the suggestion of Wairegi and van Asten (2011) that nutrient interactions with other factors are important in determining highland banana bunch weights.

3.4.2. Potassium, rainfall and nitrogen effects on dry matter allocation plasticity

The mean total DM observed in the current study varied from 3 to 5 kg plant^{-1} (Fig. 3.3A). As for the bunch yield, DM allocation at harvest stage was driven by K and water (Table 3.3). Evidence for the dominant role of K in driving DM accumulation, and the lack of N effect at harvest stage in the field trials (Table 3.3) was corroborated by the results from on-farm pre-harvest stage sampling (Table 3.4). This supports earlier reports that K is important in banana DM production and allocation especially to the bunches, which may suffer up to 80% DM reduction due to K deficiency (Turner and Barkus,1980).

Drought stress reduces DM production (Firth et al., 2003) and yield in bananas (van Asten et al., 2011). It is thus surprising that K increased total DM irrespective of whether wet or dry conditions prevailed in the current study (Fig. 3.3). This may be due to the role K plays in osmotic adjustment, a mechanism by which plants adapt to drought stress conditions (Cutler et al., 1977). Osmotic adjustment is the net accumulation of solutes (osmolytes), which enables plants to function at reduced leaf water potentials. Accumulation of K in the leaves of drought stressed banana plantlets in a glasshouse study was credited with minimising the impact of the imposed stress on their DM production (Mahouachi, 2009). Under conditions of limited K supply, organic solutes take over the role of K in osmotic adjustment. The solutes, derived from photosynthates in competition with the plant's growth requirements, are energetically less efficient than K when used for osmotic adjustment (Kusaka et al., 2005).

The significant K × CRF interaction effects on DM allocation (Table 3.3) in the current study may therefore be attributed to the role of K in maintaining the plant water relations such that its metabolism is not adversely affected under drought stress. However, van Asten et al. (2011) did not observe significant interaction effects between K and cumulative rainfall on bunch mass in their study. van Asten et al. (2011) computed cumulative rainfall 12 months before the date of harvest, while in the current study it was computed 12 months after the date of planting/emergence. With an average crop cycle duration of approximately 19 months in the current study, there is only 5 months' overlap of cumulative rainfall with that of van Asten et al. (2011). Drought stress in the current study was thus more likely to have been experienced at an earlier phenological stage compared with that in the study by van Asten et al. (2011). The degree of osmotic adjustment is much greater in young leaves compared with old leaves (Kameli and Lösel, 1995; Alves and Setter, 2004). From the observed difference between the current study

and that by van Asten et al. (2011), it is probable that K-mediated osmotic adjustment mitigates drought-induced DM production and yield losses in highland banana if the drought occurs early (i.e. in the first 6 months from emergence) rather than late in the growth cycle.

Significant reduction in the aerial shoot to corm DM ratio without K input at harvest stage (Table 3.3), especially under dry conditions (Fig. 3.3) suggests that there is DM allocation plasticity in response to K deficiency among highland banana in line with the functional equilibrium model; i.e. plants invest relatively more fresh assimilates in the subterranean corm when deficient in K. The similar aerial shoot to corm DM ratio at harvest stage between plants that experienced dry and those that experienced wet conditions suggest that drought-stressed highland banana plants do not preferentially invest fresh DM in the corm. At harvest stage, plants that received N also had similar aerial shoot to corm DM ratios as those that did not receive N input (Table 3.3) suggesting lack of DM allocation plasticity with respect to N deficiency. Significant difference in aerial shoot to corm DM ratio at pre-harvest stage (Table 3.4) and results from allometric analysis with respect to the corm mass fraction at pre-harvest stage (Fig. 3.4A) confirmed DM allocation plasticity with respect to not only K- but also N-deficiency. The similarity in slope for logarithm-transformed corm mass fraction regressed on logarithm-transformed total DM among plants subjected to different magnitudes of water stress (Fig. 3.4B) confirms lack of DM allocation plasticity in response to drought stress in highland banana.

Dry matter allocation plasticity in favour of below-ground biomass structures in response to K and/or N deficiency is in line with the functional equilibrium (Brouwer, 1962; Davidson, 1969; McCarthy and Enquist, 2007). This, however, contradicts the finding by Ericsson and Kähr (1993) who reported DM allocation plasticity in favour of the shoots in response to K deficiency in *Betula pendula* seedlings. Limited K supply hampers carbon assimilation effectively rendering CO_2, an above-ground resource, limiting to DM production (Ericsson, 1995), which explains increased allocation to above-ground structures with K deficiency (Ericsson and Kähr, 1993). In the current study however, the role of K in maintaining plant water relations through osmotic adjustment seems to take precedence over its role in carbon assimilation. This also explains why drought stress per se did not induce preferential DM allocation to below-ground biomass structures, contrary to observations in other crops (Chartzoulakis et al., 1993; Slot et al., 2012), but rather accentuated it under low K supply (Fig. 3.3).

From the findings in this study, it can be hypothesised that highland banana exhibit risk-averse behaviour with respect to assimilate investments into subterranean structures in response to drought stress but not to K and N deficiency. Bananas are very sensitive to limited soil water supply but seem to rely on a mechanism that is primed for conserving water in their tissues (Turner et al., 2007) rather than seeking to exploit reserves further away in the soil. This is through rapid closure of the stomata (Robinson, 1996), to the detriment of photosynthesis and productivity (Turner et al., 2007). In terms of species survival in an ecosystem with a strong seasonal rainfall distribution, temporal retardation of growth and development under drought improves the plant's chances of progressing vegetatively to the next generation using assimilates that would otherwise have been invested in an uncertain search for more water further in the soil profile. Banana roots have poor penetrating power and their exploration of the soil profile is dependent on the soil physical properties (Roque, 2003), which are even less conducive when dry. Investment of assimilates in root system growth may thus not assure the plant of increased water supply as efficiently as waiting for the next rainy season in a suspended phenological state.

Osmotic adjustment in the presence of adequate K supply lowers the leaf water potential threshold for stomatal closure, which permits continued photosynthesis and growth despite the drought stress (Blum, 1996). This explains why combined drought stress and K deficiency led to prolonged cycle duration compared with when the plants had either adequate K supply or experienced wet conditions (Fig. 3.1). This finding is in line with Okech et al. (2004) who reported prolonged highland banana cycle duration due to K deficiency and drought in southwestern Uganda. Unlike water, the supply of nutrients in nature does not follow defined seasonal patterns, along which the bananas could tailor their growth cycles over phylogeny as a survival strategy against periods of low nutrient supply. The banana plants therefore invest assimilates into below-ground organs to scavenge for nutrients, but not water.

The finding that N deficient plants allocate DM to below-ground biomass fractions corroborates the numerous studies on which Thornley's Model (Thornley, 1972) was based, which remains unchallenged regarding its predictions on DM allocation plasticity with respect to N supply. However, the finding in the current study that N deficiency neither affected the bunch mass (Table 3.2) nor total DM measured at harvest (Table 3.3) and pre-harvest stage (Table 3.4) is at odds with the finding that it induced DM allocation plasticity in favour of the corm at pre-harvest stages (Table 3.4; Fig. 3.4A). Increased

respiration and other carbon costs associated with N assimilation (Plaxton and Podestá, 2006) in plants that received N in the fertilizer response trial may have masked preferential allocation of DM to the corms unlike that for plants that received no N in the farmers' fields surveyed.

3.5.   Conclusions

Potassium mitigates DM production and bunch yield losses arising from drought stress at early growth stages. Highland bananas exhibit DM allocation plasticity in favour of subterranean biomass structures in response to K and N deficiency but not to drought stress per se. Drought stress accentuates DM allocation plasticity in response to K deficiency. Highland bananas therefore respond to or seem to 'worry' more about K deficiency than drought stress. Consequently, farmers' investment in K nutrition of highland banana may present a viable entry point for mitigating both K deficiency and drought stress impacts on productivity than investments in water harvesting and irrigation systems. This however needs further agronomic and economic evaluation. It may be important to take into account carbon allocated to osmotic adjustment for simulation of water- and K-limited growth in highland banana as an additional sink term in competition with the normal structural growth of the plant.

CHAPTER FOUR

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

Abstract

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

Keywords: Growth analysis, Leaf area ratio, *Musa acuminata* AAA-EA., Net assimilation rate, Phenotypic plasiticity, Relative growth rate.

4.1.   Introduction

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

Efforts to quantitatively describe timing of flowering in bananas have focused on relating the cumulative number of leaves emerged at an assumed point of flower initiation or flower bud emergence from the pseudostem (e.g. Ndubizu et al., 1983; Mekwatanakarn and Turner, 1989). However, this approach has not been widely applied, perhaps because the cumulative number of leaves emerged at flowering varies substantially, e.g. 23 to 43 (van Asten, P.J.A., personal communication). There is thus a need to identify and elucidate plant attributes and/or environmental cues that influence the timing of flowering in bananas. Summerville (1944) proposed that flowering in bananas is initiated when the product of leaf area (square inches), leaf longevity (days), air temperature (°F) and daylight hours during the life of a leaf is at least 5.6×10^{11}. The parameters used in the model by Summerville (1944) suggest that the physiological age, and/or photoperiod and/or dry matter accumulated may be critical for flower initiation in bananas. However, Fortescue et al. (2011) reported a weak correlation between photoperiod and frequency of flowering per unit area over time at a site with a narrow photoperiod range. This finding renders photoperiod an unlikely factor in the African Great Lakes region's banana agro-ecologies, which by virtue of their equatorial location, have a narrow range of photoperiod.

Flowering in monocarpic biennial and perennial plants has been reported to be dependent on plant size, though in some species both plant size and age are influential (Klinkhamer et al., 1987 and references therein). According to life history theory, a thresh-old size or age is necessary for commencement of reproductive growth to maximise fitness. Fecundity and quality of off-spring increases when reproductive growth is delayed (Roff, 1992). However, the probability of a plant dying before attaining reproductive growth

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

In quantitative growth analysis, RGR or the change in total dry mass (W_T) per unit of W_T already present per unit time, is modelled as a product of net assimilation rate (NAR), leaf mass ratio (LMR) and specific leaf area (SLA) of a plant (Lambers et al., 1989). In this simple model, growth is envisaged to be a function of net carbon gain (through NAR) in the photosynthetic tissues (mainly leaves) and carbon allocation to the leaves relative to that allocated to the rest of the plant (LMR and SLA). Net assimilation rate is the change in W_T per unit leaf area (A_L) per unit time. Leaf mass ratio is the leaf dry mass (W_L) per unit W_T while SLA is A_L per unit W_L. Leaf mass ratio and SLA are morphological components of RGR concerned with interception of light energy while NAR is a physiological component related to the utilisation of intercepted light energy for carbon assimilation. Net assimilation rate is positively correlated with rate of photosynthesis per unit A_L (Poorter and van der Werf, 1998) while LMR and SLA exhibit sensitivity to plant illumination (Evans and Poorter, 2001; Senevirathna et al., 2008).

Quantitative growth analysis based on RGR and its components is acceptable for single plant analyses because there is no crop canopy to allow more mechanistic assessment of light interception and light use efficiency. It has been used to evaluate the relative importance of plant physiological and morphological responses as coping mechanisms among cultivated plants or closely related wild species against growth-limiting factors (Galmés et al., 2005; del Amor and Cuadra-Crespo, 2012). Among the most limiting abiotic constraints to highland banana production are drought stress (van Asten et al., 2011), K and N deficiencies (Nyombi et al., 2010; Wairegi and van Asten, 2010) but there is no information about the relative importance of physiological and morphological components of RGR in modulating growth under these stresses.

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

4.2. Materials and Methods

4.2.1. Study site characterisation

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

to be deficient in both K and N from significant shifts in highland banana dry matter partitioning between above- and below-ground biomass structures in response to K and N input (Taulya, 2013).

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

4.2.2. Trial set up and data management

The trials were planted in October, 2004 with highland banana cultivar 'Kisansa' tissue culture plantlets, spaced 3 m $\times$ 3 m to give 35 plants (5 $\times$ 7 matrix) per plot, out of which 15 plants (i.e. inner 3 $\times$ 5 matrix) were used as the net plot for data collection. Between blocks, which were in general oriented across the slope, retention ditches, bordered with soil bunds on the up-slope edge, were dug alongside each plot's length to minimise transfer of treatment nutrients between plots through runoff and eroded sediments. The trials were set up in a randomised complete block design with 5 treatments and an un-amended control (N_0K_0 in Table 4.1) replicated 4 times. Details of trial management are reported in Nyombi et al. (2010).

Data collected from the first and second ratoon crops or Cycle 2 and Cycle 3, respectively between 1 January 2006 and 31 December 2007 were used for the current study. The planted crop constituting Cycle 1 were excluded from the current study because their physiological age could not be determined. The date and spatial position of emergence relative to the location of the mother plant for each sucker on a given mat in the net plot was recorded.

Table 4.1: Description of treatments in fertilizer response trials conducted in central (Kawanda) and south western (Ntungamo) Uganda.

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

(Column group header: Treatment)

At most, 3 plants of different generations (Cycles) were maintained per mat at a given time. Excess suckers were periodically removed. Records for suckers selected to grow as Cycle 2 or 3 were kept on individual plant basis. These included periodic growth monitoring parameters and dates of flowering (i.e. emergence of the flower bud out of the pseudostem) and harvest. The growth parameters, assessed at approximately 4-week intervals, were plant height (cm) as the length from ground level up to the vertex of insertion into the pseudostem of the youngest pair of leaves and girth at base (cm) as the circumference around the pseudostem at ground level.

At each growth monitoring data collection routine (hereafter referred to as 'event'), A_L, W_L and W_T per plant were estimated from plant height and/or girth data using allometric functions reported in Nyombi et al. (2009). The allometric functions were developed from plants sampled from the same trials as the study herein reported. At each site, an automatic weather station (HOBO®; Onset Computer Corporation, Massachusetts, USA) was installed for recording daily rainfall and air temperature data. The physiological age, TSUM (°C d) of each plant at a given event n days after emergence, was computed as the growing degree days from Eq. 4.01:

$$T_{SUM} = \sum_{i=1}^{i=n} \max\left(0, \frac{T_{MIN(i)} + T_{MAX(i)}}{2} - T_{BASE} \right) \quad \text{... Eq. 4.01}$$

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

Growth analysis was performed on data for events falling between 6 and 4 months pre-flowering because the plants were still within the exponential growth phase, which is assumed in Eq. 4.02. Plants were considered to be at 6, 5 and 4 months pre-flowering if the event occurred within the ranges 194 to 166, 165 to 136 and 135 to 106 d, respectively before the date of flowering. The total dry mass per plant and physiological age at successive events were used to estimate the RGR ($^{\circ}$Cd^{-1}) for each plant in the net plot following the classical approach to growth analysis (Eq. 4.02) according to Hunt (2003).

$$RGR = \left(1/W_T\right) \times \left(dW_T/dT_{SUM}\right) \equiv \left(\ln W_{T(i)} - \ln W_{T(i-1)}\right)\Big/\left(T_{SUM(i)} - T_{SUM(i-1)}\right) \ldots\ldots\ldots\ldots\text{ Eq. 4.02}$$

where $W_{T(i)}$ and $W_{T(i-1)}$ are the total dry masses (kg) of the plant at the current and immediate preceding event, respectively, while $T_{SUM(i)}$ and $T_{SUM(i-1)}$ are the physiological ages ($^{\circ}$Cd) of the plant at the current and immediate preceding event, respectively. The absolute growth rate, AGR (kg $^{\circ}$Cd^{-1}) was estimated per plant using Eq. 4.03, while NAR (kg m^{-2} $^{\circ}$Cd^{-1}), LMR (kg kg^{-1}) and SLA (m^2 kg^{-1}) were estimated for each plant in the net plot using Eqs. 4.04, 4.05 and 4.06, respectively.

$$AGR = dW_T/dT_{SUM} \equiv \left(W_{T(i)} - W_{T(i-1)}\right)\Big/\left(T_{SUM(i)} - T_{SUM(i-1)}\right) \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{ Eq. 4.03}$$

$$NAR = \frac{1}{A_L} \times \frac{dW_T}{dT_{SUM}} \equiv \frac{\left(\ln A_{L(i)} - \ln A_{L(i-1)}\right)}{\left(A_{L(i)} - A_{L(i-1)}\right)} \times \frac{\left(W_{L(i)} - W_{L(i-1)}\right)}{\left(T_{SUM(i)} - T_{SUM(i-1)}\right)} \ldots\ldots\ldots\ldots\text{ Eq. 4.04}$$

$$SLA = A_{L(i)}\Big/W_{L(i)} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{ Eq. 4.05}$$

$$LMR = W_{L(i)}\Big/W_{T(i)} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{ Eq. 4.06}$$

where $T_{SUM(i)}$, $T_{SUM(i-1)}$ and $W_{T(i)}$ are as defined for Eq. 4.02; $A_{L(i)}$ and $A_{L(i-1)}$ are the leaf area (m^2) at the current and immediate preceding event, respectively; $W_{L(i)}$ and $W_{L(i-1)}$ are the leaf dry mass (kg) at the current and immediate preceding event, respectively.

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

4.2.3. Data analysis

From a preliminary analysis of the data, contrasts between 150 kg N ha^{-1} yr^{-1} (treatment $N_{150}K_{600}$; Table 4.1) and 400 kg N ha^{-1} yr^{-1} (treatments $N_{400}K_{600}$, $N_{400}K_0$ and $N_{400}K_{250}$; Table 4.1) for plant height and girth at base at a given event and site were not significant. Likewise, contrasts between 250 kg K ha^{-1} yr^{-1} (treatment $N_{400}K_{250}$; Table 4.1) and 600 kg K ha^{-1} yr^{-1} (treatments $N_{400}K_{600}$, N_0K_{600} and $N_{150}K_{600}$; Table 4.1) for height and girth at base at a given event were also not significant. Variances for plant height and girth at base for treatments $N_{400}K_{600}$, N_0K_{600}, $N_{150}K_{600}$ and $N_{400}K_{250}$ were homogenous but different from those for treatments N_0K_0 and $N_{400}K_0$, which in turn had homogenous variances at a given site. For the purpose of this study therefore, plants from $N_{400}K_0$ were isolated in a group that received N but not K, while those from N_0K_{600} were isolated in a group that received K but not N. Plants from N_0K_0 were isolated in another group that received no external nutrient inputs while those from $N_{400}K_{600}$, $N_{150}K_{600}$ and $N_{400}K_{250}$ were pooled in a group that received both N and K.

Physiological and chronological age (number of days from emergence to flowering) at flowering data were subjected to analysis of variance (ANOVA) using unbalanced treatment structure with crop cycle and blocks (replication) as confounding variables in GenStat 15.0 (Payne et al., 2003). The sequence of factors (Site, K and N) in the ANOVA did not affect the output. To investigate the possibility that differences in threshold total dry mass at flowering between sites underlay rejection of the null hypothesis that physiological age at flowering is independent of site effects, boundary line analysis was used to explore the relationship between maximum physiological age at flowering and total dry mass at flowering, separately for each site. The points defining the upper limit of the data cloud in a scatterplot of physiological age vs. total dry mass at flowering (Fig. 4.1) were identified following the BOLIDES algorithm, excluding outliers identified using the rectangle criterion (Schnug et al., 1996). The boundary points

were then fitted to a model developed based on the assumption that highland banana plants delay flowering to maximise accumulation of total dry mass while their physiological age at flowering approaches an asymptotic maximum A $^{\circ}$Cd.

Based on the rational gambling decision rule described by Metcalf et al. (2003) for flowering in monocarpic perennial plants, the model expressed in Eq. 4.07 was assumed to describe the optimal solution to the trade-off between delaying flowering and curtailing further dry mass accumulation in highland banana above the threshold total dry mass for flowering.

$$y_i = A \times (x_i - C)\big/\big[B + (x_i - C)\big]$$ .... Eq. 4.07

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

The model parameters A, B and C were estimated using numerical optimisation conditioned on minimising the coefficient of variation of the root mean square error (CRMSE) between observed and predicted maximum physiological age at flowering. The CRMSE was computed according to Eq. 4.08. Correspondence between observed and fitted optimisation model predictions of boundary points was evaluated using the squared correlation coefficient (R^2) computed using Eq. 4.09.

$$C_{RMSE} = \left[\frac{1}{n}\sum_{i=1}^{n}\left(y_i^o - y_i^p\right)^2\right]^{0.5}\Big/\bar{y}_i^o$$ .... Eq. 4.08

$$R^2 = 1 - \left[\sum_{i=1}^{n}\left(y_i^o - y_i^p\right)^2\Big/\sum_{i=1}^{n}\left(y_i^o - \bar{y}_i^o\right)^2\right]$$ .... Eq. 4.09

where y_i^o and y_i^p are the observed and predicted maximum physiological age ($^{\circ}$Cd); $\bar{y}_i^o$ is the mean observed maximum physiological age ($^{\circ}$Cd).
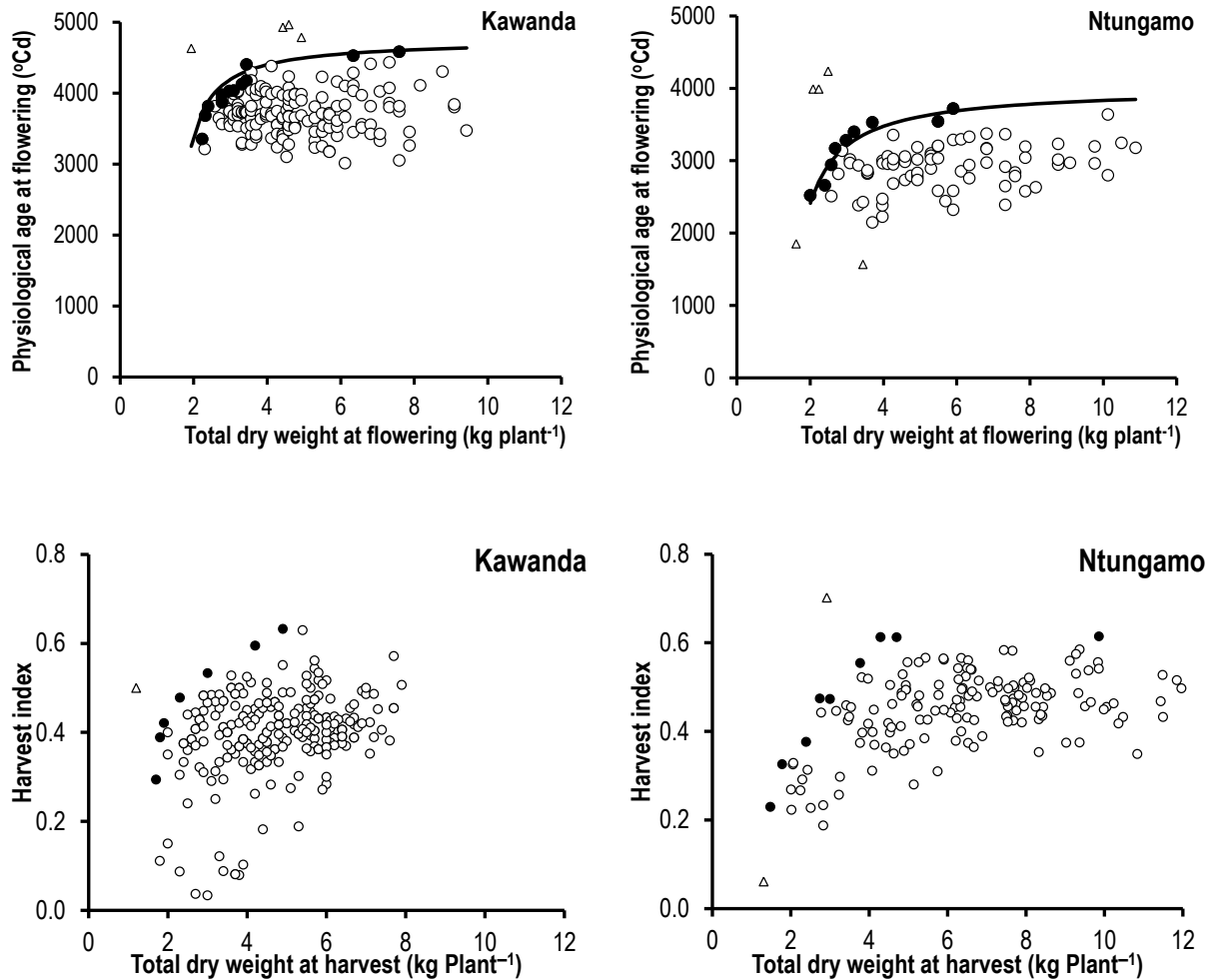
Fig. 4.1: Boundary points for the relationship between maximum physiological age vs. total dry mass at flowering, and harvest index vs. total dry mass at harvest of E. African highland banana in central (Kawanda) and south-western (Ntungamo) Uganda, respectively.

Filled circles are boundary points while open triangles are outliers based on the rectangle criterion (Schnug et al., 1996).

The threshold dry weight was also computed from the relationship between harvest index and total dry weight per plant, which is described by a hyperbolic function. The intercept of this relationship is the threshold dry weight required for a plant to flower (Moot, 1997). The harvest index was computed as the ratio of bunch dry mass to the total dry mass. Points defining the upper limit of the data cloud in a scatter plot of harvest index (ratio of bunch dry matter to total dry weight) vs. total dry weight (Fig 4.1) were identified using the BOLIDES algorithm, excluding outliers identified using the rectangle criterion (Schnug et al., 1996). Taking only the boundary points, the inverse of the

harvest index was subjected to linear regression against the inverse of total dry weight to obtain the threshold dry weight as the inverse of the intercept.

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

Analysis of variance following unbalanced treatment structure and adjusting for cycle and block effects as confounding variables in GenStat 15.0 (Payne et al., 2003) was used to evaluate the effect of CRF_{28}, K and N on absolute growth rate, RGR and its components between 4 and 6 months pre-flowering separately for each site. The sequence of factors (CRF_{28}, K and N) in the ANOVA did not affect the output. Growth response coefficients were computed using Eq. 4.10 (Poorter and Nagel, 2000) for the factors that increased RGR and its components to evaluate the relative contribution of morphological and physiological components to RGR at each site.

$$GRC_X = \left(\ln X_H - \ln X_L\right)\big/\left(\ln RGR_H - \ln RGR_L\right) \dots\dots\dots\dots\dots\dots\dots\dots\text{Eq. 4.10}$$

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

According to Poorter and Nagel (2000), the sum of growth response coefficients is one, if RGR and its components are well estimated at the different levels of the influential factor. The greater the value of the growth response coefficient for a given RGR component, the higher the contribution of that component to the observed decrease in RGR with respect to the influential factor at the growth-limiting low level. When a given component has a growth response coefficient greater than one, its effect on RGR is

counterbalanced by negative growth response coefficients for one or both of the remaining components in a trade-off manner.

4.3. Results

4.3.1 Rate of banana phenological development

Plants grown at Ntungamo flowered at a younger physiological age than those grown at Kawanda by 739 °Cd. However, plants grown at Kawanda flowered at an older chronological age than those grown at Ntungamo by 51 days. The physiological age at harvest for plants grown at Ntungamo was also younger than that for plants grown at Kawanda by 949 °Cd while the reverse was true for chronological age at harvest, which was older for plants grown at Ntungamo than for plants grown at Kawanda by 60 days. Likewise, bunch filling duration for plants grown at Ntungamo was shorter than that for plants grown at Kawanda by 217 °Cd with respect to physiological time but 7 days longer with respect to chronological time (Table 4.2).

The physiological and chronological age at flowering and harvest for plants that received no N were both greater than the corresponding values for plants that received N (Table 4.2) but there was no difference in bunch-filling duration due to N. On its own, K had no effect on rate of phenological development. However, plants grown at Ntungamo that received K had younger physiological age at flowering and at harvest than those that received no K. There was no difference in physiological age at flowering between K rates for plants grown at Kawanda. There was also no difference in chronological age at harvest between K rates for plants grown at Kawanda (Fig. 4.2).

Plants grown at Ntungamo required a threshold total dry mass (parameter *C*, Eq. 4.07) of 1.45 kg per plant to flower, which was similar to the corresponding value of 1.56 kg per plant for plants grown at Kawanda (Table 4.3). These values were similar to 1.37 and 1.47 kg per plant obtained for Kawanda and Ntungamo (Fig. 4.3), respectively using the method by Moot (1997). The characteristic total dry mass at half the asymptotic maximum physiological age at flowering (parameter B, Eq. 4.07) for plants grown at Ntungamo (0.38 kg per plant) was greater than that for plants grown at Kawanda by 0.14 kg per plant. However, the asymptotic maximum physiological age at flowering (parameter A, Eq. 4.07) for plants grown at Kawanda (4761 °Cd) was older than that for plants grown at Ntungamo by about 750 °Cd (Table 4.3).

Table 4.2: Effects of potassium (K) and nitrogen (N) on rate of phenological development and bunch-filling duration of East African highland bananas in central (Kawanda) and south western (Ntungamo) Uganda.

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

[z]Adjusted for crop cycle and replication effects; s.e = standard error of mean; Means for a given factor in the same column followed by the same letter are not significantly different (P>0.05); −K = 0 kg K ha⁻¹ yr⁻¹ applied; +K = 250 to 600 kg K ha⁻¹ yr⁻¹ applied; −N = 0 kg N ha⁻¹ yr⁻¹ applied; +N = 150 to 400 kg N ha⁻¹ yr⁻¹ applied. All interactions after S × K (not shown) were not significant.
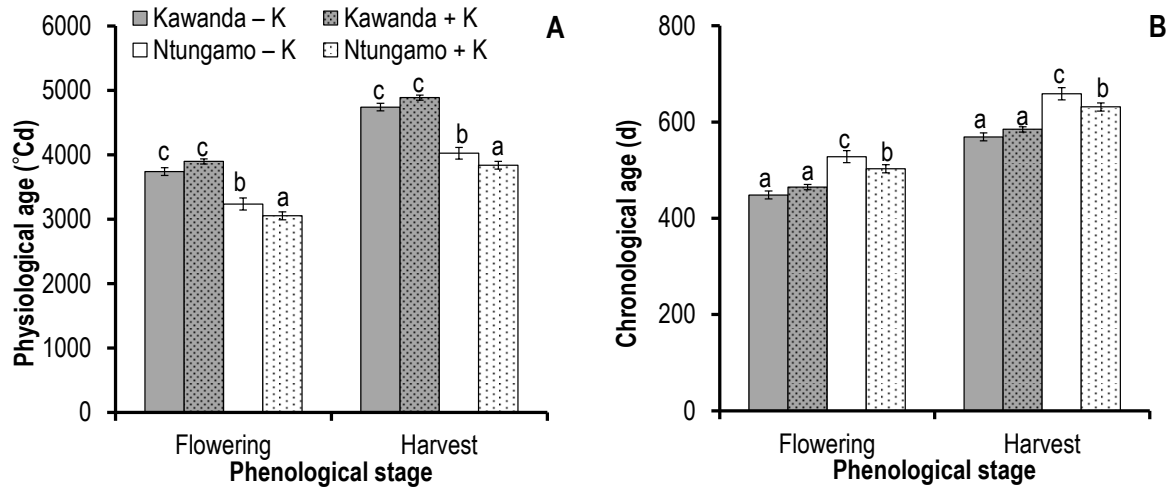
Fig. 4.2: Site × potassium (K) interaction effects on physiological age (**A**) and chronological age (**B**) at flowering and harvest stage of East African highland banana over 2 crop cycles in central (Kawanda) and south western (Ntungamo) Uganda.

Means are adjusted for crop cycle and replication effects; Error bars are standard errors of means; Means crowned with the same lower case letter at a given phenological stage are not significantly (P>0.05) different; −K = 0 kg K ha^{-1} yr^{-1} applied; +K = 250 to 600 kg K ha^{-1} yr^{-1} applied.

Table 4.3: Comparison of numerical optimisation model parameter estimates in central (Kawanda) and south western (Ntungamo) Uganda.

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

Parameter C (kg per plant) is the threshold total dry mass for flowering; B (kg per plant) is an empirical characteristic dry mass halfway to parameter A, and; A (^{o}Cd) is the potential physiological age at flowering; se = standard error of mean; CRMSE = mean coefficient of variation for the root mean square error from jacknifed pseudo values; R^2 = mean square correlation coefficient from jacknifed pseudo values; df = degrees of freedom, ^{z}adjusted for non-homogeneous variances; t^{ns} = Not significant (2-tailed) at 95.0% confidence level; t^{**} and t^{***} = significant (2-tailed) at 99.0 and 99.9% confidence levels, respectively.
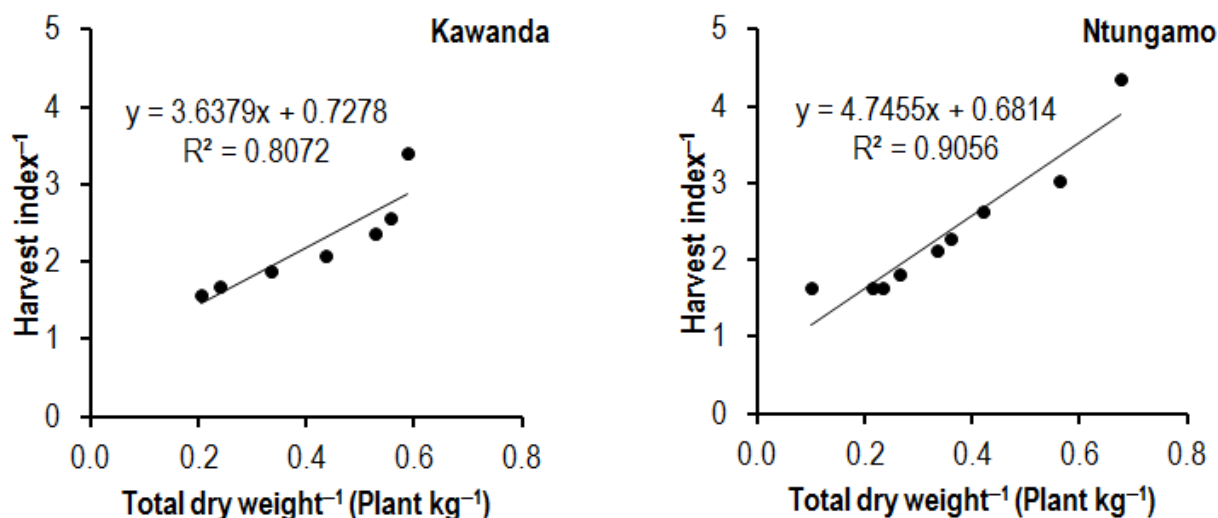
Fig. 4.3: Relationship between harvest index and total dry weight at harvest of East African highland banana in central (Kawanda) and south western (Ntungamo) Uganda.

Threshold dry mass for flowering is the inverse of the intercept at each site according to Moot, 1997.

4.3.2. Effect of rainfall, potassium and nitrogen on growth

Compared at the same phenological stage relative to flowering, plants that received K had greater total dry mass than those that received no K by 30 to 80% between 6 months pre-flowering and 3 months post-flowering (Fig 4.4A). Leaf dry mass exhibited similar trends and magnitudes of change as total dry mass in response to K (data not shown). Leaf area on the other hand increased by up to 26% with K application between 6 months pre-flowering and 3 months post flowering (Fig 4.4D). Compared at the same phenological stage between 6 months pre-flowering and 3 months post-flowering, CRF_{28} and N had no effect on total dry mass (Fig. 4.4B and 4.4C, respectively) and leaf area (Fig. 4.4E and 4.4F, respectively). Plants that received no K at Ntungamo were generally more stunted than corresponding plants at Kawanda. From 3 to 1 months pre-flowering, plants that received K at Ntungamo had higher total dry mass and larger leaf area than corresponding plants at Kawanda but from flowering stage up to 3 months post-flowering, this difference was no longer significant (data not shown).

Absolute growth rates from 6 to 4 months pre-flowering were mainly affected (in descending order of magnitude) by CRF_{28}, Site and K. Wet conditions in the 28 day-period preceding an event between 6 and 4 months pre-flowering gave thrice the absolute growth rate relative of dry conditions. Plants grown at Ntungamo had twice the absolute growth rate of those grown at Kawanda.
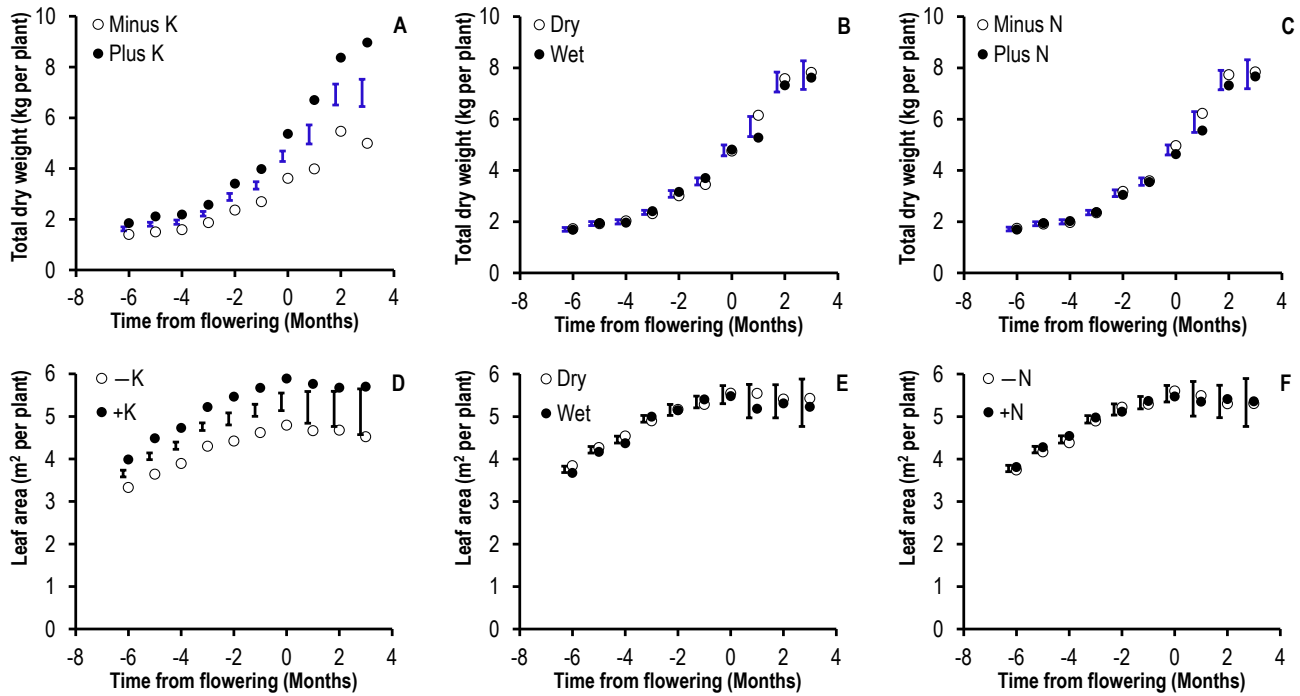
Fig. 4.4: Effects of potassium (K), rainfall and nitrogen (N) on total dry mass (**A, B and C,** respectively) and leaf area (**D, E and F,** respectively) of East African highland banana between 6 months pre-flowering and 3 months post-flowering in Uganda.

Means are adjusted for crop cycle and replication effects; Bars alongside each pair of means are least significant differences at 95% confidence level; −K = 0 kg K ha^{-1} yr^{-1} applied; +K = 250 to 600 kg K ha^{-1} yr^{-1} applied; −N = 0 kg N ha^{-1} yr^{-1} applied; +N = 150 to 400 kg N ha^{-1} yr^{-1} applied; Wet is cumulative rain fall received in preceding 28-day period (CRF$_{28}$) ≥ 84 mm; Dry is CRF$_{28}$ < 84 mm.

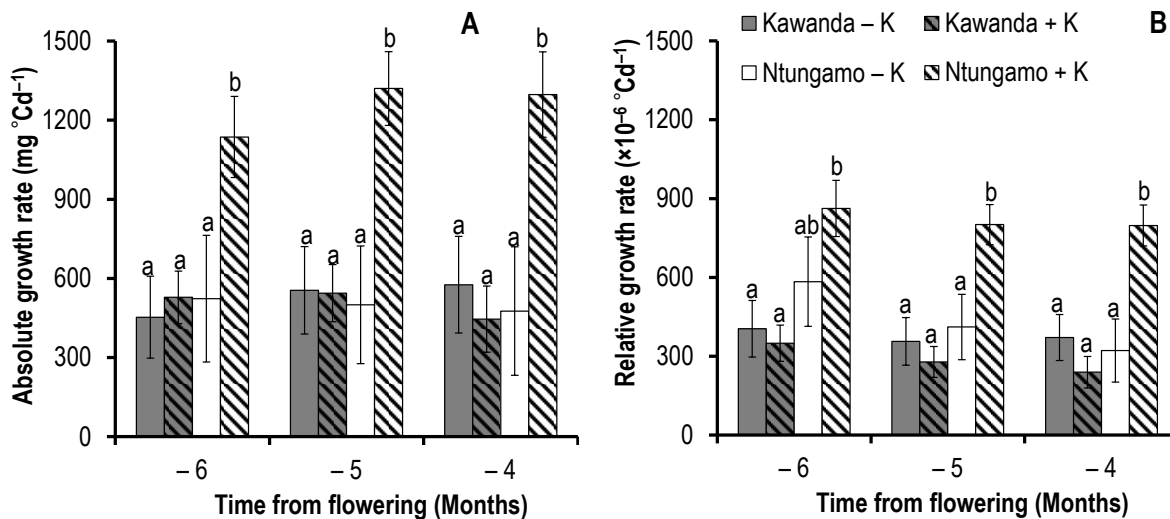**Fig. 4.5:** Site × potassium (K) interaction effects on absolute growth rate (**A**) and relative growth rate (**B**) of East African highland banana at Kawanda (central Uganda) and Ntungamo (south-western Uganda).

Means crowned with the same lower case letter at a given time from flowering are not significantly (P>0.05) different −K = 0 kg K ha^{-1} yr^{-1} applied; +K = 250 to 600 kg K ha^{-1} yr^{-1} applied.

Table 4.4: Variation of absolute growth rate and relative growth rate of East African highland banana at 6, 5 and 4 months pre-flowering with site, potassium (K) rainfall (CRF_{28}) and nitrogen (N) input.

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

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

Table 4.5: Variation of net assimilation rate and specific leaf area of East African highland banana at 6, 5 and 4 months pre-flowering with site, potassium (K) rainfall (CRF_{28}) and nitrogen (N) input.

| | | Net assimilation rate (mg m⁻² (°Cd)⁻¹) | | | | | | Specific leaf area (m² kg⁻¹) | | | | | |
| | | 6 Months pre-flowering | | 5 Months pre-flowering | | 4 Months pre-flowering | | 6 Months pre-flowering | | 5 Months pre-flowering | | 4 Months pre-flowering | |
Factor	Level	n	ᶻMean ± se	n	ᶻMean ± se	n	ᶻMean ± se	n	ᶻMean ± se	n	ᶻMean ± se	n	ᶻMean ± se
Site	Kawanda	205	160 ± 23.1 a	162	138 ± 21.6 a	146	122 ± 23.2 a	205	11.9 ± 0.12 a	162	11.9 ± 0.13 a	146	12.3 ± 0.15 a
	Ntungamo	118	321 ± 35.8 b	117	289 ± 28.2 b	110	285 ± 30.1 b	118	12.7 ± 0.19 b	117	12.7 ± 0.17 b	110	12.7 ± 0.20 a
Potassium	−K	99	176 ± 36.9 a	83	160 ± 32.3 a	76	144 ± 33.7 a	99	12.7 ± 0.19 b	83	13.1 ± 0.20 b	76	13.3 ± 0.22 b
	+K	219	238 ± 23.3 b	196	218 ± 20.1 b	180	212 ± 22.1 b	219	12.0 ± 0.12 a	196	11.9 ± 0.12 a	180	12.1 ± 0.15 a
CRF_{28}	Dry	210	119 ± 24.1 a	188	121 ± 20.9 a	160	104 ± 22.5 a	210	12.3 ± 0.13 a	188	12.3 ± 0.13 a	160	12.6 ± 0.15 a
	Wet	108	410 ± 34.1 b	91	365 ± 30.1 b	96	338 ± 31.7 b	108	12.0 ± 0.18 a	91	12.0 ± 0.19 a	96	12.4 ± 0.21 a
Nitrogen	−N	123	233 ± 34.1 a	105	177 ± 29.8 a	99	209 ± 32.9 a	123	12.0 ± 0.18 a	105	12.3 ± 0.18 a	99	12.5 ± 0.22 a
	+N	195	209 ± 24.2 a	174	215 ± 20.9 a	157	181 ± 22.4 a	195	12.3 ± 0.13 a	174	12.2 ± 0.13 a	157	12.5 ± 0.15 a
Source of variation													
Crop cycle (C)			<0.001		0.494		0.650		<0.001		<0.001		<0.001
Replication (Rep)			0.280		0.115		0.720		0.055		0.066		0.072
C × Rep			0.719		0.217		0.595		0.111		0.022		0.006
Site (S)			<0.001		<0.001		<0.001		0.069		0.007		0.383
Potassium (K)			0.003		0.026		0.161		<0.001		<0.001		<0.001
CRF_{28}			<0.001		<0.001		<0.001		0.025		0.439		0.717
Nitrogen (N)			0.682		0.122		0.904		0.159		0.415		0.870
S × K			0.265		0.010		0.003		0.747		0.130		0.009

ᶻMeans were adjusted for site, cycle and replication effects; se = Standard error of mean; Means for a given factor in the same column followed by the same letter are not significantly different (P>0.05); −K = 0 kg K ha⁻¹ yr⁻¹ applied; +K = 250 to 600 kg K ha⁻¹ yr⁻¹ applied; CRF_{28} = cumulative rainfall received in preceding 28 days; Dry is CRF_{28} < 84 mm; Wet is CRF_{28} ≥ 84 mm; −N = 0 kg N ha⁻¹ yr⁻¹ applied; +N = 150 to 400 kg N ha⁻¹ yr⁻¹ applied; All interactions after S × K (not shown) were not significant.
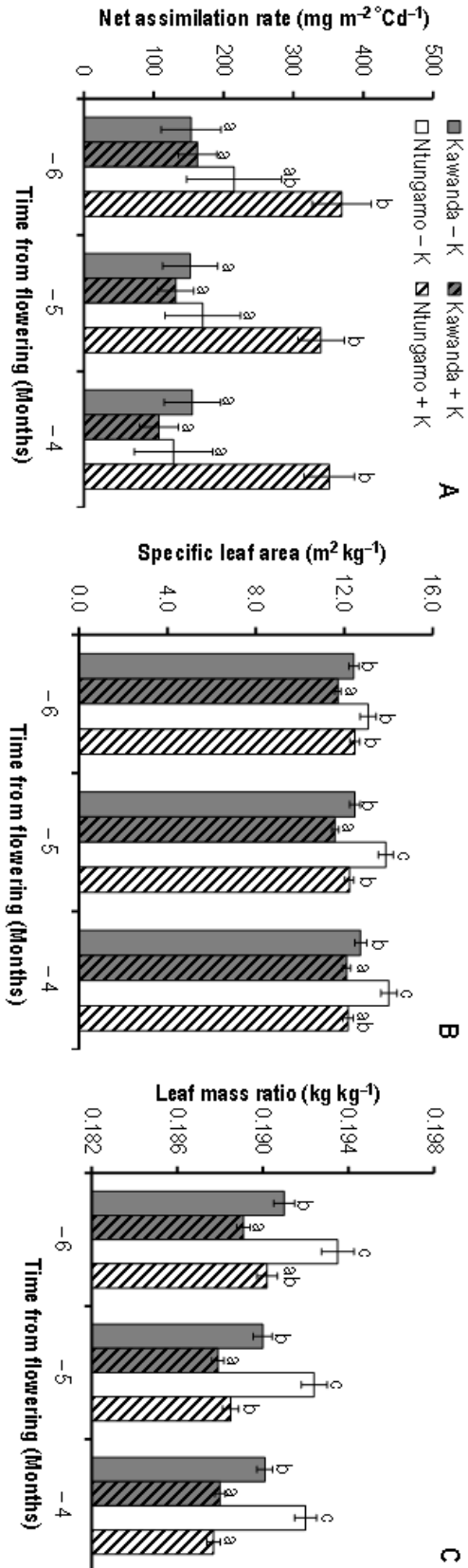
Fig. 4.6: Site × potassium (K) interaction effects on net assimilation rate (**A**), specific leaf area (**B**) and leaf area ratio (**C**) of East African highland banana at Kawanda (central Uganda) and Ntungamo (south-western Uganda).

Means are adjusted for crop cycle and replication effects; Error bars are standard errors of means; Means crowned with the same lower case letter at a given time from flowering are not significantly (P>0.05) different −K = 0 kg K ha⁻¹ yr⁻¹ applied; +K = 250 to 600 kg K ha⁻¹ yr⁻¹ applied.

In general, the absolute growth rate for plants that received K was approximately 1.5 times greater than that for plants that received no K but the effect was only significant at 6 and 5 months pre-flowering (Table 4.4). Plants that received no K at Ntungamo had lower absolute growth rate than their counterparts that received K. Between K rates, plants grown at Kawanda had similar absolute growth rates (Fig. 4.5). The effect of N on absolute growth rate was not significant (Table 4.4).

The effects and trends observed on absolute growth rate were also exhibited on RGR (Table 4.4, Fig. 4.5) and its physiological component NAR (Table 4.5, Fig. 4.6). The morphological components of RGR displayed different trends in direction and order of magnitude with respect to Site, CRF_{28}, K and N. From 6 to 4 months pre-flowering, plants that received no K had 6 to 10% greater SLA than plants that received K. Plants that received no K allocated about 1% more ($P<0.001$) of their total dry matter to the leaves (LMR) compared with plants that received K (data not shown) with this effect being significantly stronger for plants grown at Ntungamo than for corresponding plants grown at Kawanda (Fig 4.6).

4.3.3. Contribution of relative growth rate components

Net assimilation rate accounted for the largest proportion ($\geq$ 90%) of the observed increase in RGR at both sites in response to wet conditions. In response to K, however, NAR contributed only 38% to the observed increase in RGR at Kawanda while SLA contributed 49% (Table 4.6). At Ntungamo, the largest proportion of the observed change in RGR in response to K was due to NAR (Table 4.6). However, the effect of NAR on RGR was counterbalanced by a 10% opposing change in RGR due to SLA at Ntungamo in response to K. Leaf mass ratio had no contribution to the observed RGR change in response to K supply at Ntungamo (Table 4.6).

Table 4.6: Growth response coefficients for net assimilation rate, specific leaf area and leaf mass ratio of East African highland banana 6 to 4 months pre-flowering with respect to potassium and rainfall (CRF_{28}) at Kawanda (central Uganda) and Ntungamo (south-western Uganda).

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

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

4.4. Discussion

4.4.1. Trade-off between physiological and chronological age

The highland banana plants in this study exhibited phenotypic plasticity with respect to age at flowering and harvest across the experimental sites (Table 4.2). As expected, Kawanda's higher effective temperature led to lower chronological age at flowering and at harvest than corresponding values at Ntungamo (Table 4.2). However, if physiological age would have been the same across sites, then Ntungamo plants should have taken about 121 days more than Kawanda plants instead of the 51 days observed (Table 4.2). Therefore, contrary to Hypothesis 1 in the current study, flowering (and harvest) was greatly hastened at Ntungamo in physiological time (Table 4.2). This phenotypic plasticity with respect to physiological age at flowering and harvest suggests that size or total dry mass already accumulated by the plant may matter a lot in highland banana development, as has been shown to be the case with other monocarpic biennials and perennials (Klinkhamer et al., 1987). Growth and development in plants are governed by the rate of metabolic processes, which in turn are dependent on temperature and size (Gillooly et al., 2001). Since there was no difference in the size (as total dry mass) at flowering and threshold size for flowering (Table 4.3) between the sites, it is plausible that difference in growth rate, rather than size per se was responsible for the observed phenotypic plasticity in physiological age at flowering across the sites.

The higher characteristic total dry mass (parameter B value) and younger asymptotic maximum physiological age at flowering (parameter A value) for plants grown at Ntungamo compared with corresponding values for plants grown at Kawanda (Table 4.3) indicate that the absolute crop growth rate for plants grown at Ntugngamo was about 88% faster than that of plants grown at Kawanda. This coincides with the results from ANOVA on absolute crop growth rate between 4 and 6 months pre-flowering (Table 4.4). Turner and Lahav (1983) reported bananas to have a smaller NAR and reduced accumulation of total dry mass with rise in day temperature above 25 °C, which they attributed to increase in maintenance respiration. Between 30 and 70% of fresh photo-assimilates are lost on the same day due to maintenance respiration (van der Werf et al., 1994; Atkin et al., 1996). The degree of thermal acclimation, which can alter the relative change in rates of photosynthesis and respiration in plants with increase in ambient temperature, has been shown to vary with plant functional groups and species (Larigauderie and Korner 1995; Niu et al. 2008). In general, however, the rate of maintenance respiration increases faster than the rate of photosynthesis with rising

temperature (Liang et al., 2013) leading to a reduction in NAR and hence slower rate of dry mass accumulation with increase in temperature. Indeed, the NAR at Ntungamo was faster than that at Kawanda (Table 4.5). The faster absolute growth rate at Ntungamo may thus have been due to lower maintenance respiration carbon costs charged against photo-assimilates under the cooler ambient temperature regimes at Ntungamo than those at Kawanda. This may have enabled Ntungamo plants to attain the threshold size for flowering sooner than Kawanda plants leading to the observed phenotypic plasticity in physiological age at flowering and at harvest across the sites.

Differences in absolute growth rate as determined by the rates of photosynthesis and maintenance respiration may also explain the significant Site × K interactions on physiological age at flowering and at harvest (Fig. 4.2). Potassium stimulates photosynthesis through activation of photosynthetic enzymes and loading of photo-assimilates into the phloem for translocation to various sinks thereby removing the negative feedback, which the assimilates' accumulation in leaves exerts on photosynthesis (Pettigrew, 2008; Gerardeaux et al., 2010). However, the effect of K input on total dry mass accumulation through increased photosynthesis may have been masked at Kawanda due to size-induced increase in maintenance respiration carbon costs (Amthor, 1984; Gillooly et al., 2001). Kawanda plants that received K were on average about 20 to 40% greater in total dry mass than their counterparts that received no K (data not shown). The combined effect of warmer temperature and greater size may have increased maintenance carbon costs charged against photo-assimilates to such an extent that differences in the NAR between K rates at Kawanda were masked. With similar NAR (Table 4.5) and hence similar crop growth rates (Fig. 4.5A) between K rates, plants required similar amount of time to attain the threshold size for flowering resulting in similar physiological age at flowering and harvest at Kawanda, unlike at Ntungamo (Fig. 4.2).

The cumulative amount of rainfall received over a 28-day period preceding an event tripled the absolute growth rate (Table 4.4). Banana plants are particularly sensitive to soil water supply and rapidly close their stomata under constrained water supply from the soil (Turner et al., 2008; Carr, 2009). However, CRF_{28} did not affect total dry mass accumulation (Fig. 4.4B). It is probable that the 4-week interval considered in this study was too short for substantial effects of CRF_{28} on total dry mass accumulation to be realised with only 6 months to flowering. van Asten et al. (2011) found a strong impact of drought stress within 12 months to harvest on fresh bunch yield. Fresh bunch yield is

linearly related to total dry mass of banana biomass and so it is likely that over time, drought stress delays flowering (Carr, 2009; Damour et al., 2012).

Delay in flowering without N application (Table 4.2) may have arisen from reduced light use efficiency due to N deficiency (Zhao et al., 2005). This may have resulted in reduced rate of dry mass accumulation. Plants then took longer to attain the threshold dry mass for flowering or building reserves for supporting bunch filling after flower emergence. This may also explain the similarity in total dry mass at flowering with and without N (Fig. 4.4C). These results corroborate those of Damour et al. (2012). Similar to the 0 to 450 kg N ha^{-1} yr^{-1} applied in the current study, Darmour et al. (2012) applied 0 to 420 kg N ha^{-1} yr^{-1}, but also got no difference in girth at base at flowering stage between the N rates. Girth at base is related to the total dry mass (Nyombi et al., 2009) and fresh bunch weight (Wairegi et al., 2009) of banana. Damour et al. (2012) also reported 40- and 70-day delays to flowering for the second and third crop cycle, respectively, of Cavendish bananas (cv. Grand Nain) in response to withholding N in the French West Indies.

The mean bunch filling duration (i.e. difference between age at flowering and age at harvest), was generally around 930 °Cd between N and K rates (Table 4.2). This is comparable to the 970 °Cd reported by Umber et al. (2011) and the range 950 – 1120 °Cd reported by Bugaud et al. (2009). Both studies used a base temperature of 14 °C. The mean bunch filling duration at Kawanda (1008 °Cd) was also within the range of values published in literature. However, the mean bunch filling duration at Ntungamo (791 °Cd) was rather short compared with the range reported in literature. The chornological bunch filling duration for Kawanda is comparable to the mean bunch filling duration range of 100 to 121 days reported by Bugaud et al. (2006). Given that the difference in effective temperature between Ntungamo and Kawanda was only 2.3 °C, the difference in bunch filling chronological duration (7 days) is short compared with the observed difference in growing degree days (217 °Cd). Altogether, the results suggest that apart from accumulating a certain heat sum, rapid rate of production of assimilates can to some extent reduce the physiological and chronological age to flowering and bunch maturity in highland banana.

4.4.2. Relative contribution of physiological and morphological components

Specific leaf area was significantly larger among plants that received no K compared with those that received K (Table 4.5), especially for plants grown at Ntungamo (Fig. 4.6B) where K deficiency was more pronounced. Plants that received no K exhibited a

response similar to plants subjected to shading, which increase their SLA as a morphological strategy for maximising light interception per unit of dry matter under low light intensity conditions (Poorter et al., 2009). However, plants that received no K in the current study had smaller leaf area (Fig. 4.4D). The increase in SLA is thus unlikely to have resulted from low light intensity due to increased mutual leaf shading within the canopy. Moreover, banana leaf lamina expansion, and hence leaf area, is complete by the time the leaf emerges from the pseudostem and unfurls (Turner et al., 2008). Impaired assimilate production and translocation to the developing leaves, as reported in K-deficient cotton plants (Gerardeaux et al., 2010), may have caused the increase in SLA among plants that received no K in the current study rather than mutual shading. This is supported by the higher LMR of plants that received no K, especially at Ntungamo (Fig. 4.6C). Gerardeaux et al. (2010) also observed an increase in fraction of total biomass allocated to the leaves in K-deficient cotton plants which they attributed to assimilates retained in the leaves due to impaired translocation. Similar to the responses of herbaceous species (Shipley, 2006), LMR had minimal contribution to the increase in RGR with increase in CRF_{28} and K application at both sites, according to their respective growth response coefficients unlike NAR and SLA (Table 4.6).

The inversion in the contribution of NAR to the observed increase in RGR at Kawanda with increase in CRF_{28} and K (Table 4.6) may be due to the coupling of the effects of rainfall with those of temperature, unlike with the effects of K. The mean maximum daily temperature on wet days (at least 3 mm of rainfall per day) was lower (t = 7.305; df = 728; 2-tailed significance <0.001) than that on dry days by 1.1 °C. This may have reduced maintenance respiration losses of carbon at Kawanda thus increasing NAR and its contribution to the observed increase in RGR in response to wet conditions but not in response to K. However, Kawanda plants that received K had the smallest SLA (Fig. 4.6B), which is associated with high light use efficiency. Leaves with small SLA have more layers of palisade cells (Nishio et al., 1993), which effectively increases the chloroplast density per unit leaf area and capture of photosynthetically active radiation with concomitant increase in carbon dioxide conductance (Syvertsen et al., 1995), thereby enhancing light use efficiency. Higher light use efficiency among plants that received K may thus explain the increased contribution of SLA to the observed increase in RGR compared with the contribution from NAR with respect to K at Kawanda (Table 4.6). This finding is in line with that by Nyombi (2010) whose highland banana growth simulation model revealed that plants grown at Kawanda had higher light use efficiency

than those grown at Ntungamo. Plants grown at Ntungamo with no K input had the largest SLA (Fig. 4.6B) and are thus likely to have had lower light use efficiency, which may have contributed to the negative growth response coefficients for SLA observed at Ntungamo (Table 4.6).

4.5. Conclusions

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

"Not everything that counts can be counted, and not everything that can be counted counts"- Albert Einstein

CHAPTER FIVE

5.0. Simulation of the East African highland banana soil water balance: model description and sensitivity analysis

Abstract

The aim of this study was to develop a model for designing and evaluating crop water management practices in East African Highland banana (*Musa* sp. AAA-EA, hereafter called 'banana') systems. The specific objective was to identify input parameters for model calibration. The model was adapted to the perennial banana cropping system from an annual crop framework, LINTUL2. The adapted model was used to simulate the soil water balance at two sites in Uganda with a daily time step from 1 January to 31 December in 2006 and 2007. On-site weather data and input parameter default values (either measured or derived/estimated from literature) were used. The simulations were rerun to evaluate changes in the output state variables (the soil water balance components *viz.* root zone water content, canopy transpiration, drainage and evaporation from soil) in response to ±1% changes in a given input parameter value relative to the default values (central difference method around the default value). For a given input parameter-state variable combination, sensitivity coefficients and their time-averaged arithmetic mean ($\bar{C}$) were computed for each site and each year. A component was considered insensitive to a given parameter if $-10\% < \bar{C} < +10\%$; otherwise, it was deemed to be sensitive. The components were mostly sensitive to the weather parameters rainfall, net radiation, temperature, vapour pressure and wind speed, whose $\bar{C}$ values ranged from 12 to 1340%. The $\bar{C}$ values in response to soil water content at field capacity for root zone water content and canopy transpiration were 21 to 99% and 18 to 57%, respectively. The $\bar{C}$ values in response to soil water content at permanent wilting point for root zone water content were 23 to 35%, while those for drainage and evaporation from the soil were 24 to 55% and 24 to 38%, respectively. On the contrary, the $\bar{C}$ values in response to soil water content at permanent wilting point for canopy transpiration were −19 to −14%. Evaporation from the soil was most sensitive to the crop parameters radiation extinction coefficient in the canopy and leaf area indices for Plants 1 to 3. Evaporation from the soil was the only component showing sensitivity to the mulch parameters but it accounted for less than 5% of the water flows in the soil water balance. Calibration of this model at a given site should focus on moisture contents at field capacity and at permanent wilting point, and rooting depth, assuming availability of good quality weather data.

Keywords: *Drainage, Field capacity, Permanent wilting point, Runoff, Soil water storage, Transpiration*

5.1.   Introduction

Drought stress is a major limitation in the rain-fed East African highland banana (hereafter referred to as highland banana) cropping systems of the Great Lakes region of Africa (van Asten et al., 2011). There is lack of information for optimising management interventions against the dynamic shifts in the strain between crop water requirements and water supply from the soil in these systems. Irrigation studies for generating the information are costly and time-consuming to conduct in perennial cropping systems. The soil water balance concept has been used to simulate the dynamics of crop water uptake or transpiration as a rapid and cheap means of exploring management interventions for perennial cropping systems in lieu of irrigation field experiments (van Vosselen et al., 2005; Abazi et al., 2013). The general approach involves estimation of a reference evapotranspiration, which is multiplied by a crop coefficient, to obtain the potential transpiration under non-limiting soil water supply or ideal growing conditions. Potential transpiration is multiplied by a transpiration reduction factor (0 to 1) to obtain the actual transpiration under limiting soil water supply or non-ideal growing conditions.

Several equations have been proposed for estimating reference evapotranspiration. Due to their mechanistic character, the combination type of equations such as Penman (1948) and Penman-Monteith (Monteith, 1964), which combine an energy term with a mass transfer term, are said to be more reliable than their largely empirical alternatives such as Thornwaite (1948) and Hargreaves (1974). A modified Penman-Monteith equation, referred to as the FAO 56, was recommended by FAO (Allen, 1998). It is well regarded as a tool for estimating reference evapotranspiration in plants (McMahon et al., 2013) compared with alternative equations. Several studies report satisfactory results based on the FAO 56 approach (e.g. Karam et al., 2007; Teixera et al., 2008; Suleiman et al., 2013). However, the crop coefficient varies with growth stage (Allen, 1998) and growing conditions or cultural practices (Bhattacharyya and Madhava Rao, 1985). The crop coefficient therefore needs to be determined empirically or calibrated for a specific geographical location and cultural management regime (Suleiman et al., 2013).

For purposes of determining the crop coefficient applicable under the FAO 56 guidelines (Allen, 1998), the crop growth cycle is divided into 4 distinct phenological stages namely 'initial' (0-10% ground cover), 'development' (10-100% ground cover), 'mid-season' (100% ground cover till start of senescence) and 'late-season' (start of senescence till harvest). A constant crop coefficient is assumed for the 'initial' stage. Thereafter, the crop coefficient is increased linearly during the 'development' stage up to a constant

maximum value over the 'mid-season' stage. The crop coefficient is then reduced linearly during the 'late-season' stage. The FAO 56 approach therefore assumes a phenologically homogenous crop stand with well-defined or predictable development rates. However, plants of different phenological stages co-exist at a given point in time in established highland banana crop stands. Furthermore, highland bananas exhibit phenotypic plasticity in their development (Taulya et al., 2014), especially in response to water supply (Okech et al., 2004). Therefore, the timing of the beginning- and end-points between contiguous development stages is uncertain and strongly influenced by the dynamics of water stress experienced by a given banana plant. The FAO 56 approach cannot be directly applied to the phenologically diverse established highland banana cropping system. An alternative approach which incorporates the crop effects on transpiration in an index that can be determined dynamically is required. One approach was developed by Brisson (1998). It involves simplification of the basic laws describing the transfer of water along the soil-plant-atmosphere continuum with root water uptake being estimated from an Ohm's law analogue. The approach requires the critical leaf water potential, root length density, mean root radius and bulk soil hydraulic conductivity, which are difficult to estimate empirically. This is in direct contrast to the approach in the simplified plant growth model LINTUL2, adapted from Spitters and Schapendonk (1990).

Originally developed for spring wheat, LINTUL2 simulates water-limited crop growth and production through linkage to a soil water balance model with a single soil layer delimited by the soil surface at the top and the rooting depth at the bottom. Reference transpiration is estimated using the Penman equation (Penman, 1948). Potential transpiration is estimated via attenuation of evaporative energy as a function of the leaf area index. The crop coefficient is thus not a prerequisite for computing potential evapotranspiration from the reference evapotranspiration. The transpiration reduction factor is taken to be 0 if soil water content is below the permanent wilting point. It is taken to be 1 if the soil water content is above a certain critical soil water content, which varies between the permanent wilting point and the field capacity of the soil. The transpiration reduction factor is increased linearly between the permanent wilting point and the critical water content, which in turn is a function of soil, environment and crop parameters (Eq. 5.01).

$$\theta_{cr} = \theta_{pw} + \frac{ET_p}{ET_p + TC}\left(\theta_{fc} - \theta_{pw}\right) \quad \text{...Eq. 5.01}$$

where θ_{cr}, θ_{pw} and θ_{fc} is the critical water content (m³ m⁻³), permanent wilting point (m³ m⁻³) and field capacity (m³ m⁻³), respectively; ET$_p$ is the potential transpiration rate (mm d⁻¹) and TC is the transpiration constant (mm d⁻¹).

The transpiration constant is an index for drought tolerance of the crop, with smaller values indicating increasing sensitivity to drought. As such, the critical water content takes care of the crop-specific effects in simulating crop water uptake, analogous to the crop coefficient used in the FAO 56 method. The critical water content approach in LINTUL2 is in line with the observation that the crop coefficient depends on both the potential transpiration and the soil water content. Plants may struggle to meet a high transpiration demand (i.e. on days with high potential transpiration rate), leading to a less-than-expected actual transpiration rate despite an adequate soil moisture supply close to the field capacity. On days with a low potential transpiration rate, the actual transpiration rate may equal the potential transpiration rate despite very low soil moisture contents close to the permanent wilting point (Denmead and Shaw, 1962). This approach facilitates a dynamic adjustment in the transpiration reduction factor, which is compatible with the phenotypic plasticity and phenological heterogeneity in established banana stands. The broad objective of this study was to adapt the LINTUL2 water balance model to the perennial and phenologically heterogeneous highland banana cropping system. The specific objective was to identify the model input parameters that have the most influence on the soil water balance of highland banana and thus need to be quantified or calibrated accurately for reliable simulation. The influence of the model parameters was evaluated by testing how much a given model output changed per unit change in a specific model input parameter relative to the default value.

5.2. Materials and Methods

In the original LINTUL2 model, water inflow into the rooted soil layer is from rainfall and irrigation, less the interception by the crop canopy and surface runoff. A tipping bucket mechanism is used to compute water inflow into the root zone (Ittersum et al., 2003). Within a given time step, water added by rainfall or irrigation may fill the rooted soil layer to field capacity from the top downwards. If increase in soil water storage from inflow exceeds field capacity within the same time step, the excess drains below the root zone. If the inflow rate is greater than the drainage rate within a given time step, the soil water content rises up to saturation from the bottom of the rooting depth upwards and thereafter, additional inflow is lost as surface runoff. Upward capillary rise and lateral flows are assumed to be negligible. However, growth of the root system can contribute to

the soil water input through an increase in the rooting depth by which the root system explores wet soil that was previously below the root zone. In the event of drought stress, there is increased allocation of newly-produced dry matter to the root system at the expense of the shoot biomass. Water outflow from the soil layer is through deep percolation or drainage, evaporation from the soil surface and by crop uptake or transpiration. Some adaptations (Fig. 5.1) were made on LINTUL 2 to suit the highland banana crop system.
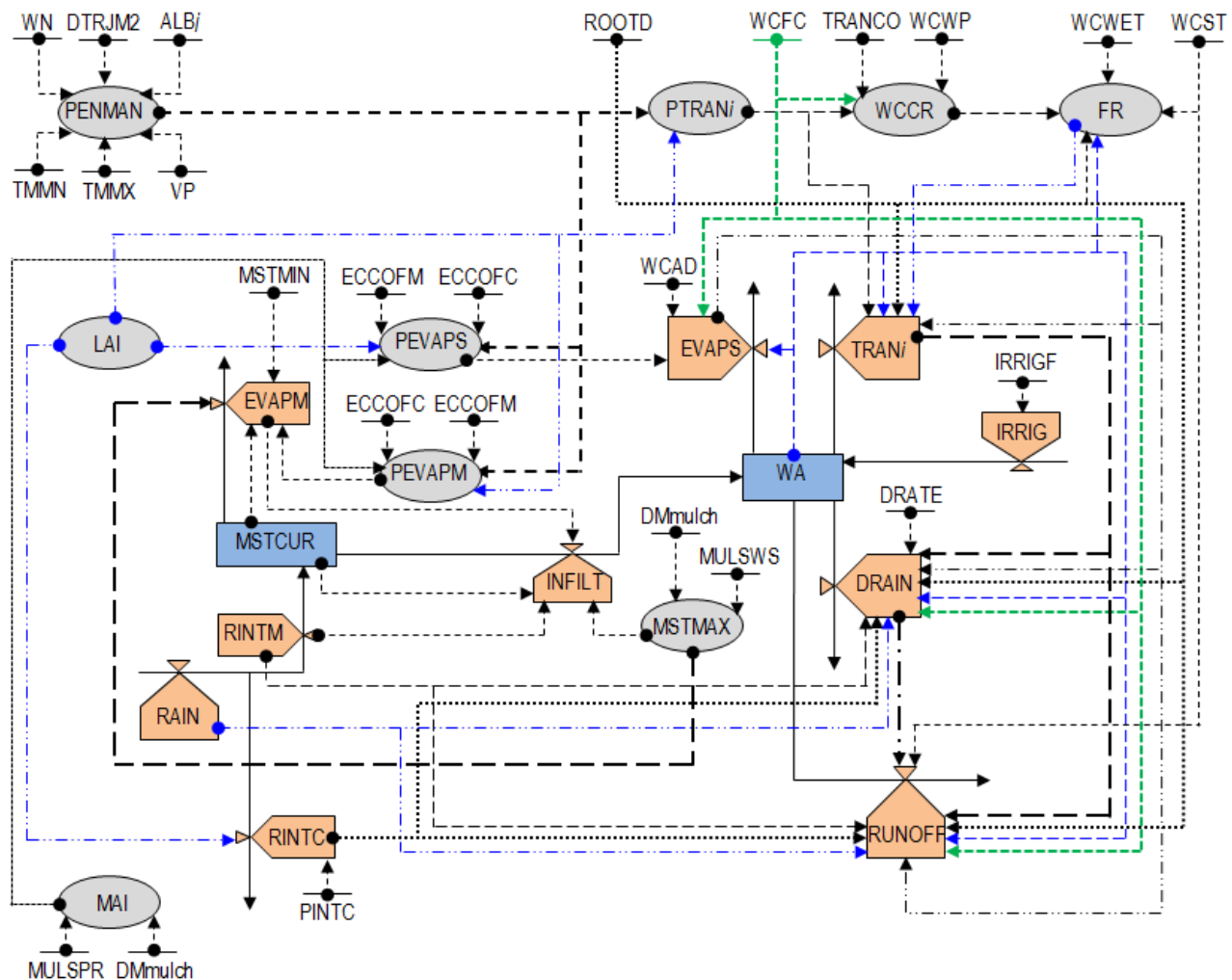

Figure 5.1: Relational diagram for the soil and mulch water balance model adapted for a mulched East African highland banana cropping system.

Codes are defined in Appendix 5.

The adaptations made to the LINTUL2 soil water balance model (Fig 5.1) to represent the highland banana system were: (1) inclusion of a three-layer canopy with one layer for each of the three plants (mother plant or Plant 1, daughter plant or Plant 2 and granddaughter plant or Plant 3) that constitute a banana mat; (2) inclusion of a mulch layer on the soil surface to mimic the self-mulching nature of an established highland banana crop stand; (3) negligible changes in rooting depth in an established highland banana crop stand where root growth and death rates are assumed to be in equilibrium; and (4) assumption that there is no increase in dry matter allocation to the root system against shoot growth due to drought stress (Taulya, 2013).

5.2.1. Description of the adapted soil water balance model

The rate of change in soil water storage in the root zone was quantified as the difference between soil water inflow and outflow (Eq. 5.02).

$$dW_t/dt = \left(R_g - \sum_{j=1}^{3} R_j - M + I \right) - \left(R_o + D + E_a + \sum_{j=1}^{3} T_{aj} \right) \quad \text{..Eq. 5.02}$$

where dW_t/dt is the rate of change in soil water storage in the rooting zone; R_g is the rainfall; R_j is the rate of rainfall interception in canopy layer $j = 1$, 2 or 3 of the banana mat; M is the rate of rainfall interception in the mulch layer; I is the rate of irrigation; R_o is the rate of surface runoff; D is the rate of drainage beyond the rooting depth; E_a is the rate of evaporation from the soil, and; T_a is the actual canopy transpiration rate of the three plants that comprise the banana mat. All terms are in mm d^{-1}.

5.2.1.1. Rainfall interception rates in crop canopy and mulch

Rainfall interception in the crop canopy R_j was computed as the sum of interceptions in the three canopy layers. For each canopy layer, interception was computed as the minimum of either the supply capacity from the rainfall incident on the canopy layer or the canopy's rainfall storage capacity, which was assumed to be directly proportional to the leaf area index (Equation 5.03). Stem flow was not considered in this model, although Cattan et al. (2007) reported that 18-26% of the incident rainfall reaches the ground through stem flow resulting in 28-fold amplification of incident rainfall at the base of the pseudostem compared with elsewhere under a banana canopy. Ignoring the stem flow effects was justified based on the fact that root distribution was assumed to be uniform throughout the root zone yet in reality, it tapers off both horizontally and vertically

(Araya et al., 1998), matching the canopy interception and stem flow-induced rainfall distribution heterogeneity under a banana canopy.

$$R_1 = \min(R_g, P_1 \times LAI_1)$$
$$R_2 = \min(\max\left[0., R_g - R_1\right], P_2 \times LAI_2)$$
$$R_3 = \min(\max\left[0., R_g - R_1 - R_2\right], P_3 \times LAI_3)$$

....Equation 5.03

where R_1, R_2 and R_3 is rainfall interception rate (mm d^{-1}) in the canopy of Plant 1, 2 and 3, respectively; R_g is the rainfall (mm d^{-1}) recorded; P_1, P_2 and P_3 is the rainfall interception coefficient in the canopy or maximum rainfall interception rate (mm d^{-1}) per unit leaf area index for Plant 1, 2 and 3, respectively; LAI_1, LAI_2 and LAI_3 is the leaf area index of Plant 1, 2 and 3, respectively.

It was assumed that water stored in the canopy evaporated within one time step, chosen as one day. This is reasonable given the tendency for illuminated banana leaves to fold downwards (Thomas and Turner, 2001), which, together with their waxy surface, minimises the amount of water stored in the canopy (Bassette and Bussière, 2008). In contrast, the mulch layer rests horizontally on the ground surface, and receives attenuated solar radiation transmitted through the canopy, which may be insufficient to evaporate all intercepted water in the mulch within one day. A mini water balance was therefore included to keep track of the amount of water stored in the mulch, recharged solely by mulch interception but depleted by evaporation from mulch during all the time the mulch is wet, and infiltration into the soil upon filling up the maximum water storage capacity of the mulch. Rainfall interception by the mulch was envisaged to cease immediately the maximum storage capacity of the mulch was filled up and henceforth, additional rainfall infiltrated into the soil. The maximum water storage capacity in mulch was estimated as a product of the specific water storage by mulch and the mulch dry mass per unit area of soil surface. Rainfall interception rate in the mulch was estimated as the difference between incident rainfall and interception in the canopy.

5.2.1.2.   Drainage and surface runoff rate

In the tipping bucket approach adopted for this model, drainage was calculated first (before surface runoff) as a function of the field capacity of the soil and the amount of water stored in the soil (Eq. 5.04). Effectively, drainage was computed as the difference between the rates of recharge and depletion of soil water storage in the root zone with reference to the field capacity. Drainage rate was set to 0 if the result from Eq. 5.04 was

less than 0. Drainage rate was set to a predefined maximum positive value D_{MX} if the result from Eq. 5.04 was greater than D_{MX}, the soil's maximum drainage rate or saturated hydraulic conductivity, which is a characteristic of a given soil.

$$D = \frac{(W_t - W_{fc})}{\Delta t} + (I + R_g - R_j - M - E_a - T_a)$$ ....Eq. 5.04

where D is the rate of drainage (mm d^{-1}); W_t and W_{fc} is the amount (mm) of water in the soil at the current moisture content and at field capacity, respectively; I, R_g, R_j, M_i, E_a and T_a are as defined (mm d^{-1}) for Equation 5.02; Δt is the time step of integration (d).

At a high rate of soil water recharge, the drainage rate may be inadequate to keep the soil water storage at or below field capacity. In that case, the amount of water stored in the root zone will increase up to the point of saturation. Upon saturation, additional recharge is converted to surface runoff (Eq. 5.05).

$$R_o = \max\left(0, \frac{(W_t - W_s)}{\Delta t} + (I + R_g - R_j - M - E_a - T_a - D)\right)$$ ....Eq. 5.05

where R_o is the rate of runoff (mm d^{-1}); W_t and W_s is the amount (mm) of water in the soil at the current moisture content and at saturation, respectively; I, R_g, R_j, M_i, E_a, and T_a and D, are as defined (mm d^{-1}) for Eq. 5.02; Δt is the time step of integration (d).

5.2.1.3. Evaporation and transpiration

5.2.1.3.1. Reference evaporation and transpiration rate

The Penman equation (Penman, 1948) was used to compute reference evaporation and transpiration rates (Eq. 5.06). In the energy term, the surface albedo for mulch was assumed to be the same as that for soil during computation of the reference evaporation rate from mulch and soil (Eq. 5.07). Likewise, the reference transpiration rate was computed using the surface albedo for green vegetation in the energy term (Eq. 5.07). With only weather variables (temperature, wind speed and vapour pressure), the mass transfer or drying term was identical for both reference evaporation and reference transpiration (Eq. 5.08).

$$ET_{rj} = \frac{\Delta}{\Delta + \gamma} \times \frac{R_{net}}{\lambda} + \frac{\gamma}{\Delta + \gamma} \times \frac{E_{air}}{\lambda}$$ ....Eq. 5.06

where ET_{rj} is the reference evapotranspiration rate (mm d^{-1}) for surface j (= mulch, soil or canopy); Δ is the slope of the saturated vapour pressure-temperature curve (kPa °C^{-1}); γ is the psychrometric coefficient (kPa °C^{-1}); R_{net} is the net radiation function (J m^2 d^{-1}); λ is the latent heat of vaporisation for water (J kg^{-1}); E_{air} is the aerodynamic function quantifying mass transfer (J m^{-2} d^{-1}).

$$R_{net} = (1 - AL_j) R_s - \sigma (273.15 + T)^4 \max\left(0, 0.55\left[1 - \frac{VP_a}{VP_s}\right]\right)$$ ....Eq. 5.07

where R_{net} is the net radiation (J m^{-2} d^{-1}); AL_j is surface albedo for surface j (= mulch, soil or green vegetation); R_s is the incident short wave length radiation (J m^{-2} d^{-1}) on the evaporating surface or transpiring canopy; σ is the Stefan-Boltzmann constant (J m^{-2} d^{-1} K^{-4}); T is daily average temperature (°C); VP_a is actual vapour pressure (kPa), and; VP_s is saturated vapour pressure (kPa).

$$E_{air} = (VP_s - VP_a) 2.63 (1 + 0.54u)$$ ....Eq. 5.08

where u is the average wind speed (m s^{-1}) at 2-m height.

Saturated vapour pressure was computed from Eq. 5.09, while the slope of the vapour pressure-temperature curve was estimated from Eq. 5.10.

$$VP_s = 0.611 e^{\frac{17.4T}{239+T}}$$ ....Eq. 5.09

$$\Delta = \frac{4158.6 \times VP_s}{(239 + T)^2}$$ ....Eq. 5.10

5.2.1.3.2. Potential evaporation and transpiration rate

The potential evaporation rates from mulch (Eq. 5.11) and from soil (Eq. 5.12) were computed by attenuating their respective reference evaporation rates using extinction functions applied sequentially to the canopy and mulch layers. The extinction functions were based on the assumption that evaporation was driven by energy absorbed at the evaporating surface, which was estimated as the difference between incident and transmitted energy at a given layer.

$$ET_{pM} = \max\left(0, \left[ET_{rM} \times e^{-EC_C(LAI1+LAI2+LAI3)} \times \left(1 - e^{-EC_M \times MAI}\right) \right]\right) \quad \text{.........................Eq. 5.11}$$

where ET_{pM} is the potential evaporation rate from mulch (mm d^{-1}); ET_{rM} is the reference evaporation rate (mm d^{-1}) for mulch; LAI_1, LAI_2 and LAI_3 are the leaf area indices for Plant 1, 2 and 3, respectively; MAI is the mulch area index; EC_C and EC_M is extinction coefficient for radiation in the canopy and mulch, respectively.

$$ET_{pS} = \max\left(0, \left[ET_{rS} \times e^{-EC_C(LAI1+LAI2+LAI3)-EC_M \times MAI} \right]\right) \quad \text{...Eq. 5.12}$$

where ET_{pS} is the potential evaporation rate from soil (mm d^{-1}); ET_{rS} is reference evaporation rate (mm d^{-1}) for soil; LAI_1, LAI_2, LAI_3, MAI, EC_C and EC_M are as defined for Eq. 5.11.

The mulch area index was computed as a product of the total dry mass of mulch per unit area and the adjusted specific mulch area, which according to Scopel et al. (2004), takes into account clumping and overlapping of the mulch materials. Similar to potential evaporation rate, potential transpiration was computed for each plant by applying sequential extinction through overlying canopy layers (Eq. 5.13 to 5.15). It was assumed that half of the rainfall intercepted in each canopy layer evaporates before the available energy is channelled to transpiration. The potential transpiration rate was thus reduced by half of the rainfall interception in each canopy layer (Eq. 5.13 to 5.15) to reflect energy expended in canopy drying.

$$ET_{p1} = \max\left(0, \left[ET_{r1} \times \left(1 - e^{-EC_C \times LAI1}\right) - 0.5R_1 \right]\right) \quad \text{..Eq. 5.13}$$

$$ET_{p2} = \max\left(0, \left[ET_{r2} \times e^{-EC_C \times LAI1} \times \left(1 - e^{-EC_C \times LAI2}\right) - 0.5R_2 \right]\right) \quad \text{....................................Eq. 5.14}$$

$$ET_{p3} = \max\left(0, \left[ET_{r3} \times e^{-EC_C \times (LAI1+LAI2)} \times \left(1 - e^{-EC_C \times LAI3}\right) - 0.5R_3 \right]\right) \quad \text{....................................Eq. 5.15}$$

where ET_{p1}, ET_{p2} and ET_{p3} are the potential transpiration rates (mm d^{-1}) for Plant 1, 2 and 3, respectively; ET_{r1}, ET_{r2} and ET_{r3} are the reference transpiration rates (mm d^{-1}) for Plant 1, 2 and 3, respectively; R_1, R_2 and R_3 are the rainfall interceptions in the canopy for Plant 1, 2 and 3, respectively.

5.2.1.3.3. Actual evaporation and transpiration rate

The ratio of the readily evaporable amount of water currently stored in mulch to maximum readily evaporable water storage capacity of the mulch was applied as a reduction factor to the potential evaporation rate from mulch to quantify the actual evaporation rate from mulch (Eq. 5.16). It was assumed that only water stored in the mulch above a certain minimum amount is readily evaporable under normal environmental conditions. It was also assumed that the evaporable water stored in the mulch was progressively depleted starting from the more exposed upper mulch layers and proceeding towards the less exposed bottom mulch layers. The evaporable water stored deeper in the mulch was considered more difficult to evaporate due to attenuation of radiation at the mulch surface and build-up of humid air within the mulch. Furthermore, decomposition of the mulch, which produces water-philic by-products, was assumed to be more advanced at the mulch-soil interphase deeper in the mulch layer, hence the reduction in rate of evaporation from the mulch as it progressively became drier from the top, downwards. The dynamics of mulch decomposition are not included in the soil water balance model.

$$ET_{aM} = ET_{pM} \times \frac{W_{tM} - W_{MN}}{W_{MX} - W_{MN}} \quad \text{...Eq. 5.16}$$

where ET_{aM} is actual evaporation rate (mm d^{-1}) from mulch; ET_{pM} as previously defined; W_{tM} is the current water storage (mm) in the mulch; W_{MX} and W_{MN} are respectively the maximum and minimum water storage (mm) of the mulch.

The evaporation reduction factor (0 to 1; Fig 5.2) for soil was computed as the ratio of readily evaporable soil water to the maximum amount of evaporable water the soil can store. Water stored in the soil between the air dry moisture content and that at field capacity was considered to be the maximum amount of evaporable water, while the amount of readily evaporable water was the difference between the amount of water stored in the soil at the current moisture content and that at air dry moisture content. The actual evaporation from the soil was therefore computed from Eq. 5.17.

$$ET_{aS} = ET_{pS} \times \frac{\theta_t - \theta_{ad}}{\theta_{fc} - \theta_{ad}} \quad \text{...Eq. 5.17}$$

where ET_{aS} is actual evaporation rate (mm d^{-1}) from soil; ET_{pS} as previously defined; θ_t, θ_{fc} and θ_{ad}, is the current soil water content (m^3 m^{-3}), field capacity (m^3 m^{-3}) and air-dry water content (m^3 m^{-3}), respectively.
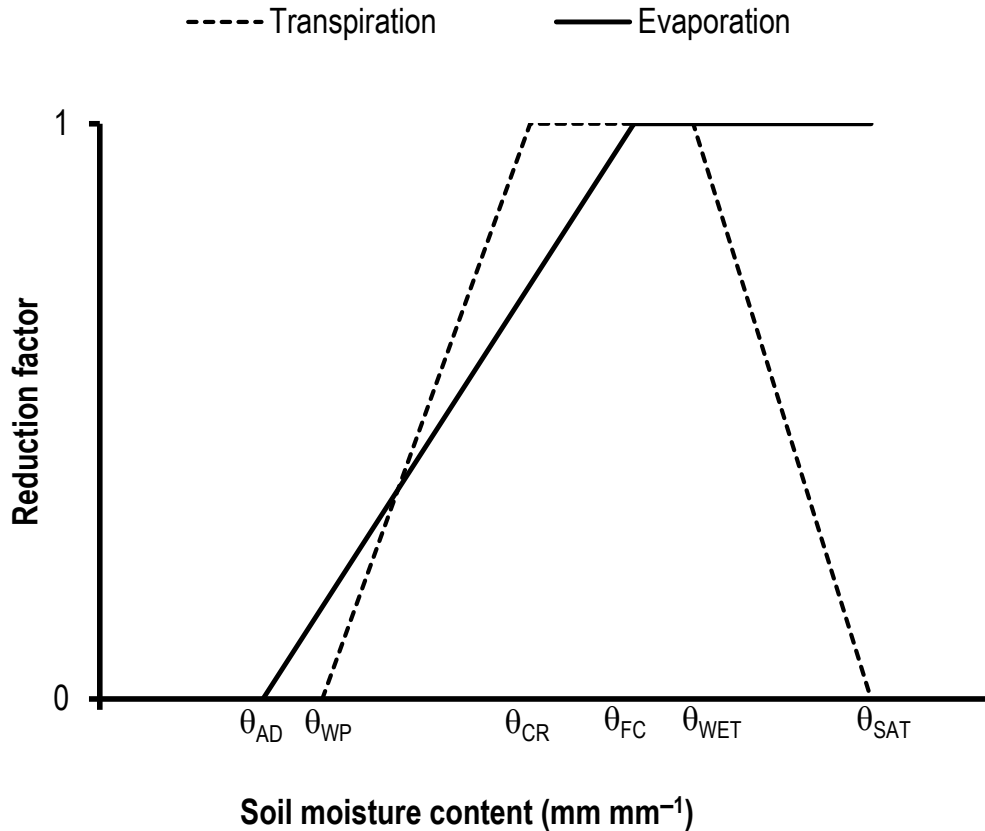

Figure 5.2: Relationship between soil moisture content and transpiration or evaporation reduction factors.

θ_{AD} = Air-dry moisture content; θ_{WP} = Permanent wilting point; θ_{CR} = Critical moisture content below which a reduction in transpiration is induced; θ_{FC} = Field capacity; θ_{WET} = Wet moisture content above which there is reduction in transpiration due to shortage of oxygen; θ_{SAT} = Saturated moisture content.

Similar to actual evaporation, actual transpiration was computed as the product of potential transpiration and a reduction factor. Four soil water content situations were considered in quantifying the transpiration reduction factor, *viz.* the permanent wilting point, critical water content, wet moisture content and saturated moisture content (Fig 5.2). At the permanent wilting point the soil was too dry and at the saturated moisture content too wet for transpiration to occur and hence the transpiration reduction factor was set to 0. At or above the critical water content (Eq. 5.01) up to the wet moisture content,

water uptake from the soil was unimpeded and thus could meet the evaporative demand rate under the prevailing environmental conditions. Therefore, the transpiration reduction factor was set to 1 for situations between the critical and wet soil moisture content.

Below the critical water content, the plant was assumed to experience drought stress, while above the wet moisture content, the plant's physiological processes were deemed to be so impaired by poor soil aeration that transpiration was constrained. The transpiration reduction factor was thus increased linearly from 0 at permanent wilting point, to 1 at the critical water content, and linearly reduced from 1 at the 'wet' moisture content to 0 at saturation. When the soil moisture content was less than the critical soil water content, Equation 5.18a was used. When the soil moisture content was greater than the wet soil water content, Eq. 5.18b was used to quantify the actual transpiration.

$$T_{ai} = ET_{pi} \times \frac{\theta_t - \theta_{pw}}{\theta_{cr} - \theta_{pw}}$$ ....Eq. 5.18a

$$T_{ai} = ET_{pi} \times \frac{\theta_{sd} - \theta_t}{\theta_{sd} - \theta_w}$$ ....Eq. 5.18b

where T_{ai} is the actual transpiration rate (mm d^{-1}) for Plant i = 1, 2 or 3; ET_{pi} is potential transpiration rate for Plant i = 1, 2 or 3; θ_{sd}, θ_t, θ_w, θ_{cr} and θ_{pw}, is the saturated water content (m^3 m^{-3}), current water content (m^3 m^{-3}), wet water content (m^3 m^{-3}), critical water content (m^3 m^{-3}) and permanent wilting point (m^3 m^{-3}), respectively.

5.2.2. Model parameterisation

Categorised under 'crop', 'mulch' and 'soil', a total of 19 parameters (Table 5.1) were selected for the sensitivity analysis. Wherever possible, measured values were used as the default setting. The measured values were taken from fertilizer response trials conducted on-station at Kawanda in central Uganda and on-farm at Ntungamo in south western Uganda (Nyombi et al., 2010; van Asten et al., 2011). The measured parameters were leaf area indices for Plant 1, 2 and 3 (Table 5.1). These were taken as the maximum leaf area indices observed on plants at flowering, in the mid- and early-vegetative stages, respectively in the fertilizer response trials.

Table 5.1: Default values for crop, mulch and soil parameters applied during the sensitivity analysis.

Category	Code (Symbol in text equations)	Description	Default value	Source
Crop	ALBC (AL_i)	Canopy surface albedo	0.25	cf. Carrer et al., 2014
Crop	ECCOFC (EC_C)	Radiation extinction coefficient in canopy	0.5	cf. Leriche et al., 2001
Crop	LAI1 (LAI1)	Leaf area index for plant 1	5 ha ha^{-1}	Measured
Crop	LAI2 (LAI2)	Leaf area index for plant 2	3 ha ha^{-1}	Measured
Crop	LAI3 (LAI3)	Leaf area index for plant 3	1.5 ha ha^{-1}	Measured
Crop	PINTC (R_j)	Rainfall interception coefficient in canopy	0.25 mm ha ha^{-1} d^{-1}	Estimate
Crop	TRANCO (TC)	Transpiration constant	5 mm d^{-1}	Estimate
Mulch	ALBS (AL_i)	Mulch/soil surface albedo	0.15	cf. Carrer et al., 2014
Mulch	ECCOFM (EC_M)	Radiation extinction coefficient in mulch	0.4	cf. Leriche et al., 2001
Mulch	MULSPR	Adjusted specific mulch area	0.00038 ha kg^{-1}	Scopel et al. (2004)
Mulch	MSTMIN (W_{MN})	Air-dry water content of mulch	0.3 mm	Estimate
Mulch	DMmulch	Mulch soil cover	3000 kg DM ha^{-1}	Estimate
Soil	WCAD (θ_{ad})	Air-dry moisture content	0.01 m^3 m^{-3}	cf. Carsel, 1988; Jacobsen and Schjønning, 1993
Soil	WCFC (θ_{fc})	Field capacity moisture content	0.33 m^3 m^{-3}	cf. Mbah, 2012
Soil	DRATE	Maximum drainage rate	50 mm d^{-1}	Estimate
Soil	WCWP (θ_{wp})	Wilting moisture content	0.11 m^3 m^{-3}	cf. Dodd and Lauenroth, 1997
Soil	WCWET (θ_w)	Wet moisture content, when plants start suffering from oxygen shortage	0.37 m^3 m^{-3}	Estimate
Soil	WCST (θ_{sd})	Saturated moisture content	0.42 m^3 m^{-3}	cf. Carsel, 1988; Jacquemin and Noilhan, 1990
Soil	ROOTD	Effective rooting depth	0.5 m	cf. Carr, 2009

Leaf area (in m^2) per plant was determined from girth data using the allometric functions reported in Nyombi et al. (2009), which were developed from destructive sampling in the fertilizer response trials at Ntungamo. Leaf area index was then computed as the ratio of leaf area per plant to the area per plant (9 m2) in the fertilizer response trials. Where measurements on some parameters were not available, values from the literature were

used as default settings for the sensitivity analysis. Estimated values were used for parameters that were neither measured in the fertilizer response trials nor available from literature (Table 5.1).

The water balance at the two experimental sites of the fertilizer response trials was simulated using the model written in the Fortran Simulation Translator (FST) computer language with daily weather data recorded at each site from 1 January 2006 to 31 December 2007.

5.2.3. Sensitivity analysis

Sensitivity coefficients in response to ±1% change in each selected parameter for pertinent state variables of the soil water balance were computed using the central difference method around the default value (Eq. 5.19).

$$C_{s,p,t} = \frac{\partial \ln S_t}{\partial \ln P} \approx \frac{\left(S_{t,P\_max} - S_{t,P\_min}\right)\big/S_{t,P\_default}}{\left(P_{max} - P_{min}\right)\big/P_{default}} \quad \text{...Equation 5.19}$$

where $C_{s,p,t}$ is the sensitivity coefficient for state variable S, in response to a change in the default setting of parameter P on day t; S_{t,P_max} and S_{t,P_min} is the magnitude of state variable S when the default value of parameter P is respectively increased and reduced by 1%; $S_{t,P\_default}$ is the magnitude of state variable S with parameter P set at its default value ($P_{default}$); P_{max} and P_{min} are the values of parameter P when its default value is increased and reduced by 1%, respectively.

The pertinent states (variable S) were respective daily integrals of canopy transpiration (i.e. total transpiration from all three plants on a banana stool), drainage and evaporation from the soil. Soil water content in the rooting zone was also considered a pertinent state in the sensitivity analysis. Time-averaged arithmetic means ($\bar{C}$) for the sensitivity coefficients for each state-parameter combination were computed for the period 1 January to 31 December for each year at each site for comparative purposes. A state variable was considered to be insensitive to a given parameter if $-10\% < \bar{C} < +10\%$; otherwise, it was deemed to be sensitive to the parameter.

5.3. Results

5.3.1. Overview of soil water balance components at default parameter values

The annual total rainfall received at Kawanda was 1366 and 1633 mm in 2006 and 2007, respectively, while that received at Ntungamo was 1318 and 817 mm. This averaged about 4 mm d^{-1} at both sites except at Ntungamo in 2007 where it was only 2.2 mm d^{-1} (Table 5.2). With initial soil moisture content at field capacity, the change in root zone water storage at both sites during both years averaged between −0.23 and −0.06 mm d^{-1}. Transpiration was the largest source of water outflow from the root zone, at a mean rate of about 2 mm d^{-1} followed by drainage (Table 5.2). Irrespective of site or year, cumulative annual transpiration from Plant 1, 2 and 3 accounted for approximately 94, 5 and 1% of the annual cumulative canopy transpiration. Regardless of site or year, there was little evaporation from the soil, ranging from 0 to 0.028 mm d^{-1} (Table 5.2) and there was no runoff generated at all (Data not shown). Interception in Plant 1, 2 and 3 canopy layers accounted for 57 to 61, 27 to 29 and 12 to 14% of the canopy rainfall interception, depending on site and year (Data not shown).

Table 5.2: Mean daily rates of soil water balance components assuming default input parameter settings at Kawanda (central Uganda) and Ntungamo (south western Uganda) in 2006 and 2007.

Parameter	Mean rate, mm d^{-1} (Minimum – Maximum)			
	Kawanda		Ntungamo	
	2006	2007	2006	2007
Rainfall	3.74 (0.00 – 86.00)	4.47 (0.00 – 46.00)	3.61 (0.00 – 78.00)	2.24 (0.00 – 33.81)
Δ root zone water storage	-0.06 (-13.97 – 50.54)	-0.23 (-4.49 – 33.25)	-0.09 (-4.38 – 37.72)	-0.19 (-4.16 – 30.89)
Canopy transpiration	2.21 (0.00 – 4.77)	2.18 (0.00 – 4.47)	2.09 (0.09 – 4.36)	1.77 (0.19 – 4.14)
Drainage	0.78 (0.00 – 50.00)	1.58 (0.00 – 40.95)	0.88 (0.00 – 45.25)	-
Evaporation from soil	0.012 (0.000 –0.027)	0.014 (0.000 – 0.028)	0.013 (0.001 – 0.026)	0.010 (0.002 – 0.023)
Interception in canopy	0.788 (0.000 – 2.375)	0.908 (0.000 – 2.375)	0.709 (0.000 – 2.375)	0.636 (0.000 – 2.375)
Evaporation from mulch	0.009 (0.000 – 0.018)	0.009 (0.000 – 0.016)	0.010 (0.000 – 0.015)	0.009 (0.000 – 0.015)

Δ root zone water storage = change in root zone water storage

5.3.2. Sensitivity of root zone water content

Root zone water content was mostly sensitive to the weather parameters; rainfall, net radiation, temperature and vapour pressure, as well as the soil parameters; soil water content at field capacity and permanent wilting point at both sites and years.
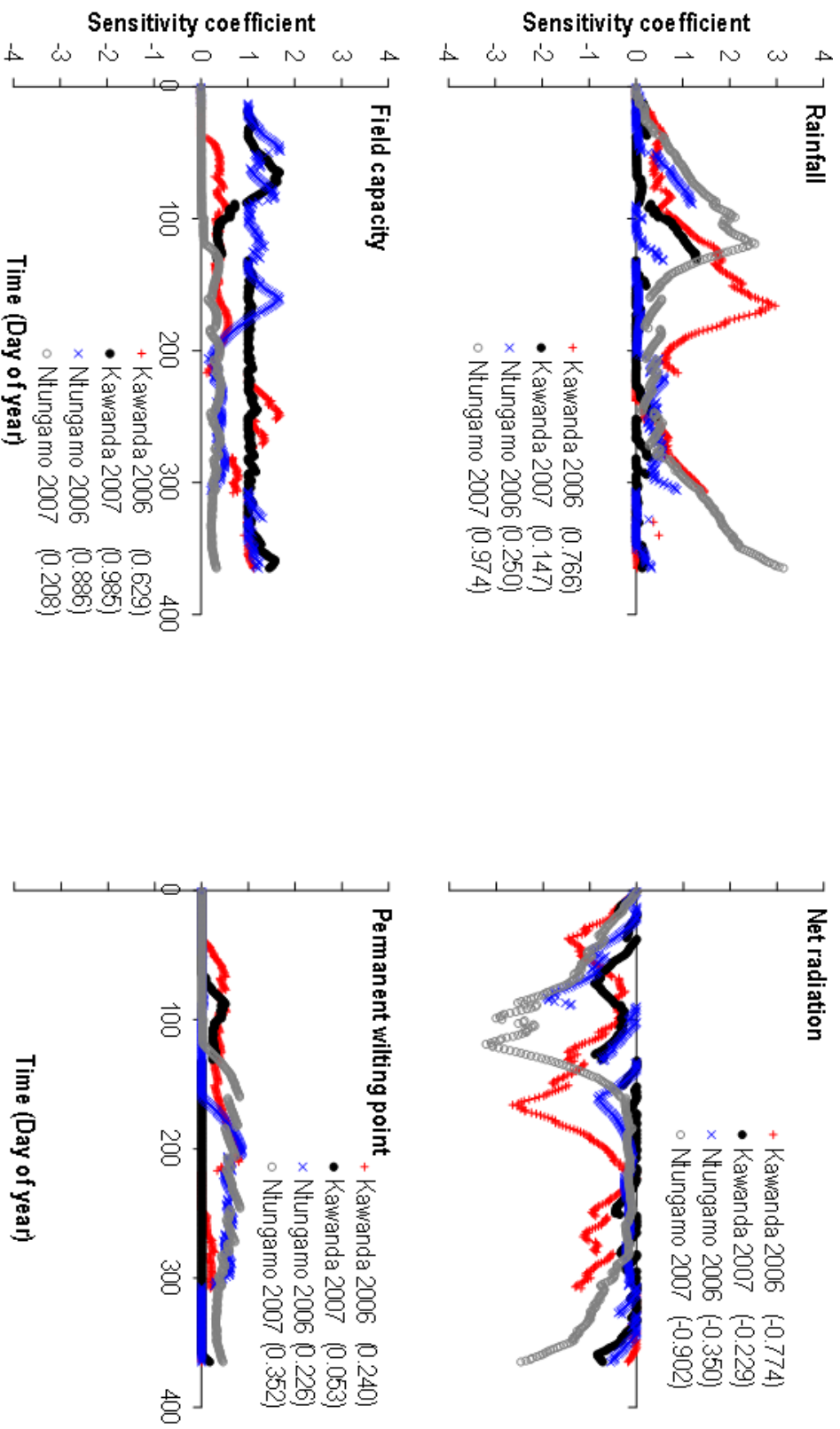
Figure 5.3: Sensitivity of root zone water content to ±1% change (central difference method around the default value) in rainfall, daily radiation, soil water content at field capacity and soil water content at permanent wilting point relative to their respective default values at Kawanda (central Uganda) and Ntungamo (south western Uganda) in 2006 and 2007.

Figures in parentheses next to the legends are mean sensitivity coefficients averaged over a year.

The sensitivity of soil water content to rainfall was more or less the direct opposite of that to net radiation. Likewise, the sensitivity of soil water content to temperature was roughly the direct opposite of that to vapour pressure. The sensitivity coefficient for root zone water content to rainfall was on average 15 to 77% at Kawanda and 25 to 97% at Ntungamo. On the contrary, that for root zone water content to net radiation was −77 to −23% and −90 to −35% at Kawanda and Ntungamo, respectively (Fig 5.3). The sensitivity coefficients of root zone water content to temperature and vapour pressure followed the same trend as those to rainfall and net radiation, respectively, but with smaller magnitudes (Data not shown).

Among the soil parameters, root zone water content was most sensitive to soil water content at field capacity with average sensitivity coefficients between 21 and 99%. Root zone water content sensitivity coefficients to soil water content at permanent wilting point were on average between 22 and 35%, excluding Kawanda 2007 where the coefficient was not sensitive (Fig 5.3). The sensitivity coefficient for root zone water storage to rooting depth was −46 and −13% at Kawanda in 2006 and Ntungamo in 2007, respectively. Root zone water content was also sensitive to canopy surface albedo with mean sensitivity coefficients of 25.5, 11.6 and 30.4% at Kawanda in 2006, Ntungamo in 2006 and Ntungamo in 2007, respectively. However, root zone water content was generally not sensitive to the rest of the crop parameters and all mulch parameters (Data not shown).

5.3.3. Sensitivity of canopy transpiration

Canopy transpiration was more sensitive to the weather parameters compared with either the soil or crop parameters but exhibited no sensitivity to any of the mulch parameters. Its sensitivity coefficients to rainfall and net radiation were 38 to 106% and 54 to 123%, respectively (Fig 5.4). Canopy transpiration was, however, not sensitive to rainfall and net radiation in 2007 at Kawanda and Ntungamo, respectively. The sensitivity coefficients for canopy transpiration to vapour pressure and soil moisture content at field capacity were between 10 and 74%, while those to average temperature and soil moisture content at permanent wilting point were between −63 and −10%. However, canopy transpiration was not sensitive to soil moisture content at permanent wilting point and field capacity in 2007 at Kawanda and Ntungamo, respectively.
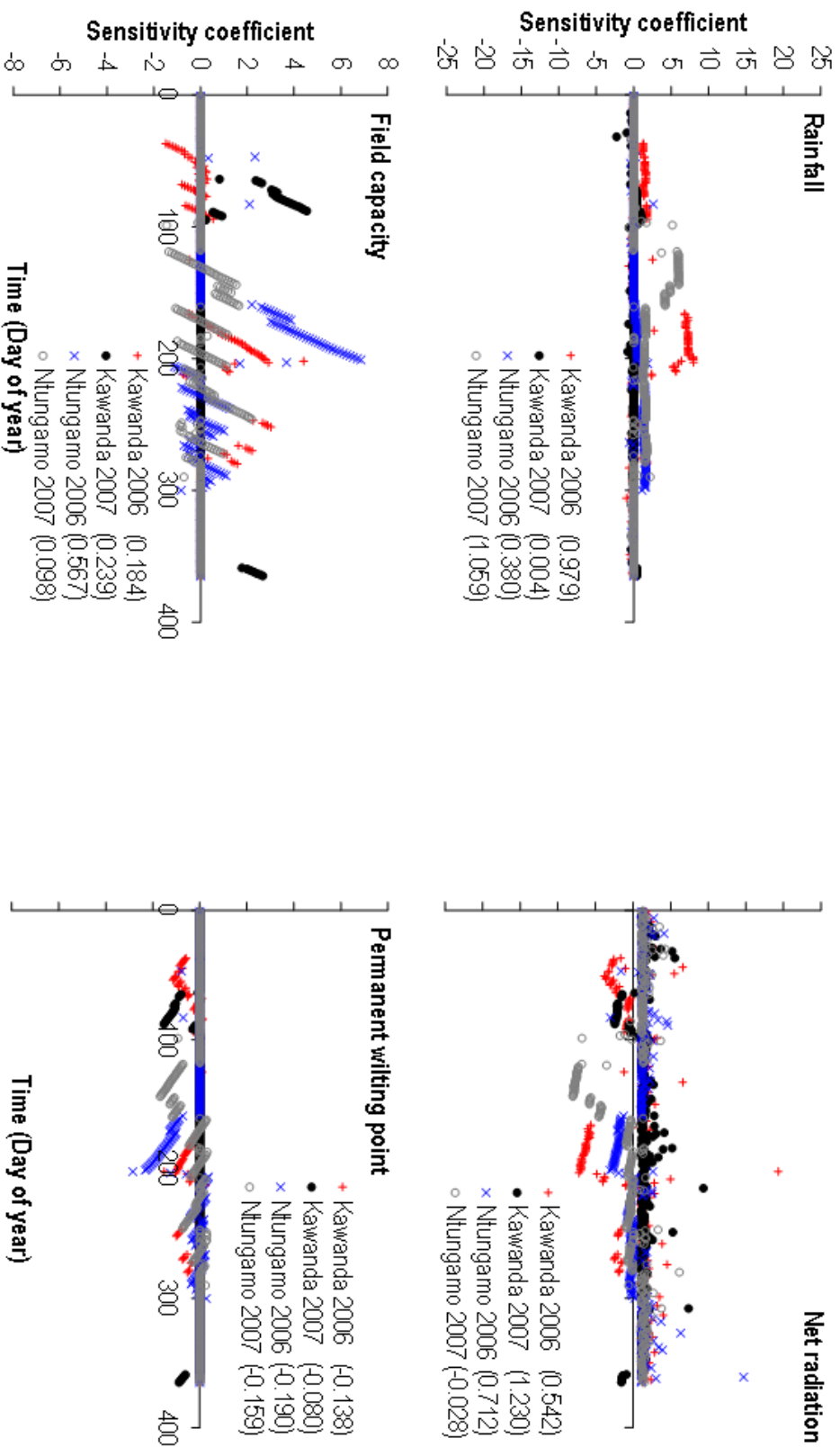
Figure 5.4: Sensitivity of canopy transpiration to ±1% change (central difference method around the default value) in rainfall, net radiation, soil water content at field capacity and soil water content at permanent wilting point relative to their respective default values at Kawanda (central Uganda) and Ntungamo (south western Uganda) in 2006 and 2007.

Figures in parentheses next to the legends are mean sensitivity coefficients averaged over a year.

On average, canopy transpiration's sensitivity coefficients to rooting depth were between 16 and 37% at Kawanda in 2007 and Ntungamo in 2006, respectively, while those to Plant 1 leaf area index were −28 and −12% at Kawanda in 2006 and Ntungamo in 2007, respectively (Data not shown). Its sensitivity coefficients to canopy rainfall interception coefficient were on average −50, −22, −24 and −29% at Kawanda in 2006, Kawanda in 2007, Ntungamo in 2006 and Ntungamo in 2007, respectively. Canopy transpiration's sensitivity coefficients to canopy surface albedo were −20, −41 and −24% at Kawanda in 2006, Kawanda in 2007 and Ntungamo in 2006, respectively, while those to radiation extinction coefficient in the canopy were 12.3, 14.9 and 12.1% at Kawanda in 2006, Kawanda in 2007 and Ntungamo in 2006, respectively. Canopy transpiration was not sensitive to canopy surface albedo and canopy radiation extinction coefficient at Ntungamo in 2007 (Data not shown).

5.3.4. Sensitivity of drainage

Drainage was more sensitive to the weather parameters compared with either the soil or crop parameters. It's sensitivity coefficients to rainfall and daily average temperature were respectively 600 to 900% and 300 to 400%, while those to daily radiation and vapour pressure lay between −300 and −500% (Table 5.3).

The smallest sensitivity coefficients among the weather parameters were on average −22.7, −142.1 and −38.7% for wind speed at Kawanda in 2006, Kawanda in 2007 and Ntungamo in 2006, respectively (Table 5.3). Among the soil parameters, drainage was sensitive to soil water content at field capacity, soil water content at permanent wilting point and rooting depth while among the crop parameters, it was sensitive to crop canopy surface albedo, canopy rainfall interception coefficient, and leaf area index for Plant 1, 2 and 3. Drainage's sensitivity coefficients to soil water content at field capacity and rooting depth were on average, 30 to 164% and 27 to 110% (Table 5.3), respectively. It's sensitivity coefficients to soil water content at permanent wilting point were 55 and 24% in 2006 at Kawanda and Ntungamo, respectively (Table 5.3).

Drainage's sensitivity coefficient to canopy rainfall interception coefficient were −135 to −318%, while those to canopy surface albedo were between 110 and 276% (Table 5.3). At a given site in a given year, drainage's sensitivity coefficients were greatest and least for Plant 1 and Plant 3 leaf area index, respectively (Table 5.3).

Table 5.3: Time-averaged sensitivity coefficients of drainage in response to ±1% change (central difference method around the default value) in weather, soil and crop parameters relative to their respective default values at Kawanda (central Uganda) in 2006 and 2007 and Ntungamo (south western Uganda) in 2006.

Parameter	Time averaged sensitivity coefficient (Minimum – Maximum)		
	Kawanda 2006	Kawanda 2007	Ntungamo 2006
Weather			
Rainfall	13.405 (0.000 – 66.954)	6.601 (1.106 – 60.087)	7.801 (1.150 – 66.085)
Net radiation	-8.350 (-53.889 – 0.000)	-4. 791 (-53.623 – -0.051)	-5. 843 (-70.643 – -0.003)
Temperature	6.783 (-7.337 – 71.865)	4.144 (-0.458 – 61.949)	2.974 (0.006 – 39.409)
Vapour pressure	-6.623 (-63.321 – 5.398)	-3.961 (-51.811 – 0.238)	-3.441 (-44.112 – -0.006)
Wind speed	-0.257 (-1.613 – 0.019)	-0.267 (-4.324 – 0.004)	-0.401 (-5.347 – 0.000)
Soil			
Rooting depth	-1.097 (-19.703 – 0.000)	-0.268 (-12.084 – 0.000)	-0.853 (-12.477 – 0.000)
Field capacity	-1.643 (-29.513 – 0.000)	-0.299 (-12.084 – 0.000)	-1.089 (-18.704 – 0.000)
Permanent wilting point	0.545 (0.000 – 9.803)	0.031 (0.000 – 1.838)	0.235 (0.000 – 6.225)
Crop			
Canopy rainfall int. coefficient	-3.175 (-15.911 – 0.000)	-1.350 (-17.993 – -0.043)	-1.394 (-14.740 – -0.042)
Canopy rad. ext. coefficient	-0.673 (-6.673 – 0.000)	-0.290 (-2.293 – -0.010)	-0.283 (-4.011 – 0.099)
Canopy surface albedo	2.759 (0.000 – 17.788)	1.085 (0.018 – 5.712)	1.327 (0.046 – 8.773)
Leaf area index for plant 1	-1.895 (-15.483 – 0.000)	-0.811 (-9.600 – -0.023)	-0.840 (-9.884 – -0.030)
Leaf area index for plant 2	-1.303 (-8.720 – 0.000)	-0.554 (-7.074 – -0.017)	-0.558 (-5.909 – -0.015)
Leaf area index for plant 3	-0.649 (-4.360 – 0.000)	-0.276 (-3.539 – -0.009)	-0.279 (-2.956 – -0.008)

Int. = interception; rad. = radiation; ext. = extinction. Note that there was no drainage at Ntungamo in 2007.

5.3.5. Sensitivity of evaporation from the soil

Evaporation from the soil was most sensitive to the crop parameters radiation extinction coefficient in the canopy and leaf area index for Plant 1, 2 and 3. Irrespective of site or year, its sensitivity coefficients to radiation extinction coefficient in the canopy and leaf area index for Plant 1 were on average −480 and −260%, respectively. The sensitivity coefficient for evaporation from soil to Plant 2 leaf area index was about −150%, while that to radiation extinction coefficient in mulch, adjusted specific mulch area and mulch surface cover was on average about −46%, irrespective of site or year (Table 5.4).

Table 5.4: Time-averaged sensitivity coefficients of evaporation from the soil in response to ±1% change (central difference method around the default value) in crop and mulch parameters relative to their respective default values at Kawanda (central Uganda) and Ntungamo (south western Uganda) in 2006 and 2007.

| Parameter	Time averaged sensitivity coefficient (Minimum – Maximum)			
	Kawanda		Ntungamo	
	2006	2007	2006	2007
Crop				
Radiation extinction coefficient in canopy	-4.775 (-4.862 – -4.747)	-4.775 (-4.780 – -4.744)	-4.775 (-4.794 – -4.726)	-4.784 (-4.907 – -4.735)
Canopy surface albedo	0.269 (0.000 – 0.913)	0.079 (0.000 – 0.322)	0.122 (0.000 – 0.675)	0.320 (0.000 – 1.188)
Leaf area index for plant 1	-2.574 (-2.789 – -2.498)	-2.515 (-2.604 – -2.498)	-2.527 (-2.619 – -2.499)	-2.604 (-2.933 – -2.500)
Leaf area index for plant 2	-1.548 (-1.686 – -1.500)	-1.509 (-1.566 – -1.499)	-1.517 (-1.581 – -1.500)	-1.572 (-1.793 – -1.500)
Leaf area index for plant 3	-0.774 (-0.843 – -0.750)	-0.755 (-0.783 – -0.750)	-0.759 (-0.791 – -0.750)	-0.786 (-0.896 – -0.750)
Canopy rainfall interception. coefficient	-0.124 (-0.467 – 0.005)	-0.024 (-0.176 – 0.005)	-0.049 (-0.200 – 0.005)	-0.180 (-0.716 – 0.000)
Mulch				
Radiation extinction coefficient in mulch	-0.456 (-0.459 – -0.454)	-0.456 (-0.457 – -0.454)	-0.456 (-0.459 – -0.455)	-0.456 (-0.458 – -0.454)
Mulch/soil surface albedo	-0.215 (-0.507 – -0.176)	-0.203 (-0.342 – -0.176)	-0.211 (-0.390 – -0.179)	-0.209 (-0.381 – -0.178)
Adjusted specific mulch area	-0.456 (-0.459 – -0.454)	-0.456 (-0.457 – -0.454)	-0.456 (-0.459 – -0.455)	-0.456 (-0.458 – -0.454)
Mulch surface cover	-0.458 (-0.465 – -0.455)	-0.456 (-0.463 – -0.454)	-0.457 (-0.463 – -0.455)	-0.460 (-0.469 – -0.455)
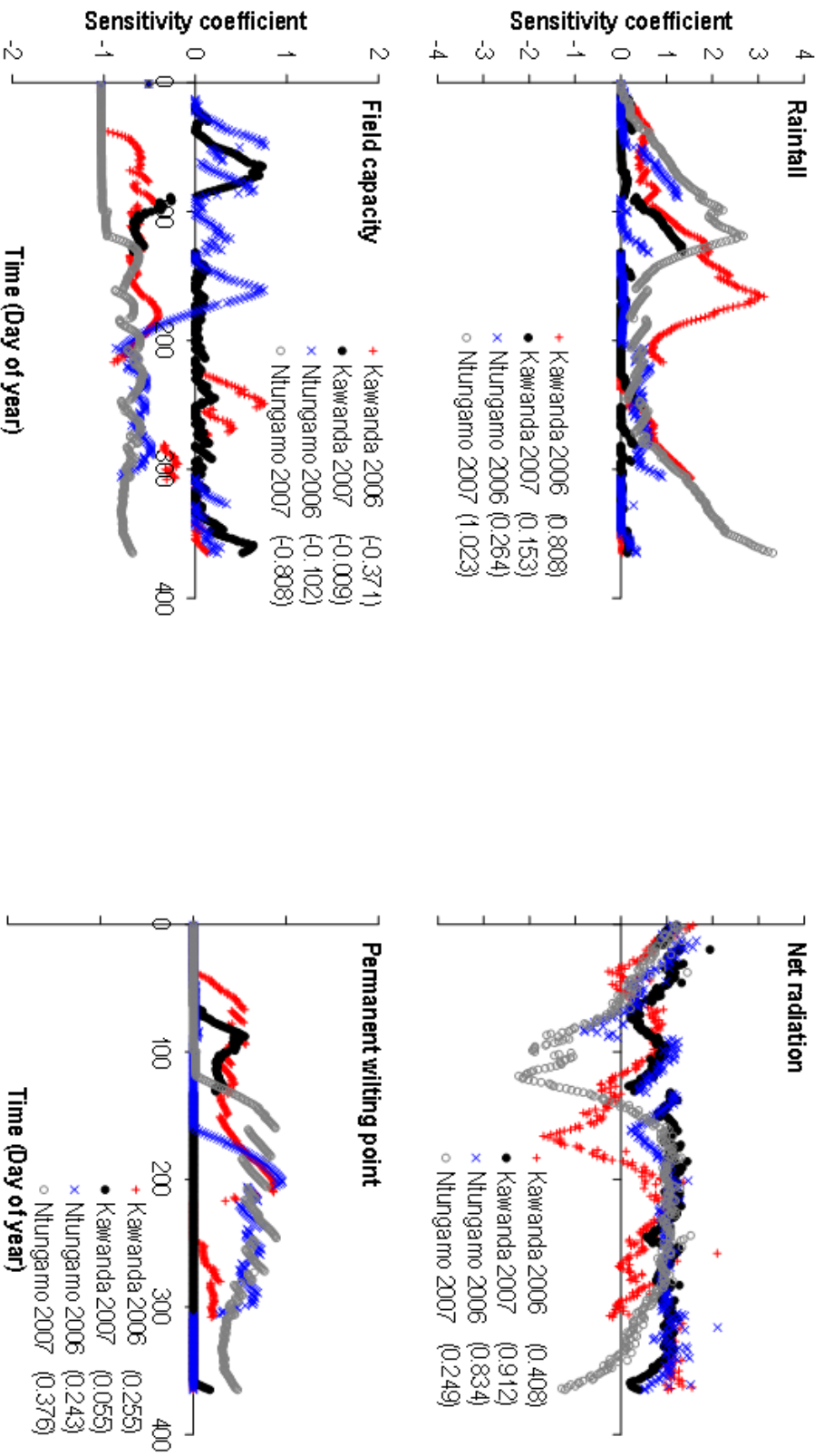
Figure 5.5: Sensitivity of evaporation from soil to ±1% change (central difference method around the default value) in rainfall, net radiation, soil water content at field capacity and at permanent wilting point relative to their respective default values at Kawanda (central Uganda) and Ntungamo (south western Uganda) in 2006 and 2007.

Figures in parentheses next to the legends are mean rates averaged over a year.

The sensitivity coefficients for evaporation from soil to rainfall and net radiation were 26 to 100% and 25 to 90%, respectively (Fig 5.5), while those to vapour pressure were 15 to 69% (Data not shown). On the contrary, its sensitivity coefficients to average daily temperature were −69 to −12% (Data not shown).

Among the soil parameters, evaporation from the soil was most sensitive to soil water content at field capacity and at permanent wilting point. Its sensitivity coefficients to soil water content at field capacity were −81 to −10% (Fig 5.5), excluding Kawanda in 2007 when the coefficient was not sensitive. Its sensitivity coefficients to soil water content at permanent wilting point were 24 to 38%, excluding Kawanda in 2007 when a non-sensitive coefficient was observed. The sensitivity coefficient for evaporation from the soil to soil surface albedo averaged about −20% (Table 5.4).

5.4.   Discussion

Ntungamo was drier than normal in 2007 when compared with the 900 to 1150 mm of mean annual total rainfall expected at the site according to Hijmans et al. (2005). This may explain the lack of drainage at Ntungamo in 2007, unlike in 2006. The mean canopy transpiration rate of 2 mm d^{-1} was comparable with the 2 to 3 mm d^{-1} measured by Lu et al. (2002) in Darwin, Australia. However, it was small compared with the mean values reported for other banana cultivars grown elsewhere in the tropics, for example 5.7 to 9.2 mm d^{-1} in Honduras (Arscott et al., 1965), 3.3 to 4.0 mm d^{-1} in Brazil (Bassoi et al., 2004) and 2.6 to 4.3 mm d^{-1} in Brazil (Montenegro et al., 2008) as reviewed by Carr (2009). The maximum rate of evaporation from the soil (0.028 mm d^{-1}) in the current study was only one third of the maximum rate of evaporation from the soil in a shaded but non-mulched banana system in Israel, which was reported to be 0.105 mm d^{-1} (Tanny et al., 2005). The low evaporation from soil observed in this study may have been due to attenuation of net radiation through the three-layered crop canopy as well as in the mulch layer before reaching the soil surface (Eq. 5.12). This is supported by the observation that evaporation from the soil was most sensitive to net radiation extinction coefficient in the crop canopy (Table 5.4).

Transpiration, the dominant process for water removal from the root zone, was driven by atmospheric demand and limited by soil water supply in this model. The atmospheric demand was determined by the amount of radiation arriving at a given canopy layer and the drying power of the wind (Eqs. 5.06 to 5.10) while soil water supply was determined by the soil water content. This explains why over 90% of the canopy transpiration was

due to Plant 1, through whose canopy the incident net radiation energy diminished exponentially (Eq. 5.13) before reaching the underlying Plant 2 and Plant 3 canopies. Consequently, transpiration was sensitive to the parameters that determine either evaporative demand (radiation, temperature and vapour pressure) or limitation to transpiration (soil water content at field capacity and at permanent wilting point) as well as rainfall (Fig 5.3 and Fig 5.4), which recharges the soil water storage capacity and hence offsets the limitation to transpiration due to sub-optimal soil water content. Limitation to transpiration due to excessive soil water content (Eq. 5.18a) was rarely encountered at both sites and both years in this study, hence the lack of sensitivity of transpiration to the wet soil water content.

The apparent relationships between the sensitivity of root zone water content to rainfall, net radiation (Fig 5.3), temperature and vapour pressure (Section 5.3.2) suggest dependent or interactive effects in the processes through which these parameters influence root zone soil water content. Whereas rainfall replenishes soil water content, radiation provides the energy for conversion of liquid to gaseous water; the first step in evapotranspiration, which was the main process for depletion of soil water content. Temperature, determines the gaseous water molecules' kinetic energy, while vapour pressure sets up the gradient that drives the gaseous water molecules' departure from the evaporating sites on the leaf/soil surfaces (Penman, 1948). There are thus feed forward and feedback loops through which rainfall, radiation, temperature and vapour pressure interact to influence the process of evapotranspiration, which in turn explain the observed relationships in patterns of sensitivity of root zone water content to the weather parameters. Kawanda was exceptionally wet in 2007 (Fig 5.2) having received a cumulative gross rainfall of 1633 mm, which was above the mean total annual rainfall of between 1150 and 1400 mm expected at this site (Hijmans et al., 2005). This explains why canopy transpiration was not sensitive to rainfall but was most sensitive to radiation at Kawanda in 2007 (Fig 5.4). On the contrary, canopy transpiration was sensitive to rainfall and insensitive to net radiation at Ntungamo in 2007, which was exceptionally dry. This highlights the importance of the balance between atmospheric evaporative demand and soil water supply in modifying sensitivity of canopy transpiration to the weather variables in this model.

Drainage was more sensitive to rainfall than to the soil water content at field capacity (Table 5.3). The rate of drainage can be conceptualised as a process determined by the rate of water supply from rainfall that drives the infiltration rate in conjunction with other

factors that influence the rate at which the soil's water content at a given point in time changes around field capacity. The infiltration rate, which recharges water content to field capacity prior to on-set of drainage in this model, may be limited by surface sealing and/or crusting (Inbar et al., 2014). Surface sealing and crusting, however, was not considered in this model since the soil surface is mulched and is thus not prone to surface sealing and/or crusting (Assouline, 2004). Processes that deplete the soil water storage relative to the field capacity moisture content are the other important factors that determine the rate of drainage, besides rainfall. These factors include weather parameters that influence evapotranspiration and soil parameters that influence the amount of water that can be stored in the root zone. This explains the sensitivity of rate of drainage to radiation, average temperature, vapour pressure, rooting depth and soil water content at field capacity (Table 5.3). However, the soil parameters appear to have merely limited the drainage process, which seems to have been principally driven by rainfall and the weather parameters controlling evapotranspiration.

The results indicate that a deep rooting zone with high available water capacity arising from a good soil structure are important in increasing water uptake and hence banana yields. Deep tillage to break up shallow indurated soil layers and building soil organic matter through addition of organic materials so as to increase the available water capacity of the soil are thus important cultural practices for managing the crop water requirements and banana productivity as surmised by Zake (1993). The soil organic matter dynamics, their associated available water capacity dynamics and soil water conservation through a thin dry topsoil layer were not simulated. The soil water conserving effect of a thin dry topsoil layer was represented by the surface mulch layer. Nevertheless, the mulch layer had minimal impact on root zone water content due to reduced availability of energy at the soil surface. A deep root zone and high available soil water capacity only serve to offset the limitations to transpiration, which were less important compared with the driving factors of environmental evaporative demand and water supply to the root zone through rainfall (Fig 5.4). The results therefore imply that irrigation could be more important than mulching for increasing transpiration and, hence, banana yields in Uganda where inadequate rainfall regimes prevail. The model, after calibration, can be used to quantify the crop water requirements in order to guide irrigation management for optimising banana productivity in Uganda.

5.5. Conclusions

The East African Highland banana soil water balance components were sensitive to the weather parameters rainfall, radiation, temperature, vapour pressure and wind speed. Where weather stations are installed, high quality data on these weather parameters are readily available. Then the degree of uncertainty in the soil parameters, rather than in the measured weather data, determine the accuracy and reliability of the soil water balance simulated by the model. The soil parameters to which the water balance components exhibited sensitivity were rooting depth and moisture contents at field capacity and at permanent wilting point. Sensitivity was also exhibited to the crop parameters canopy surface albedo, radiation extinction coefficient in the canopy, leaf area indices for Plant 1, 2 and 3, especially regarding drainage and evaporation from the soil. Only the negligible evaporation from the soil was sensitive to the mulch parameters. Calibration of this model at a given site should pay attention to the soil parameters rooting depth and moisture contents at field capacity and at permanent wilting point, which are notorious for their wide variability and yet are not routinely measured in surveys due to methodological challenges.

'As far as the laws of mathematics refer to reality, they are not certain, and as far as they are certain, they do not refer to reality'- Albert Einstein

CHAPTER SIX

6.0. Water-limited production of East African highland banana cropping systems: experiments and simulations

Abstract

Drought stress is a major constraint in East African highland banana (*Musa* spp. AAA-EA) in Uganda. The specific objectives of this study were to quantify the yield gap due to drought stress and to estimate the contribution of self-mulch to mitigation of the drought stress impact on yields. A soil water balance was linked to the potential production model (LINTUL-BANANA1) of highland bananas. The model was calibrated and tested against empirical data from fertilizer response field trials at Kawanda (central Uganda) and Ntungamo (south-western Uganda). Individual plant data on growth and yield components were collected. Weather data were collected using an HOBO® automatic meteorological station installed at each site. Soil water storage data were collected in Blocks 1 and 3 at Ntungamo and Blocks 1 and 4 at Kawanda using a Deviner2000®. The model was calibrated to match simulated with observed total dry matter and soil water storage using data from in Block 1 at Ntungamo. The calibrated model was tested on four plants that emerged on the same date in the same plot of Block 3 at Ntungamo and Block 4 at Kawanda. The model was further tested for reliability in simulating yield components using 20 and 23 plants from Kawanda and Ntungamo trials, respectively, which were randomly selected from plots that received 150-400 kg N and 250 – 600 kg K ha^{-1} yr^{-1}. The calibrated and tested model was used to simulate growth and yield under rain-fed conditions vs. that with soil moisture maintained at field capacity to quantify the yield gap due to drought stress. It was also used to simulate rain-fed growth and yield with and without self-mulch to quantify mitigation of mulching on drought stress impact. In both simulation trials, the plants for each scenario were paired by date of emergence. Data were analysed using paired t-test and analysis of variance. The model accurately predicted total dry weight (RMSE <0.09; r^2 > 0.85). However, simulated corm and leaf dry matter were only 27 and 37% of their observed values, respectively, while the simulated pseudostem and bunch dry matter were double their respective observed values. Therefore, simulated yields were interpreted on the basis of percentages. The drought stress yield gap across sites was 55% and was wider (74%) at Kawanda than at Ntungamo (41%). Self-mulch reduced the drought stress yield gap by 10% at Kawanda, but had no effect at Ntungamo. The model needs further calibration of the soil water balance parameters defining available water capacity and crop parameters defining dry matter partitioning between the plant structures for accurate simulation of yield components. Adding nutrient limitations, especially potassium, to the model is also recommended for comprehensive evaluation of the contribution of mulch to drought stress mitigation and sustaining highland productivity in the low-input production systems of Uganda.

Keywords: *Light interception, light use efficiency, mulch, specific leaf area, Uganda.*

6.1. Introduction

Drought stress is a major limitation to the hitherto rain-fed East African highland banana (hereafter called 'highland banana') cropping systems of Uganda (van Asten et al., 2011). Information on the water requirement of a crop (Slabbers, 1980) and yield gap due to drought stress is necessary to make economically rational choices from a collection of feasible agronomic management techniques against drought stress in a given cropping system. The optimal rainfall for bananas is reported to be 1300 mm yr^{-1} (Robinson, 1996). However, van Asten et al. (2011) reported increase in highland banana fresh bunch weight with increase in cumulative rainfall beyond 1500 mm yr^{-1} in the 365-day period preceding the date of harvest. This suggests that the crop's optimal rainfall in the major agro-ecological zones of Uganda is over 25% greater than the reported optimal value.

Studies on the management of crop water requirements in highland banana cropping systems have focused on crop growth/yield impacts of mulching (McIntyre et al., 2000; 2003; Ssali et al., 2003) and use of different mulch materials (Bananuka et al., 2000). There has also been an irrigation experiment aimed at characterising banana genotypes' drought tolerance mechanisms for crop improvement purposes (Bananuka et al., 1999). Systematic characterisation of the dynamics of crop water requirements in different pedo-climatic zones to inform choice of management interventions against drought stress in highland banana cropping systems is yet to be done. If drought stress impacts on growth and productivity are to be minimised, the chosen management intervention should enable the crop to match its actual transpiration with demands imposed by the prevailing weather conditions. Actual crop transpiration is limited by soil hydraulic property-dependent available soil water supply. Water requirements are thus spatially and temporally variable, hence the need for systematic exploration of the dynamics of crop water requirements at multiple representative locations over extended periods of time.

Due to the unique nature and physiology of bananas, conventional methods for determining the crop water status are beset with practical challenges (Turner and Thomas, 1998) in as much the same way as those for determining the whole plant actual water uptake or transpiration under field conditions (Liu et al., 2008). These challenges are exacerbated by the fact that a range of soil water supply scenarios has to be tested on a range of soil types across the major agro-ecological zones featuring the highland banana cropping systems. Furthermore, crop water uptake should be linked to crop growth and yield if data that have a bearing on the requisite management interventions are to be generated. Irrigation studies are thus important in this regard. Multi-location irrigation studies for generating such information for highland banana

cropping systems are expensive and need a long period of time to conduct, given banana's perennial growth habit. These challenges can, to some extent, be overcome with appropriate crop growth models linked to a well-calibrated soil water balance simulation framework (van Vosselen et al., 2005).

Brisson et al. (1998a) attempted to model banana growth in response to soil water supply but their simulation framework is inappropriate for established highland banana system (see Chapter 1, Section 1.3 for details), which is typically self-ratooning. This motivated Nyombi (2010) to develop a light interception and utilisation-based banana growth model for potential growth, LINTUL-BANANA1, which captures the self-ratooning and phenological heterogeneity of established banana fields in Uganda. However, LINTUL-BANANA1 simulates highland banana growth and production under conditions of no growth limitation from water, nutrients or pest/disease constraints. The current study linked a soil water balance simulation framework to LINTUL-BANANA1 to simulate water-limited banana growth and production. The specific objectives of this study were to 1) quantify banana yield gap due to drought stress; 2) evaluate the contribution of banana self-mulch (i.e. internally-generated mulch material) cover to mitigating highland banana yield loss due to drought stress in Uganda's rain-fed system. The following null hypotheses were tested: 1) There is no difference between potential and water-limited banana yields. 2) There is no difference between water-limited highland banana yields with and without self-mulch. 3) There is no difference between cumulative transpiration with and without self-mulch under water-limited growing conditions.

6.2. Materials and Methods

6.2.1. LINTUL-BANANA1 description and adaptation for water-limited scenario

Details of the underlying equations and their justification are presented in Nyombi (2010), while the relational diagrams summarising the model are presented in Appendix 6A-C. Implemented in Fortran Simulation Translator with a daily time step, the model assumes an established banana plantation in which each banana mat is synchronised and consists of three plants of different generations or crop cycles, namely: a mother (Plant 1), daughter (Plant 2 or Sucker 1) and granddaughter (Plant 3 or Sucker 2) plant. Dry matter (DM) accumulation or growth, and ultimately, development of Plant 1 (Appendix 6A) and Plant 2 (Appendix 6B), is driven by a function of photosynthetically active radiation (PAR) intercepted, daily effective temperature and light use efficiency. Interception of PAR is an exponential function of the leaf area index and a constant light extinction coefficient in the canopy, which also determines the amount of PAR that is transmitted to the underlying canopy layer/s. Intercepted PAR is quantified as the difference between incoming and outgoing PAR.

The leaf area index is estimated by the integrated difference between its growth and death rates. Leaf area index growth rate for Plant 1 depends on the proportion of total DM allocated to the leaves and a constant specific leaf area. After Plant 2 attains a heat sum of 960 ^{o}Cd, its leaf area index growth rate is computed in the same way as for Plant 1. Before Plant 2 attains 960 ^{o}Cd, its leaf area index is computed in the same way as for Plant 3 when the latter is at or older than 360 ^{o}Cd. The leaf area index growth rate for Plant 3 (Appendix 6C) is a product of the daily effective temperature, relative growth rate of leaf area and the existing leaf area index. Before 360 ^{o}Cd, Plant 3 is assumed to have no functional leaves and therefore neither growth nor death in its leaf area index occurs. The leaf area index death rate is a product of the existing leaf area index and a constant relative death rate, assuming normal leaf senescence under non-limiting growing conditions.

A proportion of the gross DM production rate for Plant 1 is allocated to Plant 2 until Plant 1 initiates flowering at 2423 ^{o}Cd. The remainder of the gross DM production rate is the Plant 1 net DM accumulation rate upon which Plant 1 root and shoot growth depend. Plant 1 also receives DM re-allocated from its predecessor's corm. The growth of Plant 2 partly depends on DM apportioned to it from Plant 1 and partly on DM from its own photosynthesis. The growth of Plant 3 depends on DM allocated to it from Plant 2 via two temperature sum-dependent functions. Plant 3 also gets DM from its own photosynthesis after developing functional leaves. For a given plant, the DM allocated to the shoot is partitioned to the corm, pseudostem, leaves and bunch (only for Plant 1) according to temperature sum-dependent coefficients. Harvest takes place when Plant 1 is aged 3600 ^{o}Cd, upon which event, the existing Plant 2 is automatically converted to Plant 1 and the existing Plant 3 automatically becomes Plant 2. At harvest, the DM in Plant 1 corm is instantly partitioned into two states; one is for re-allocation to the new Plant 1 and the other degrades to soil organic matter. However, the soil organic matter dynamics are yet to be added to the model. During the growth of the plants, the dead leaves are pruned and their DM contributes to self-mulch while dead root DM contributes to soil organic matter. At harvest, the DM in the pseudostem and that in all existing leaves (dead or functional) contribute to self-mulch, while DM in all roots for Plant 1 adds to soil organic matter.

The water balance model described in Chapter 5 was linked to LINTUL-BANANA1 in such a manner that the simulated leaf area indices from the latter were the inputs in the former. The ratio of simulated actual to potential transpiration was computed as a moisture stress index (Spitters and Schapendonk, 1990), which in turn was an input in the LINTUL-BANANA1 part of the model (Fig 5.1 and Appendix 6A-C). The moisture stress index (TRARF in the model) was assumed to reduce light use efficiency linearly since limited soil water supply induces stomatal closure (Thomas

and Turner, 1998) and over time, increased photochemical damage of chlorophyll (Thomas and Turner, 2001) in bananas. The moisture stress index was also assumed to linearly reduce the relative growth rate of leaf area index based on the observation that drought stress stops emergence of Cavendish banana leaves (Turner and Thomas, 1998). The moisture stress index reduces the accumulation of temperature sum by the plant in line with the observed delay in development due to drought stress (Okech et al., 2004).

6.2.2. Model sensitivity analysis

Sensitivity analysis was done as described in Section 5.2.3. However, the output variables considered were the leaf area index and total dry matter for Plant 1, 2 and 3, bunch weight and soil water content in response to selected soil and crop input parameters, whose respective default values are given in Table 6.1. The soil water balance module was found to be sensitive to soil water content at field capacity and permanent wilting point. The soil water content at field capacity and at permanent wilting point for each fertilizer response trial site (Kawanda and Ntungamo, see Section 6.2.3) were estimated from soil texture and soil organic matter content using pedotransfer functions (Eqs. 6.01 and 6.02) recommended by Pidgeon (1972).

$$FC = 7.38 + 0.16Si + 0.30Cl + 1.5OM \text{ .... Eq. 6.01}$$

$$PWP = -4.19 + 0.19Si + 0.39Cl + 0.90OM \text{ .... Eq. 6.02}$$

where *FC* and *PWP* are respectively the gravimetric field capacity and permanent wilting point moisture content of the soil; *Si*, *Cl* and *OM* are the percentage silt, clay and organic matter contents of the soil.

The gravimetric water FC and PWP values (*w%*) from Eqs. 6.01 and 6.02 were converted to volumetric water content ($\theta\%$) using measured bulk density (ρ_{b}, g cm^{-3}) based on equation 6.03, assuming the density of soil water (ρ_w) to be 1 g cm^{-3}.

$$\theta\% = w\% \times \rho_b / \rho_w \text{ .... Eq. 6.03}$$

The dry matter partitioning coefficients in LINTUL-BANANA1, parameter initial values and weather variables were not considered in the model sensitivity analysis, whose objective was to identify parameters for the model calibration.

6.2.3. Model calibration and testing

Model calibration and testing was based on data collected from two fertilizer response trials. Site characterisation, trial design and management are described in Section 3.2.2. Additionally, access tubes were installed in each experimental plot in 2 out of the 4 blocks at each site to monitor root zone soil water storage using a Deviner2000$^{®}$ probe and data logger (Sentek Environmental Technologies, Stepney, South Australia)

once a week. An automatic weather station (HOBO®; Onset Computer Corporation, Massachusetts, USA) was installed at each site to collect data on rainfall, solar radiation, temperature, vapour pressure and wind speed on a daily basis.

Table 6.1: Values for crop and soil parameters applied during the sensitivity analysis.

Category	Model Code	Description	Pre-calibration value	Post-calibration value
Crop	ALBC1	Plant 1 canopy surface albedo	0.25	0.25
Crop	ECCOFC1	Radiation extinction coefficient in Plant 1 canopy	0.5	0.5
Crop	LAIstop_exp	Leaf area index (LAI) above which exponential growth in LAI stops	0.88 ha ha^{-1}	0.88 ha ha^{-1}
Crop	LUE1_0	Light use efficiency for Plant 1	0.00333 kg MJ^{-1} PAR	0.0025 kg MJ^{-1} PAR
Crop	RDR1	Plant 1 relative leaf area death rate	0.0214 d^{-1}	0.0280 d^{-1}
Crop	RDR2	Plant 2 relative leaf area death rate	0.0094 d^{-1}	0.0094 d^{-1}
Crop	RGRL1_0	Plant 1 relative leaf area growth rate	0.0077 °Cd^{-1}	0.0023 °Cd^{-1}
Crop	RGRL2_0	Plant 2 relative leaf area growth rate	0.0077 °Cd^{-1}	0.0023 °Cd^{-1}
Crop	RGRL3_0	Plant 3 relative leaf area growth rate	0.0077 °Cd^{-11}	0.0023 °Cd^{-1}
Crop	SLA1	Specific leaf area for Plant 1 LAI	0.0012 ha kg^{-1} DM	0.0013 ha kg^{-1} DM
Crop	SLA2	Specific leaf area for Plant 2 LAI	0.0012 ha kg^{-1} DM	0.0014 ha kg^{-1} DM
Crop	SLA3	Specific leaf area for Plant 3 LAI	0.0012 ha kg^{-1} DM	0.0021 ha kg^{-1} DM
Crop	TRANCO	Transpiration constant	500,000 kg ha^{-1} d^{-1}	500,000 kg ha^{-1} d^{-1}
Crop	TSUM3stop_exp	Physiological age of Plant 3 at cessation of LAI exponential growth	960 °C d	960 °C d
Soil	WCAD (θ_{ad})	Air-dry moisture content	0.01 m^3 m^{-3}	0.01 m^3 m^{-3}
Soil	WCFC (θ_{fc})	Field capacity moisture content at Kawanda (at Ntungamo)	0.32 (0.24) m^3 m^{-3}	0.32 (0.24) m^3 m^{-3}
Soil	DRATE	Maximum drainage rate	500,000 kg ha^{-1} d^{-1}	500,000 kg ha^{-1} d^{-1}
Soil	WCWP (θ_{wp})	Wilting moisture content at Kawanda (at Ntungamo)	0.20 (0.10) m^3 m^{-3}	0.20 (0.10) m^3 m^{-3}
Soil	WCWET (θ_{w})	Wet moisture content	0.37 m^3 m^{-3}	0.37 m^3 m^{-3}
Soil	WCST (θ_{sd})	Saturated moisture content	0.42 m^3 m^{-3}	0.42 m^3 m^{-3}
Soil	ROOTD	Effective rooting depth	0.5 m	0.5 m

The fertilizer response trials were planted between November 2004 and January 2005. Data for model calibration and testing were from plots that received 150 to 400 kg N ha^{-1} yr^{-1} and 250 to 600 kg K ha^{-1} yr^{-1}, because the model assumes optimal conditions with respect to nutrients.

Records for suckers selected to complete the growth cycle were kept on individual plant basis. These included periodic growth monitoring parameters and dates of sucker emergence, flowering (i.e. emergence of the flower bud out of the pseudostem) and harvest. The growth parameters, assessed at approximately 4-week intervals, were plant height (length from ground level up to the vertex of insertion into the pseudostem of the youngest pair of fully unfurled leaves) and girth at base. At each growth monitoring data collection routine (hereafter referred to as 'event'), leaf area (m^2) and total dry weight (kg) per plant were estimated from the plant height and/or girth data using allometric functions developed from individual plants sampled from the fertilizer response trial at Ntungamo and farmers' fields in south-western and central Uganda (Nyombi et al., 2009).

During calibration, the model was initialised with the default values of input parameters for the soil water balance specified in Chapter 5. However, the soil water contents at field capacity and permanent wilting point, were replaced with values estimated from Equations 6.01 to 6.03. Remaining within limits of ranges reported in literature, the parameters to which the model was sensitive were adjusted, one at a time and in descending order of their relative sensitivity coefficients. This was done through trial and error so as to minimise the difference between observed and simulated soil water content and total dry matter. Data from Block 1 at Ntungamo were used for model calibration.

The calibrated model was tested on 4 plants that emerged on 20th Feb 2006 from the same plot in Block 3 of the Ntungamo trial and 4 plants that emerged on 17th Apr 2005 from the same plot in Block 4 at Kawanda. In both cases, the plot used for model testing received 400 kg N and 600 kg K ha^{-1} yr^{-1}. The model was further tested for reliability in simulating yield parameters using 20 and 23 plants from the Kawanda and Ntungamo trials, respectively, which were randomly selected from plots that received 150 – 400 kg N and 250 – 600 kg K ha^{-1} yr^{-1}. The selected plants had dates of emergence falling between beginning of February and end of July at each site.

Performance of the calibrated model was qualitatively evaluated using 1:1 plots of predicted vs. observed values for soil water content and total dry matter. Quantitative performance of the calibrated model was evaluated using the squared correlation coefficient (r^2, Eq. 6.04) and the normalised root mean square error (RMSE, Eq. 6.05) between simulated and observed values of soil water content and total dry matter.

$$r^2 = 1 - \left[\sum_{i=1}^{n} \left(x_i^o - x_i^p \right)^2 \middle/ \sum_{i=1}^{n} \left(x_i^o - \overline{x}_i^o \right)^2 \right] \quad \text{...}\text{Eq. 6.04}$$

$$RMSE = \frac{\left[\sum_{i=1}^{n} \left(x_i^o - x_i^p \right)^2 \right]^{0.5} \middle/ n}{\overline{x}_i^o} \quad \text{...}\text{Eq. 6.05}$$

where x_i^o and x_i^p are the ith observed and predicted values for a given variable (soil water content, total dry matter, leaf area or leaf dry matter), respectively, and $\overline{x}_i^o$ is the mean of all the n observed values for a given variable.

6.2.4. Evaluation of drought stress yield gap and mitigation due to self-mulch

The calibrated and tested model was used to generate data from two simulation trials. In one simulation trial, growth and yield under rain-fed conditions was compared against growth and yield with soil moisture maintained at field capacity. The second trial compared rain-fed growth and yield with and without self-mulch of the system. In both trials, the simulated plants for each scenario were paired by date of emergence so as to have the same reference dates for integrating actual evapotranspiration.

The scenario of soil moisture maintained at field capacity was implemented by setting the irrigation factor (IRRIGF in the model) equal to 1. This made the water balance sub-model to automatically introduce extraneous water supply to top it up to field capacity at any given moment in the simulation. Setting the irrigation factor to 0 eliminated the extraneous soil water input. This led to entirely rain-fed simulated growth affected by water stress whenever water inflow to the rooting zone from rainfall fell short of the water outflow from the rooting zone. A parameter (MAIF in the model) was factored into the equation for computing mulch area index. If this parameter was set to 0, a 0 for the computed mulch area index was returned thus eliminating the effects of surface mulch in the simulation. When set to 1, the parameter allowed the model to compute the mulch area index, thereby including the effects of surface mulch on rain interception and evapotranspiration in the simulation.

Simulated bunch dry matter was divided by 0.15 to convert it to fresh bunch weight, based on the linear relationships in Fig. 6.1. Assuming a spacing of 3 m × 3 m and that there is no loss of mother plants throughout the crop cycle duration (time from sucker emergence to harvest), fresh bunch yield was computed from Eq. 6.06.

$$Y = B_{FW} \times \frac{365}{C_{DUR}} \times \frac{10000}{9} \times \frac{1}{1000} \quad \text{...}\text{Eq. 6.06}$$

where Y is the fresh bunch yield (t ha^{-1} yr^{-1}); B_{FW} is the fresh bunch weight per plant, C_{DUR} is the crop cycle duration (d).
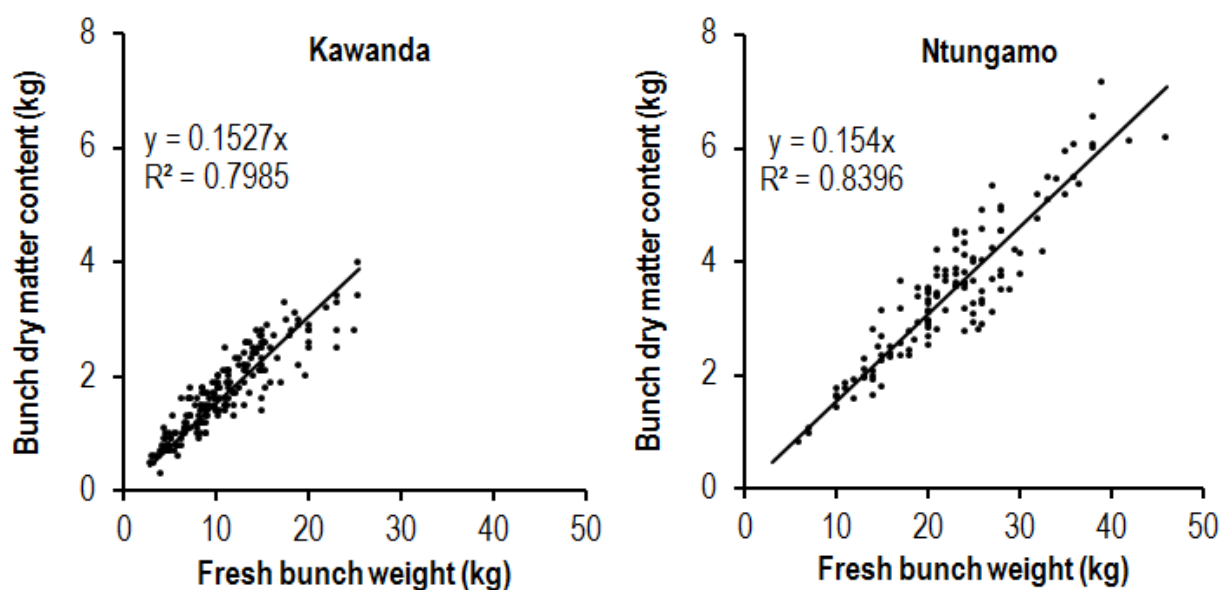
Figure 6.1: Relationship between bunch dry matter content and fresh bunch weight at Kawanda (central Uganda) and Ntungamo (South-western Uganda).

Data were from plants that received 150 – 400 kg N and 250 – 600 kg K ha^{-1} yr^{-1} in the fertilizer response trials at Kawanda and Ntungamo.

6.2.5. Data analysis

Harvest stage data on total dry mater, fresh bunch yield and its components (bunch dry mater, fresh bunch weight and cycle duration) from model testing simulations were subjected to paired t-test against observed values for plants whose dates of emergence the simulated ones' coincided with. Harvest stage data on fresh bunch yield, its components, cumulative transpiration and cumulative evaporation from the field capacity vs. rain-fed soil water supply scenario and self-mulch vs. no mulch scenario simulations were subjected to analysis of variance using unbalanced structure, adjusting for month of sucker emergence as a confounding variable.

6.3. Results
6.3.1. LINTUL-BANANA2 model calibration and performance evaluation

The model was most sensitive to Plant 1 specific leaf area and light use efficiency (Table 6.2). Plant 1 was less sensitive to the crop input parameters than either Plant 2 or Plant 3, while soil water content was the least sensitive to the crop input parameters (Table 6.2). Bunch weight and leaf area index for plant 3 were the most sensitive in 2006 and 2007, respectively, at both sites to the soil parameters root depth, water content at permanent wilting point and at field capacity. Samples taken from a well-maintained banana field at the end of the first rainy season of 2015 in central Uganda indicated that Plant 1 specific leaf area (0.013 ha kg^{-1} DM) was similar to that for Plant 2 (0.0014 ha kg^{-1} DM) but both were significantly lower than for Plant 3 (0.0021

ha kg^{-1} DM). These values were adopted in the model. Setting light use efficiency to 0.0025 kg MJ^{-1} PAR, increasing the relative death rate of Plant 1 leaf area index by 70% and reducing the relative growth rate of leaf area index for all 3 plants by 31% (Table 6.1) narrowed the discrepancy between simulated and observed total dry mass per plant. No further improvements in the model outputs were obtained by changing the remaining input parameters, and so their default values were retained.

Table 6.2: Time-averaged sensitivity coefficients of leaf area index, total dry matter, bunch weight and soil water content for the key crop input parameters SLA, LUE, WCFC and WCWP.

Input	Output	Kawanda 2006	Kawanda 2007	Ntungamo 2006	Ntungamo 2007
Plant 1 specific leaf area (SLA1)	Plant 1 leaf area index (LAI1)	0.650	0.575	0.916	0.876
	Plant 1 total dry matter (DM1)	-0.059	-0.110	0.078	0.074
	Plant 2 leaf area index (LAI2)	-0.881	-2.246	-2.422	-2.489
	Plant 2 total dry matter (DM2)	-0.856	-1.612	-1.972	-2.126
	Plant 3 leaf area index (LAI3)	-1.819	-2.354	-3.015	-2.876
	Plant 3 total dry matter (DM3)	-1.622	-1.992	-2.659	-2.631
	Soil water content (WC)	-0.003	0.001	-0.023	-0.016
	Bunch weight (Wbunch1)	-0.555	0.197	0.265	0.413
Plant 1 light use efficiency (LUE1)	Plant 1 leaf area index (LAI1)	0.577	0.524	0.806	0.784
	Plant 1 total dry matter (DM1)	0.671	0.635	0.826	0.817
	Plant 2 leaf area index (LAI2)	-0.659	-1.756	-1.874	-1.959
	Plant 2 total dry matter (DM2)	-0.705	-1.298	-1.556	-1.713
	Plant 3 leaf area index (LAI3)	-1.502	-1.956	-2.567	-2.513
	Plant 3 total dry matter (DM3)	-1.350	-1.673	-2.299	-2.329
	Soil water content (WC)	0.000	0.003	-0.016	-0.012
	Bunch weight (Wbunch1)	0.535	1.049	1.008	1.141
Water content at field capacity (WCFC)	Plant 1 leaf area index (LAI1)	-0.026	0.183	0.019	0.085
	Plant 1 total dry matter (DM1)	0.908	0.428	0.382	0.251
	Plant 2 leaf area index (LAI2)	0.257	1.468	0.520	0.807
	Plant 2 total dry matter (DM2)	0.317	1.025	0.443	0.627
	Plant 3 leaf area index (LAI3)	2.135	1.766	0.984	0.807
	Plant 3 total dry matter (DM3)	1.760	1.352	0.872	0.655
	Soil water content (WC)	0.696	0.920	0.829	0.623
	Bunch weight (Wbunch1)	2.785	0.849	1.177	0.402
Water content at permanent wilting point (WCWP)	Plant 1 leaf area index (LAI1)	0.180	-0.117	-0.023	-0.059
	Plant 1 total dry matter (DM1)	-0.753	-0.273	-0.183	-0.141
	Plant 2 leaf area index (LAI2)	-0.004	-0.942	-0.366	-0.427
	Plant 2 total dry matter (DM2)	-0.294	-0.657	-0.249	-0.324
	Plant 3 leaf area index (LAI3)	-2.267	-1.171	-0.545	-0.414
	Plant 3 total dry matter (DM3)	-1.967	-0.907	-0.489	-0.339
	Soil water content (WC)	0.276	0.100	0.257	0.331
	Bunch weight (Wbunch1)	-2.855	-0.539	-0.576	-0.212

The calibrated model accurately predicted total dry weight at a given point in time both at Kawanda and Ntungamo (Fig. 6.2). The simulated growth curve was to a great extent synchronous with the observed one at Ntungamo, but less so at Kawanda. The simulated soil water storage dynamics matched measurements at Ntungamo more closely than the corresponding relations at Kawanda. Whereas the model tended to under-estimate soil water storage at Ntungamo, the reverse was true at Kawanda (Fig. 6.3).
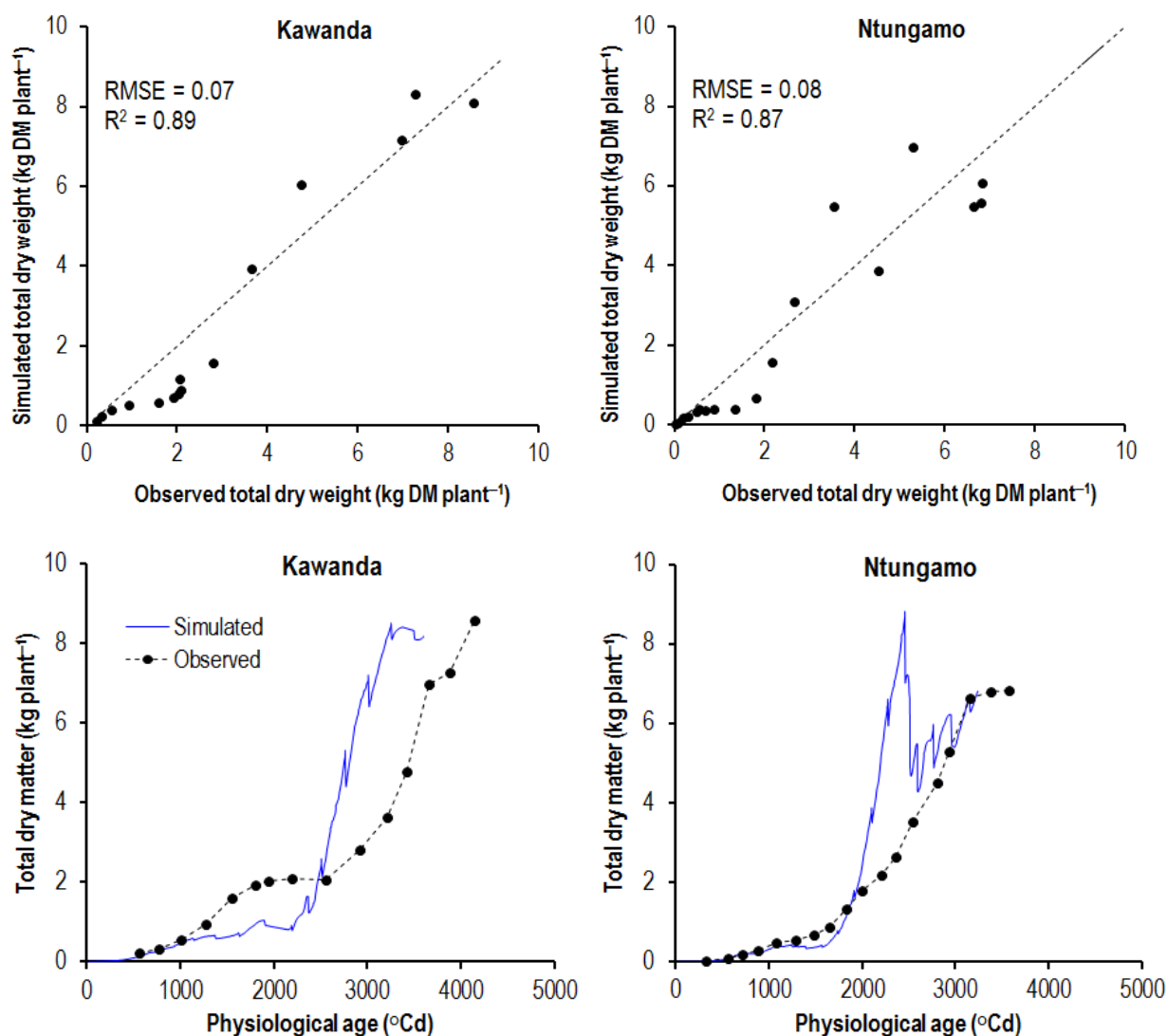

Figure 6.2: Plots for simulated vs. observed water-limited total dry weight and simulated vs. observed water-limited growth curve of East African highland banana at Kawanda, (central Uganda) and Ntungamo (south-western Uganda).

RMSE = Root mean square error. Each observed data point is a mean value from 4 plants that emerged on the same day (17th Apr 2005 at Kawanda; 20th Feb 2006 at Ntungamo) from the same experimental plot (Block 4 at Kawanda and Block 3 at Ntungamo), which received 400 kg N and 600 kg K ha^{-1} yr^{-1}. The respective soil water content plots and dynamics for these experimental plots are presented in Figure 6.3.
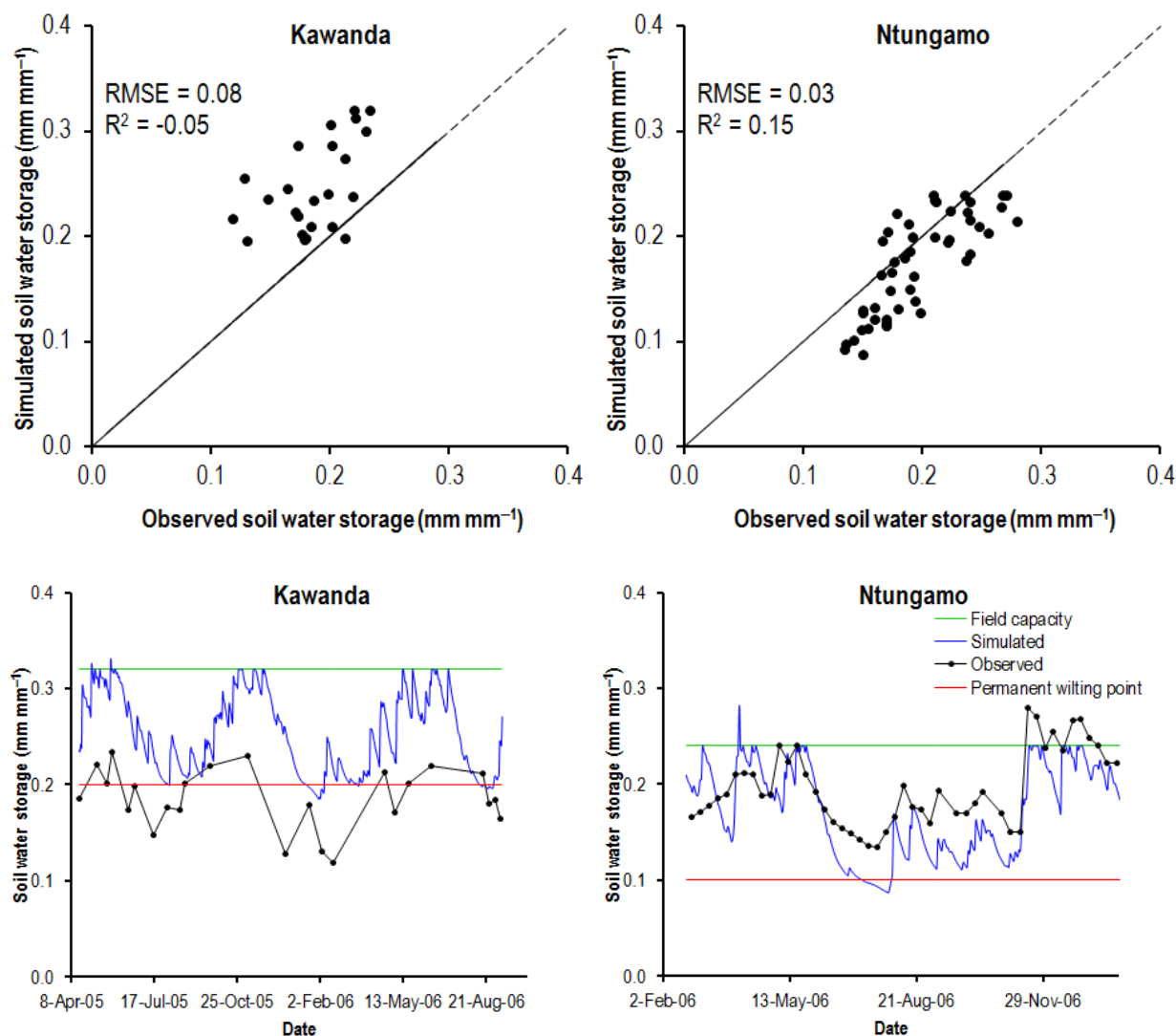
Figure 6.3: Unit plots for simulated vs. observed soil water storage and their dynamics under an East African highland banana crop at Kawanda, (central Uganda) and Ntungamo (south-western Uganda).

RMSE = Root mean square error. Each observed data point is a mean value from 4 plants that emerged on the same day (17ᵗʰ Apr 2005 at Kawanda; 20ᵗʰ Feb 2006 at Ntungamo) from the same experimental plot (Block 4 at Kawanda and Block 3 at Ntungamo), which received 400 kg N and 600 kg K ha⁻¹ yr⁻¹.

Further testing of the model revealed similarity between the simulated and observed vegetative growth duration as well as the simulated and observed cycle duration. The same was true for the total dry matter, but there were differences between the simulated and observed corm dry matter, leaf dry matter, pseudostem dry matter, bunch dry matter and bunch fresh weight (Table 6.3). The simulated fresh bunch yields were thus between 2 to 3 times the observed values (Table 6.3).

Table 6.3: Comparison of simulated and observed East African highland banana growth and yield parameters at harvest stage.

Parameter	Observed		Simulated		t(42)	Sig. (2-tailed)
	Mean	Standard error	Mean	Standard error		
Vegetative duration (d)	438.30	14.800	425.30	9.000	0.7	0.517
Bunch-filling duration (d)	130.60	1.900	137.60	3.100	-2.5	0.015
Cycle duration (d)	578.80	14.400	561.40	11.700	0.9	0.392
Corm dry matter (kg plant^{-1})	0.49	0.035	0.18	0.011	9.6	<0.000
Leaf dry matter (kg plant^{-1})	0.41	0.030	0.11	0.003	10.1	<0.000
Pseudostem dry matter (kg plant^{-1})	2.20	0.100	4.50	0.300	-10.0	<0.000
Bunch dry matter (kg plant^{-1})	2.70	0.200	6.50	0.300	-18.3	<0.000
Fresh bunch weight (kg plant^{-1})	17.60	1.300	43.50	1.700	-20.2	<0.000
Fresh bunch yield (t ha^{-1} yr^{-1})	13.20	1.200	31.20	0.80	-14.9	<0.000

Based on data from 20 and 23 randomly selected observed plants at Kawanda (central Uganda) and Ntungamo (south-western Uganda), respectively, with different dates of emergence spanning 6 months (February to July) at each site. The observed plants were from different fertilizer response trial plots, which received 150 to 400 kg N and 250 to 600 kg K ha^{-1} yr^{-1}.

6.3.2. East African highland banana yield gap under rain-fed system

Across sites, maintaining soil water storage at field capacity gave a potential fresh bunch yield of 48 t ha^{-1} yr^{-1}, while rain-fed soil moisture storage (water-limited production) gave 21 t ha^{-1} yr^{-1}. The overall simulated yield gap due to drought stress was therefore 55% across sites. However, there was a strong site × drought stress interaction effect on fresh bunch yields. The potential and water-limited fresh bunch yields at Ntungamo were higher than corresponding values at Kawanda (Fig. 6.4). The drought stress yield gap (74%) at Kawanda was almost twice that at Ntungamo. Site × soil water supply interaction effects on cumulative transpiration and cumulative evaporation from the soil were not significant. However, cumulative transpiration followed the same trends as the fresh bunch yields across sites and soil water supply scenarios (Fig. 6.4). Cumulative evaporation from the soil was almost 80% of the difference in cumulative transpiration between the rain-fed highland bananas and those maintained at field capacity at Kawanda. Self-mulch increased fresh bunch yield at Kawanda by 10% but had no effect at Ntungamo. Without self-mulch evaporation from the soil almost doubled at Kawanda (Fig 6.5). However, self-mulch had no effect on cumulative transpiration or any of the yield components.
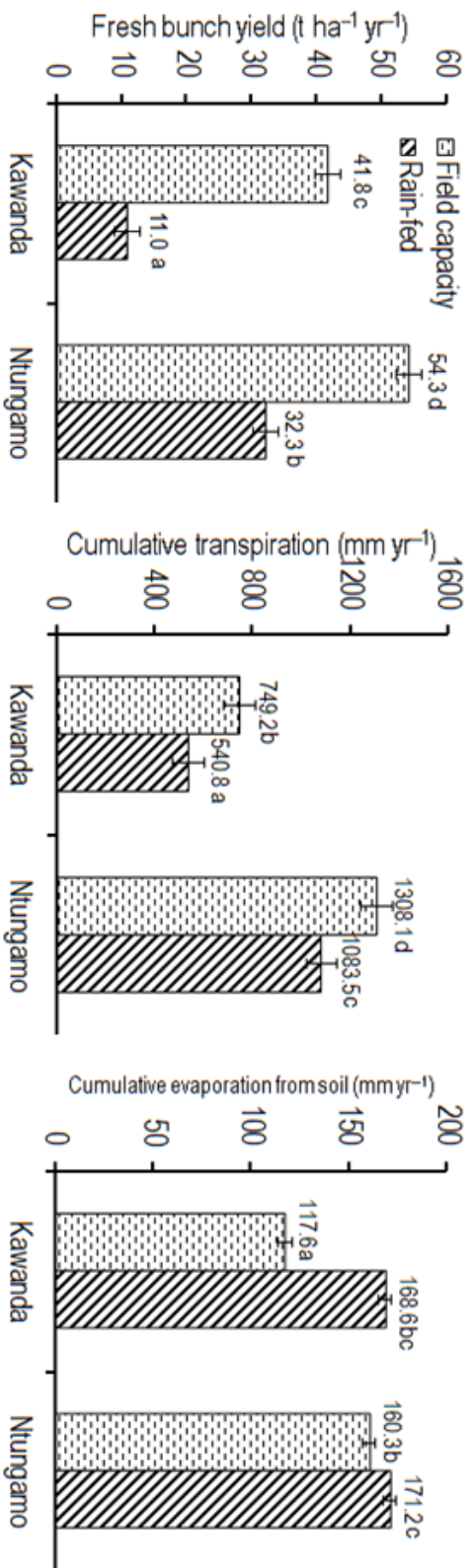
Figure 6.4: Simulated site × soil water supply interactive effects on self-mulched East African highland banana yields, cumulative transpiration and cumulative evaporation from the soil at Kawanda (central Uganda) and Ntungamo (south-western Uganda). Note the difference in y-axes of the cumulative transpiration and evaporation figures.

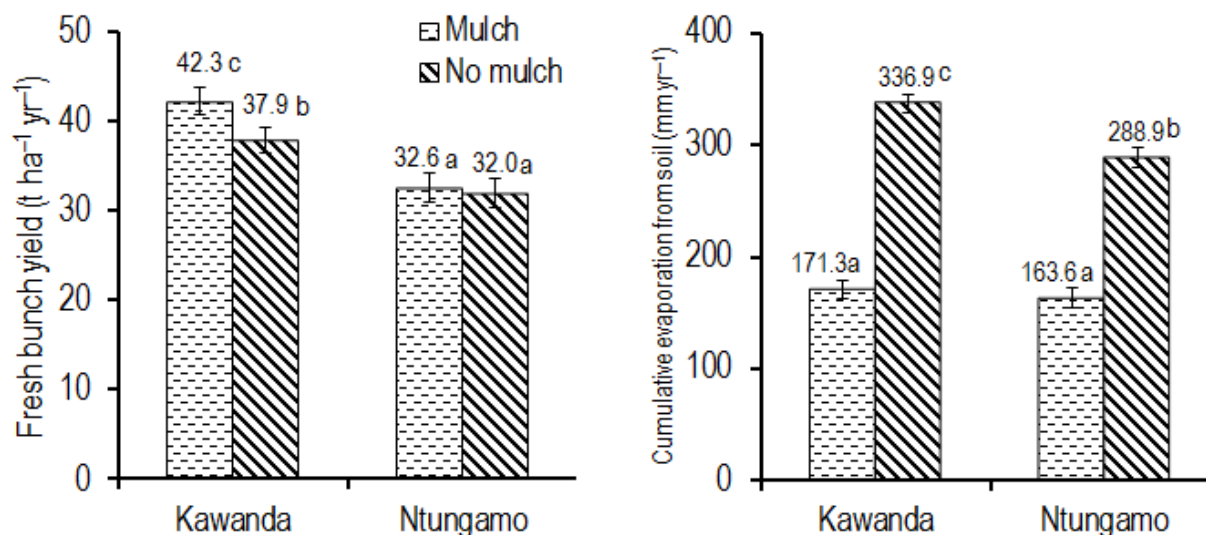*Means for a given variable followed by the same lower case letter are not significantly different at P= 0.05.*

Figure 6.5: Simulated site × soil water supply interactive effects of East African highland banana self-mulch on fresh bunch yields and cumulative evaporation from the soil at Kawanda (central Uganda) and Ntungamo (south-western Uganda).

Means for a given variable followed by the same lower case letter are not significantly different at P=0.05.

6.4. Discussion

6.4.1. LINTUL-BANANA2 model sensitivity analysis

This model is based on light interception and conversion to biomass. This explains why the model was most sensitive to Plant 1 specific leaf area and light use efficiency (Table 6.2), under whose canopy Plant 2 and Plant 3 grow. Specific leaf area determines the leaf area index (Appendix 6), which proportionately increases light interception. Utilization of the intercepted light energy to form biomass is determined by the light use efficiency. Part of the dry matter upon which Plant 2 and Plant 3 depend is from Plant 1, whose canopy also influences the amount of light energy transmitted to the underlying Plant 2 and Plant 3 canopies for their own photosynthesis. This explains why Plant 2 and Plant 3 were particularly sensitive to the plant parameters. Plant 3 emerges with no functional leaves and hence entirely depends on its mother plant (Plant 2) for assimilates that drive its growth and formation of broad leaves. The soil's moisture content at field capacity and permanent wilting point determine its available water capacity. The available water capacity in turn determines the plant's proneness to drought stress. The drought stress is programmed to reduce dry matter production, which translates into less assimilates partitioned to Plant 3 from Plant 2. This explains why Plant 3 was sensitive to the values of field capacity and permanent wilting point of the soil. It also explains why the bunch was particularly sensitive to the field capacity and permanent wilting point moisture contents of the soil since the entire amount of dry matter produced after flower initiation is allocated to bunch-filling.

6.4.2. LINTUL-BANANA2 model calibration and testing

The choice of input parameter values at calibration was within the range reported in literature. Light use efficiency for all plants at both sites was set to 0.0025 kg MJ^{-1} PAR (Table 6.1), which is within the equivalent (upon unit conversion) range of 0.00143-0.00267 kg MJ^{-1} reported by Tsegaye and Struik (2003) for enset bananas in Ethiopia. The specific leaf area values adopted for Plant 1, 2 and 3 (Table 6.1) are similar to the equivalent of 0.0015 – 0.00203 ha kg^{-1} reported by Turner and Lahav (1983) for banana (cv. Williams) in Australia, and the equivalent of 0.00135 ha kg^{-1} reported for Shima banana in Japan by Buah et al. (2000). The relative leaf area growth rate per °C adopted for all the 3 plants on a mat falls in the range reported by Navarro et al (1994). The calibrated values (0.028 and 0.0094 d^{-1}) adopted in the model are within range (0 to 0.0328 d^{-1}) of the relative leaf area death rates computed from the fertilizer response trial dataset at Kawanda and Ntungamo following the classical approach to plant growth analysis (Hunt, 2003). The calibrated parameter input values, therefore, seem realistic.

The trends in simulated soil water storage matched the observations at both sites (Fig 6.3), implying the model is adequately parameterised for simulating the soil water balance for East African highland banana. It is probable that the soil water content at field capacity and at permanent wilting point at Kawanda were over-estimated using the pedotransfer functions by Pidgeon (1972). Most of the measured soil water storage data points at Kawanda were below the calculated permanent wilting point (Fig 6.3), yet plant growth still proceeded at the site. This implies that the simulated plants were subjected to less severe moisture stress than they experienced in reality, resulting in faster simulated growth rates than observed. This explains the terminal off-set between the simulated and observed growth curves at Kawanda (Fig 6.2). Across sites however, the model accurately simulated the time to flowering or vegetative growth duration and the time to harvest or cycle duration (Table 6.3).

The model accurately simulated total dry matter per plant at both sites (Fig. 6.2). However, the distribution of the dry matter between organs was poorly simulated. The simulated leaf and corm dry matter at harvest were only 27 and 37% of the observed ones, respectively, while the simulated pseudostem and bunch dry matter were double their respective observed values (Table 6.3). This suggests that the dry matter partitioning coefficients in the model have to be determined more accurately to improve model predictions of yield components. Yield gap was thus expressed as a percentage of the absolute yield values simulated.

6.4.3. Yield gap due to drought stress and its mitigation with self-mulch

The simulated drought stress yield gap across sites (55%) is comparable to the projected drought stress yield gap of 65% by van Asten et al. (2011). The model shows that the yield gap due to drought stress was higher (74%) at Kawanda than at Ntungamo (41%), based on simulated yield data under rain-fed vs. field capacity soil water supply scenarios (Fig. 6.4). This trend is plausible because the soil at Kawanda had a higher clay content than that at Ntungamo (Nyombi et al., 2010), implying that the permanent wilting point at Kawanda is higher than that at Ntungamo, as predicted from Eq. 6.02 (Pidgeon, 1972). Even though Ntungamo had lower soil organic matter content (and hence lower field capacity moisture content) than Kawanda (Nyombi et al., 2010), the available water capacity at Kawanda was smaller than that at Ntungamo. Therefore, under rain-fed conditions, plants at Kawanda suffered greater strain in meeting their transpiration demand from limited soil water storage compared with those at Ntungamo. This is evident in the greater cumulative transpiration at Ntungamo even under rain-fed conditions, compared with that at Kawanda under field capacity growing conditions (Fig 6.4) and explains the greater drought stress yield gap at Kawanda.

The difference between cumulative transpiration under potential and rain-fed growing conditions at Kawanda was only 208.4 mm; slightly higher than the cumulative evaporation from soil under rain-fed conditions. This suggests that curtailing evaporation from the soil through adequate ground cover can contribute to mitigating the drought stress impact on crop yield at Kawanda. Greater canopy cover (i.e. higher leaf area index) and crop residue biomass channelled to surface mulch contributed to the lower evaporation from the soil under field capacity compared with that under rain-fed growing conditions at Kawanda (Fig 6.4). This explains why removal of surface mulch cover under rain-fed conditions reduced yields by 10% (Fig 6.5). The impact of self-mulch is not reflected in increased cumulative transpiration under rain-fed conditions (Data not shown). The contribution of self-mulch is likely to have been substantial during dry spells, characterised by low actual transpiration values which are not apparent in the difference between cumulative transpiration with and without surface mulch under rain-fed conditions based on average values. Even then, the contribution of self-mulch is under-estimated in this study in that it does not consider the nutrient recycling role, which may be substantial given the drought stress-mitigating effect of potassium in highland bananas (Taulya, 2013).

6.5. Conclusions

The LINTUL-BANANA2 model is adequately parameterised and accurately simulates total dry matter under rain-fed conditions but still needs calibration of the soil water

balance parameters and dry matter partitioning coefficients in order to accurately predict the yield components. Nevertheless, the model simulations corroborate the findings of van Asten et al. (2011) that drought-induced yield gaps can be as high as 65%. Furthermore, it shows that self-mulch can reduce the yield gap by at least 10%. Building nutrient limitation modules, especially for potassium, into the model will enable comprehensive evaluation of the impact of not only self-mulch but also external mulch in mitigating drought stress impact on highland banana productivity, directly through protection against evaporation of water from the soil, and indirectly through provision of K, which enables better stomatal control. Through providing nutrients, the external mulch also has implications for sustaining production well into the foreseeable future. It will also enable rapid estimation of the consumptive water use of highland banana to support decision-making on when, where and how much irrigation is economically viable besides facilitating development of water-saving production techniques in highland banana cropping systems, including identification of cultivars with high water use efficiency.

CHAPTER SEVEN

7.0. General Discussion

7.1. Introduction

Highland banana cropping systems are typically rain-fed. Low productivity is widely recognised as an issue in highland banana cropping systems of Uganda (Bekunda and Woomer, 1996; Sseguya et al. 1999; Tenywa et al., 1999). Intensification of production is long overdue to meet the food requirements of the escalating population without encroaching on land reserved for nature. A lot of research has been conducted to address various production constraints (Tushemereirwe et al., 1993; Rukazambuga et al., 1998; Barekye et al., 2000; Ssali et al., 2003; Kashaija et al., 2004) with a view to increasing highland banana productivity. Only recently did systematic analysis and prioritisation of the constraints commence to deduce interventions and guide research (e.g. Wairegi et al., 2010). Systematic constraint analysis and prioritisation requires integration of the existing knowledge about crop growth in response to eco-physiological factors and their interactions with management practices.

This thesis contributes to knowledge integration through elucidation of the highland banana response to limiting supplies of water, K and N and how their respective ameliorative inputs affect yield formation. The approach represents a paradigm shift away from literally groping and hoping for some silver bullet intervention, to retrospective scrutiny for key system drivers that are then tested and either confirmed or rejected in prospective probing of the system for best-fit bouquets of interventions. For this purpose, crop growth modelling is a critical tool that facilitates efficient exploration, extrapolation or adaptation of empirical research findings across agro-ecological zones. In this general discussion, I synthesise insights generated from retrospective scrutiny of highland banana responses to water, K and N. I also discuss how these insights are envisaged to shape development of the highland banana growth model LINTUL-BANANA as a decision support tool for the crop water and nutrient input management.

The general discussion is tailored around the research questions (Chapter 1, Section 1.4) this study set out to answer considering both the retrospective and prospective ramifications of important emerging issues. Research questions 1 and 2, were intended to rank drought stress, K and N deficiencies as constraints to highland banana and explore their interactions so as to appropriately sequence the growth model development with respect to the nutrient limitations, while Research Questions 3, 4 and 5 were for the technical aspects of model development. Research Question 6 represents the start point for prospective probing of the system but is integrated with the other research questions in this general discussion.

7.2.   Water is the main driver of highland banana growth and yield

Based on the experiments used in this study, drought stress stands out strongly as a major constraint, whose management can result in substantial increases in productivity (Chapter 2). This is reinforced by the results in Table 4.4, Table 4.5 (Chapter 4) and Fig. 6.4 (Chapter 6). However, this position seems to be contradicted by the results in Table 3.2, Fig. 3.1 and Fig. 3.2 (Chapter 3), which portray K as the driver of highland banana growth and yields. The contradiction is not helped by the title of Chapter 3, which was based on highland banana's shifts in dry matter partitioning to below-ground biomass in response to drought stress compared with that in response to K deficiency (Table 3.4 and Fig 3.4 in Chapter 3). However, this contradiction is superficial.

The increase in fresh bunch weight with cumulative rainfall received within 12 months to harvest was linear beyond 1500 mm (Fig 2.5 in Chapter 2). This suggests that the optimum annual rainfall for banana production is greater than 1500 mm. However, the first and third quartile cumulative rainfall received within 12 months from sucker emergence (CRF) by plants analysed in Chapter 3 was 1100 and 1300 mm, respectively. About a quarter and slightly more than a quarter of the plants in Ntungamo and Kawanda, respectively, received CRF of at least 1300 mm (Fig. 7.1). Therefore plants that were deemed to have grown under 'wet' conditions (CRF $\geq$ 1100 mm) were in reality only less drought stressed than those that were deemed to have grown under 'dry' conditions (CRF < 1100 mm) in Chapter 3. With such droughty growing conditions, K stood out as a driver of growth and yield because it mitigated the impact of drought stress through osmotic adjustment (Mahouachi, 2009). Therefore, improved K management on K-deficient soils, is likely to improve banana productivity and enhance water use efficiency in the rain-fed cropping systems of Uganda.

The impact of rainfall was clearer at Kawanda where the number of plants with fresh bunch yields equal to or greater than 15 t ha^{-1} yr^{-1} was distinctly higher when CRF exceeded 1300 mm (Fig. 7.1). The highest yields at Kawanda ($\approx$34 t ha^{-1} yr^{-1}) were only obtained around CRF 1500 mm (Fig 7.1). This is in line with the simulation results, which indicate a larger yield gap due to drought stress at Kawanda than at Ntungamo (Chapter 6). It also explains why response to the nutrients applied was poor, especially at Kawanda. The highest yields at Kawanda ($\approx$34 t ha^{-1} yr^{-1}) and Ntungamo ($\approx$40 t ha^{-1} yr^{-1}) from an application of 400 kg N and 600 kg K ha^{-1} yr^{-1} were small compared with attainable yields reported from other trials, such as 67 t ha^{-1} yr^{-1} in south-western Uganda (Smithson et al., 2001) in response to application of 100 kg N and 100 kg K ha^{-1} yr^{-1}. The fertilizer rates used in the trials at Kawanda and Ntungamo

were not excessive. Israeli et al. (1985) reported a yield response to 400 kg N and 400 kg K ha^{-1} season^{-1} with irrigation in a semi-arid region of Israel. Aba and Baiyeri (2015) reported an increase in crop vigour and biomass yield with an application of up to 747 kg K ha^{-1} yr^{-1} in Nigeria. Therefore, without evidence for nutrient toxicity in the trials upon which this thesis is based, it is probable that the poor soil physical conditions at Kawanda restricted root exploration of the soil profile and hence compounded the drought stress with impaired uptake of nutrients. Nevertheless, the external nutrient inputs from mineral fertilizers are crucial for sustaining productivity as is shown in Figure 3.2 (Chapter 3). Deep planting holes to loosen compact subsoil for deeper rooting (Lynch and Wojciechowski, 2015) and adding soil organic matter to increase the available water capacity may be crucial for increasing the use efficiency of fertilizer nutrients.
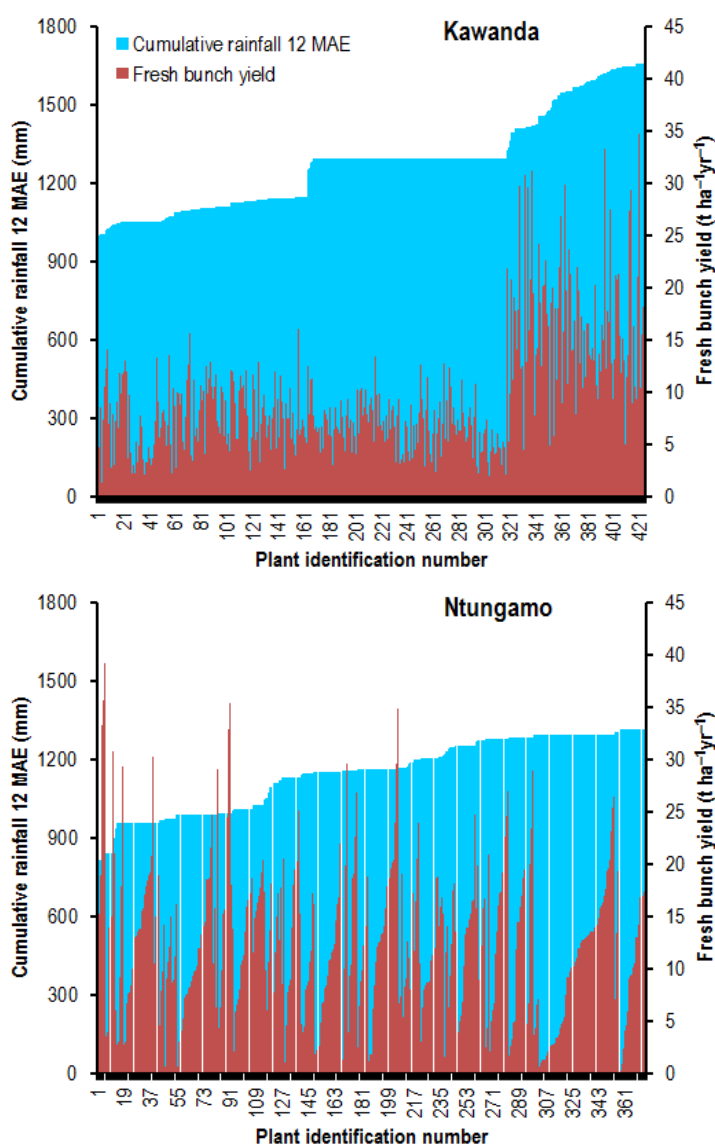

Figure 7.1: Variation in cumulative rainfall 12 months after emergence (MAE) received and fresh bunch yield in the fertilizer response trials at Kawanda (central Uganda) and Ntungamo (South-western Uganda).

Farmers are aware of the need for soil fertility management in highland banana and use a number of practices, mostly manure and mulching, but face constraints in sourcing, processing and applying the bulky organic inputs (Sseguya et al., 1999). The concept of integrated soil fertility management, which advocates for combined organic and mineral fertilizer use (Vanlauwe et al., 2010), may reduce the drudgery associated with use of sole organic inputs and the limitations of sole mineral fertilizer use in highland banana cropping systems. Mulching combined with modest doses of limiting nutrients has been found to be profitable within a 100 km radius of Kampala (Wairegi and van Asten, 2010), the Capital City of Uganda. The profitable distance limit from Kampala does not favour highland banana farmers further upcountry like in south-western Uganda, who are the major suppliers to the main urban markets in Uganda. Mulch remains as one of their main soil management inputs.

Self-mulch is the cheapest and most readily available resource, though it merely recycles the nutrients rather than replenish what is exported in the bunches. It is important to separate and quantify the water-saving and nutrient-replenishing/recycling roles of the mulch in order to design effective integrated soil fertility management packages that will ensure sustainability of the cropping system. This is one area where the growth model can complement field experiments. Already, the model has shown that self-mulch can increase highland banana yields by 10% where the soil's available water capacity is low (Fig. 6.5, Chapter 6). This may be an under-estimation of its contribution because it neither includes the nutrient-supply role of mulch nor improved infiltration through prevention of surface seal formation by incident raindrops. Whereas the leaves provide better ground cover as mulch than pseudostems, the latter contain more nutrients for recycling, especially K, than the former (Fig. 7.2).

The use of banana residues for integrated soil fertility management may not extend well into the future. There are trends towards channelling banana residues to alternative uses in Uganda (Okello et al., 2013) and elsewhere around the world (Tock et al., 2010; Pandey and Regmi 2013; Pereira et al., 2013; Santa-Maria et al., 2013). This introduces another dimension to the trade-offs involved in residue allocation, which need to be carefully analysed because mulching represents a strong entry point to improving the sustainability of the cropping system, given the substantial quantities of K they recycle in the system (Fig. 7.2). The protective role of K against banana weevil damage (Table 7.1) implies that it can be included in an integrated soil fertility and pest management package and accordingly factored into the trade-off to be resolved.
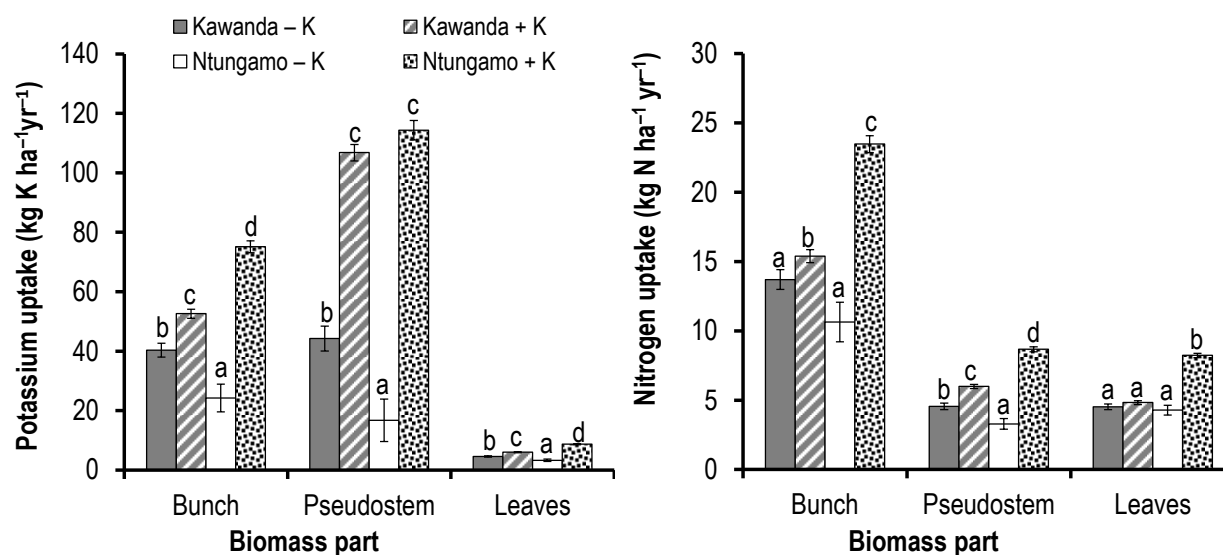
Figure 7.2: Site × potassium interaction on potassium and nitrogen uptake at harvest stage in different harvestable biomass parts of East African highland banana at Kawanda (central Uganda) and Ntungamo (south-western Uganda).

Table 7.1: Main effects of nitrogen and potassium on weevil damage and fresh bunch weight at Ntungamo, south-western Uganda.

Nutrient	Outer cylinder damage (%) mean ± se	Inner cylinder damage (%) mean ± se	Overall damage (%) mean ± se	Bunch weight (kg) mean ± se
−N	2.1 ± 0.73a	1.0 ± 0.71a	1.6 ± 0.82a	17.4 ± 0.84a
+N	5.2 ± 0.35b	2.4 ± 0.34b	3.8 ± 1.02b	17.8 ± 0.40a
−K	7.9 ± 0.88b	5.0 ± 0.86b	6.4 ± 0.80b	7.2 ± 0.99a
+K	3.7 ± 0.33a	1.4 ± 0.33a	2.5 ± 0.31a	20.2 ± 0.38b

−N = 0 kg N ha^{-1} yr^{-1} applied; +N = 150 to 400 kg N ha^{-1} yr^{-1} applied; −K = 0 kg K ha^{-1} yr^{-1} applied; +K = 250 to 600 kg K ha^{-1} yr^{-1} applied; se = standard error of mean; N = nitrogen; K = potassium; Means in the same column for the same nutrient followed by the same letter are not significantly (P>0.05) different.

Data have to be generated to support resolution of the trade-offs involved in alternative allocation strategies of the resources generated both on- and off-farm. Therefore, LINTUL-BANANA needs to contribute to a higher level integration simulation framework, for example at farm or landscape level, to support decision-making on the management of organic resources. However, the most important nutrients to highland banana (K) and other cropping systems (N) have first to be built into LINTUL-BANANA.

7.3. Highland bananas 'think' outside the box, so should their modellers

Highland bananas share some stress-adaptive mechanisms with other crops, but also have some unique features of their own, which are key for modelling the crop. Plants adapt to stressful growing conditions via morphological or physiological means. The morphological adaptations include shifts in dry matter allocation such that all growth factors are equally limiting (Bloom et al., 1985). This embodies the phenomenon of

dry matter allocation plasticity in which plants shift the allocation of dry matter between the above- and below-ground biomass parts in response to a limiting growth resource (Chapter 3). The shifts in dry matter allocation enhance the search for, and possibly, the acquisition of the limiting growth resource, while at the same time reducing the utilisation of the non-limiting growth resource. In this regard, highland bananas were found to respond differently than other plants to drought stress in that highland bananas do not increase allocation of dry matter to below-ground biomass parts (Fig 3.4). This is already built in to the model. However, highland bananas, like other plants, increase allocation of dry matter to below ground biomass in response to limiting supply of K and N (Table 3.4). This has to be built into the model, in order to simulate nutrient-limited growth.

Further experiments need to be conducted to determine the dry matter allocation coefficients in the model under well-known conditions, preferably potential and water- and/or K-limited conditions. This may be the reason for under-estimation of corm and leaf dry matter as well as over-estimation of pseudostem and bunch dry matter (Table 6.3). The experiments may be designed such that the data can be used to validate the soil water balance parameters as well. This would involve lysimeter studies for quantification of the actual transpiration and other components of the soil water balance to permit comprehensive testing and calibration. The experiments can be set up along an altitude gradient to capture shifts in ambient temperature and verify their effect on the relative importance of morphological *vis-à-vis* physiological components of relative growth rate to highland banana response to drought stress and K deficiency.

7.4. Conclusions and recommendations

Water is the most important driver of highland banana growth and yield followed by K. LINTUL-BANANA2 has been appropriately parameterised to simulate water-limited growth. However, its dry matter partitioning coefficients may need to be calibrated for accurate yield parameter simulation. Effects of K and N limitation need to be added before the model can be linked to a farm- or landscape-level simulation framework to support decision-making on integrated soil fertility management options that can sustain productivity without compromising environmental quality and ecosystem services from nature reserves.

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APPENDICES

APPENDIX 5: DEFINITION OF CODES USED IN THE WATER BALANCE RELATIONAL DIAGRAM

Code	Definition
ALBj	Canopy surface albedo
DMmulch	Mulch soil cover
DRAIN	Rate of drainage from the rooting zone
DRATE	Maximum rate of drainage
DTRJM2	Daily total radiation per square meter
ECCOFC	Radiation extinction coefficient in canopy
ECCOFM	Radiation extinction coefficient in mulch
EVAPM	Rate of evaporation from the mulch
EVAPS	Rate of evaporation from the soil
FR	Transpiration reduction factor ($0 < FR \leq 1$)
INFILT	Rate of infiltration into the soil
IRRIG	Rate of water input through irrigation
IRRIGF	Parameter controlling irrigation events
LAI	Leaf area index
MAI	Mulch area index
MSTCUR	Water storage in mulch
MSTMAX	Maximum water storage capacity of mulch
MULSPR	Adjusted specific mulch area
MULSWS	Mulch specific water storage
PENMAN	Subroutine to compute PEVAPM, PEVAPS and PTRANi
PEVAPM	Potential evaporation from mulch
PEVAPS	Potential evaporation from soil
PINTC	Rainfall interception coefficient in canopy
PTRANi	Potential transpiration from Plant i (= 1, 2 or 3)
RAIN	Rate of water input through rainfall
RINTC	Rate of rainfall interception in crop canopy
RINTM	Rate of rainfall interception in mulch
ROOTD	Effective rooting depth
RUNOFF	Rate of surface runoff
TMMN	Minimum temperature
TMMX	Maximum temperature
TRANCO	Transpiration constant
TRANi	Transpiration from Plant i (= 1, 2 or 3)
VP	Vapour pressure of the air
WA	Actual amount of water stored in the soil
WCAD	Air-dry moisture content
WCCR	Critical moisture content below which a reduction in transpiration is induced
WCFC	Field capacity moisture content
WCST	Saturated moisture content
WCWET	Wet moisture content, when plants start suffering from oxygen shortage
WCWP	Wilting moisture content
WN	Wind speed at 2-m height

APPENDIX 6: NOTES ON RELATIONAL DIAGRAMS

The relational diagram consists of 3 parts corresponding with the three plant stages: mother plant, sucker 1 and sucker 2. Each relational diagram is horizontally divided into 3 sections, corresponding to the stages of model development. The first section (extreme left) deals with gross dry matter (**DM**) production, followed (mid-section) by that dealing with DM partitioning between the shoot and the root while the last (extreme right) section deals with DM partitioning between the shoot biomass structures. The connection between the three relational diagrams is indicated by the grey symbols.

Light interception

Daily Total Radiation, **DTR** is converted to photosynthetically active radiation (PAR) incident on the canopy of Plant 1 as **PARIN1** using parameter **fPAR**, which is the proportion of DTR that is PAR. A proportion of PARIN1 is transmitted through the canopy of Plant 1 as **PAROUT1**. The amount of PAR intercepted by Plant i (where i is 1, 2 or 3), **PARINTi** is the difference between PARINi and PAROUTi. PAROUTi is equal to **PARINi+1**, or PAR incident on Plant i+1 canopy. PAROUTi is a function of a constant light extinction coefficient **Ki** and leaf area index, **LAIi** for Plant i.

LAIi is the difference between its growth rate, **GLAIi** and death rate, **DLAIi**. GLAIi is a product of the specific leaf area (**SLAi**), the proportion of shoot DM in the leaves (**Pleaf$i$**) and the shoot growth rate (**GWsh$i$**) for Plant i. Plant 3 undergoes an exponential growth phase during which GLAI3 is a function of the effective daily temperature (**DTEFF**) and a drought stress-dependent relative leaf area growth rate, **RGRL3**. DLAIi is a function of a constant relative death rate of leaves, **RDRi**.

Dry matter accumulation

DM accumulation or growth, and ultimately, development, proceeds as a function of PARINTi and the daily effective temperature **DTEFF**. DTEFF is the difference between the average daily temperature, **DAVTMP** and basal temperature, **TBASE**. DAVTMP is the average of the minimum temperature, **TMMN** and maximum temperature, **TMMX** on a given day. Integration of DTEFF over time gives the thermal or physiological age, **TSUMi** for Plant i.

Plant 1 (Appendix 6A) gross rate of DM production, **GDM1HLP** is a function of PARINT1 and a drought stress-dependent (**TRARF** from the water balance module) light use efficiency **LUE1**. Part of GDM1HLP is the rate of DM allocation to Plant 2, **G2from1**, while the

remainder **GDM1** is the Plant 1 net DM accumulation rate. Partitioning of GDM1HLP into G2from1 and GDM1 is controlled by a TSUM1-dependent fraction, **FSU2RED2_2**.

Plant 2 (Appendix 6B) gross rate of photosynthetic DM production, **GDM2HLP** is a function of PARINT2 and a drought stress-dependent light use efficiency, **LUE2**. Part of GDM2HLP is the rate of DM allocation to plant 3, **G3from2_1** (when plant 3 has no functional leaves), while the remainder **G2from2_1** contributes to the net DM production rate (**GDM2**) for plant 2 along with contribution from plant 1 photosynthesis (**G2from1**) and reallocation from harvested plant 1 corm (**dcorm1_to_Wsh1**). When plant 3 acquires functional leaves, the part of GDM2HLP partitioned to Plant 3 is **G3from2_2** and the remainder contributing to GDM2 is **G2from2_2**. When **G3from2_1** is active, **G3from2_2** is switched off and vice versa. Partitioning of GDM2HLP into G3from2_1 (later, G3from2_2) and G2from2_1 (later, G2from2_2) is controlled by a TSUM2-dependent fraction, **FSU2RED2_1**.

Plant 3 (Appendix 6C) growth rate (**GDM3**) is initially entirely due to DM partitioned to Plant 3 from Plant 2 before Plant 3 develops functional leaves (**G3from2_1**). After Plant 3 develops functional leaves, its growth rate is switched to a reducing amount of DM partitioned from Plant 2 (**G3from2_2**) and DM production from Plant 3 photosynthesis (**G3Photos**). G3Photos is a function of PARINT3 and a drought stress-dependent light use efficiency, **LUE3**.

TRARFi is computed in the soil water balance (Fig. 5.1) as the ratio of actual (**TRANi**) to potential transpiration (**PTRANi**). LAIi is a state variable in the main crop model that feeds back to the soil water balance as an input for simulation of potential and actual transpiration. The crop-dependent constants required in the soil water balance model are canopy surface albedo (**ALBCi**), radiation extinction coefficient in the crop canopy (**ECCOFCi**), canopy rainfall interception coefficient (**PINTCi**) and the transpiration constant (**TRANCOi**).

Dry matter partitioning

The root growth rate, **GWrt$i$** and shoot growth rate, GWsh$i$ are both functions of GDMi and a TSUMi-dependent fraction, **FrtREDi**, which controls the shoot-root partitioning of Plant i total DM, **DMi**. DM allocated to the shoot biomass structures corm, pseudostem, leaves and bunch is represented as **Wcorm$i$**, **Wpsstm$i$**, **Wleaf$i$** and **Wbunch$i$**, respectively. Their respective growth rates, **GWcorm$i$**, **GWpsstm$i$**, **GWleaf$i$** and **GWbunch1** are functions of the shoot growth rate GWsh$i$ and the corresponding TSUMi-dependent fractions **Pcorm$i$**, **Ppsstm$i$**, **Pleaf$i$** and **Pbunch1**, respectively, as the partitioning coefficient. Only DM in the roots (**Wrt$i$**) and leaves (Wleaf$i$) degrades during the growth of the plant at rates represented by **DWrt$i$** and **DWleaf$i$**, respectively. Consequently, death rate of DMi (**DWDMi)** is the sum of DWrt$i$ and

DWleaf*i*, while Plant *i* shoot DM (**WSh*i***) dies at a rate **DWSh*i*** equal to DWleaf*i*. DWrt*i* is determined by a constant relative root death rate **RDRrt*i*** while DWleaf*i* is controlled by RDR*i*. The total weight of dead roots (**WrtD*i*_Tot)** contributes to soil organic matter, while the total weight of dead leaves (**WleafD*i***) adds to surface mulch, which is envisaged to ultimately decompose to soil organic matter.

Harvest

Harvest occurs only for Plant 1 at TSUM1 equal to **TSUMHARV**. TSUMHARV instantly transforms Wrt1 into the total weight of roots of harvested plants (**Wrt1_After_Harv**), which degrades to soil organic matter at a relative decay rate, **RDRrt1_After_Harv**. At TSUMHARV, Wcorm1 is instantly partitioned by the fraction **Pcorm1_to_ReAllocation** into the weight of corm 1 DM to be re-allocated to the next Plant 1 (**Corm1_After_Harv**) and the weight of corm 1 DM to be decomposed to soil organic matter (**Corm1_Lost_After_Harv**). Corm1_After_Harv is reallocated to the new Plant 1 at the rate **dCorm1_ReAll_After_Harv**, determined by a relative reallocation rate, **RALR_Corm1_To_DM1**. Corm1_Lost_After_Harv degrades to soil organic matter at a rate **dCorm1_Lost_After_Harv** determined by a relative decay rate, **RDRCorm1_After_Harv**. Wpsstm1 and Wleaf1 are instantly transformed to the total weight of harvested pseudostem (**HarvestWpsstm**) and total weight of harvested leaves (**HarvestWleaf**), respectively, at TSUMHARV, which then contribute to the surface mulch.

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APPENDIX 6A: Relational diagram for water-limited growth of East African Highland banana Plant 1.

APPENDIX 6B: Relational diagram for water-limited growth of East African Highland banana Plant 2.

APPENDIX 6C: Relational diagram for water-limited growth of East African Highland banana Plant 3.
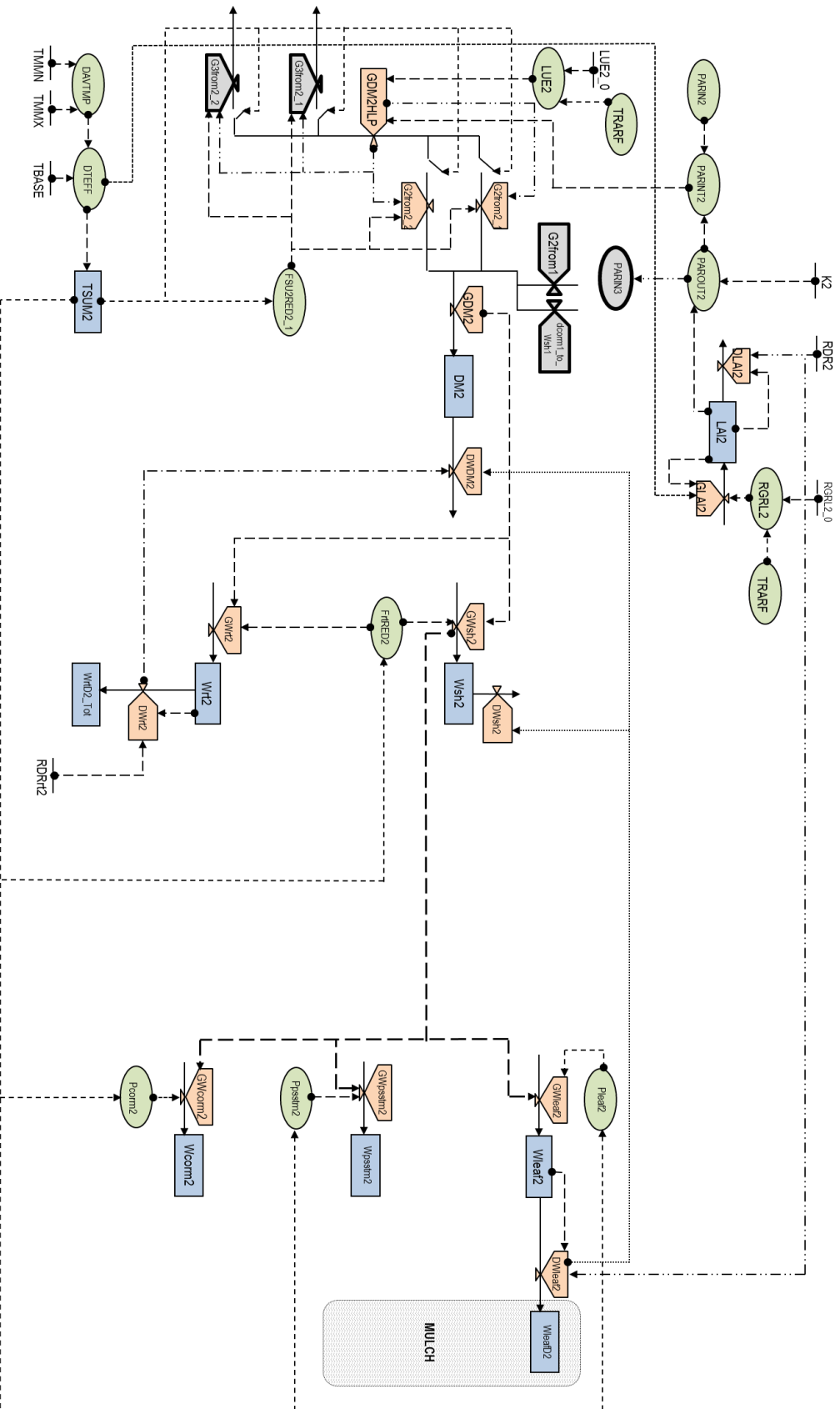
SUMMARY

The productivity of East African highland banana (hereafter called highland banana) is poor, amid an escalating population and increase in demand for this primary staple food crop in Uganda. Whereas previous research addressed constraints to highland banana production, little attention has been paid towards analysis and prioritisation of these constraints to design interventions and/or guide further research needs. This entails integration of the existing knowledge about crop growth in response to eco-physiological factors (both biotic and abiotic), and their interactions with management practices. This thesis integrated knowledge on highland banana response to limiting supplies of water, K and N in terms of growth and yield formation, so as to develop a crop growth model, and hence contribute to a decision support tool for managing crop water and nutrient requirements.

A survey of individual plants from existing farmers' fields, on-farm field experiments and on-station field/screen house experiments, were used to characterise highland banana response to limiting water, K and N supply. Based on this characterisation, an existing potential production model (LINTUL-BANANA1) was extended to simulate the water-limited highland banana growth and yield. The characterisation work started with evaluating highland banana yield gap due to drought stress using data from three fertilizer response trials. Cumulative rainfall received within 12 months to harvest (CRF_{12_H}) was computed for each bunch harvested at physiological maturity. The absolute bunch weights were divided by the 95 percentile absolute bunch weight observed at a given experimental site to convert them to relative bunch weights (RBW) and hence normalise data across sites. The RBW and CRF_{12_H} were subjected to boundary line analysis to quantify the yield gap due to drought stress. Highland banana yield gap due to drought stress was empirically determined to range from 20 to 65% and the optimum rainfall for banana production projected to be over 1500 mm yr^{-1}. The CRF_{12_H} computed included the flowering period, which was deemed critical for yield formation but excluded the early growth stages of the plant.

Cumulative rainfall received within 12 months from emergence (CRF_{12_E}) of a given sucker was also computed and used to categorise plants in fertilizer response trials conducted at two sites as having grown under either dry (CRF_{12_E} <1100 mm) or wet (CRF_{12_E} ≥1100 mm) conditions. The threshold CRF_{12_E} of 1100 mm was the third quartile CRF_{12_E} value at the drier of the 2 sites of fertilizer response trials. Potassium

mitigated drought stress impact on highland banana growth and yield. Highland bananas do not increase dry matter allocation to below-ground biomass parts in response to drought stress but do so in response to K and N deficiency. The response to K deficiency was accentuated under drought stress. The 365-day long duration over which CRF_{12_E} was computed may have been too long to detect drought stress impacts on fast growth processes. Therefore the analysis zoomed in to shorter time spans in a growth analysis of individual highland banana plants.

The growth analysis was conducted to evaluate the relative contribution of morphological (specific leaf area and leaf mass ratio) *vis-à-vis* physiological (net assimilation rate) strategies to mitigate the impact of limiting supplies of water, K and N on its relative growth rate. The growth of individual plants was monitored at four-week intervals for this analysis. The cumulative rainfall received over the 28-day period (CRF_{28}) between growth monitoring events was computed to categorise the growing conditions as either dry ($CRF_{28} < 84$ mm) or wet ($CRF_{28} \geq 84$ mm). Highland bananas relied more on net assimilation rate than dry matter allocation to the leaves (leaf mass ratio) and its utilisation to generate leaf area (specific leaf area) for light interception to mitigate the impact of limiting supply of water and K on banana relative growth rate. The threshold dry weight for flowering of highland bananas was quantified as 1.5 kg per plant.

A soil water balance module was developed and linked to the potential growth model for highland banana (LINTUL-BANANA1) to explore the crop's water-limited growth and yield gap due to drought stress in different agro-ecological zones of Uganda. The crop growth model assumes an established plantation with a maximum of 3 plants per mat, with synchronised development. Simulated drought stress was assumed to affect both growth and development. The model accurately simulated growth and soil water storage under a highland banana crop assuming non-limiting supply of K and N. The yield gap due to drought stress ranged from 40 to 74% in south-western and central Uganda, respectively. Self-mulch in the highland banana cropping system reduced the impact of drought stress on highland banana yields by 10%. This study highlights the importance of drought stress as a constraint to highland banana production in Uganda and gives insights into how empirical experimentation and crop growth simulations can complement each other to rapidly and efficiently evaluate the scope of a given constraint and to prioritise interventions.

LIST OF PUBLICATIONS

PEER-REVIEWED PUBLICATIONS

1. **Taulya, G**., van Asten, P.J.A., Leffelaar, P.A. and Giller, K.E. 2014. Phenological development of East African highland banana involves trade-offs between physiological age and chronological age. *European Journal of Agronomy* 60: 41-53.

2. **Taulya G.** 2013. East African highland bananas (*Musa* spp. AAA-EA) 'worry' more about potassium deficiency than drought stress. *Field Crops Research* 151: 45-55.

3. van Asten P.J.A., Fermont A.M. and **Taulya G**. 2011. Drought is a major yield loss factor for rainfed East African highland banana. *Agricultural Water Management* 98: 541-552

4. Nyombi, K., van Asten, P.J.A., Corbeels, M., **Taulya, G.**, Leffelaar, P.A. and Giller, K.E. 2010. Mineral fertilizer response and nutrient use efficiencies of East African highland banana (*Musa spp.*, AAA-EAHB, cv. Kisansa) in Uganda. *Journal: Field Crops Research* 117 38-50.

CONFERENCE PROCEEDINGS, BOOK CHAPTERS AND INVITED PAPERS

1. **Taulya, G**., van Asten, PJ.A., Nowakunda, K. and Kaddu-Mukasa, P. 2010. Mineral fertilizers improve the sensory quality of East African Highland bananas (*Musa* AAA-EA, cv. *Kisansa*). *Tree and Forestry Science and Biotechnology* 4(1): 93-96.

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3. **Taulya, G**., Tenywa, M.M., Majaliwa, M.J.G., Odong, T.L., Kaingo, J. and Kakone, A. 2005. Validation of pedotransfer functions for soil bulk density estimation on a Lake Victoria basin soilscape. African Crop Science Society Procedings 7(3): 1049-1056.

4. Tenywa, M.M., Majaliwa, M.J.G., Magunda, M.K., Lal, R. and **Taulya, G**. 2005. Dynamics of carbon sequestration in various agroclimatic zones of Uganda. pp.501 – 513. In: Lal, R., Stewart, B.A., Uphoff, N. and Hansen, D.O (Eds.). Climate Change and Global Food Security. Taylor and Francis, New York, USA.

5. Wanyama, I., Tenywa, M.M., **Taulya, G**., Majaliwa, M.J.G. and Ochwoh, V.A. 2005. Soil quality indexing and mapping: evaluation of a GIS-based tool on a Lake Victoria microcatchment Ferralsol African Crop Science Society Proceedings 7(3): 1033-1037.

BOOKS EDITED

1. Tenywa, J.S., **Taulya, G.**, Kawube, G., Kawuki, R., Namugwanya, M. and Santos, L. (Eds). 2011. Proceedings of the 10th African Crop Science Conference. 10-13 Oct 2011, Maputo, Mozambique.

2. Tenywa, J.S., Tenywa, M.M., Bekunda, M.A. and **Taulya, G**. (Eds). 2003. Proceedings of the Soil Science Society of East Africa 20th Conference. 2 – 6 Dec 2002. Mbale (Uganda).

3. Tenywa, M.M., Bekunda, M.A., Lufafa, A. and **Taulya, G**. (Eds.). 2003. Participatory Soil Fertility and Management in Uganda: Challenges and Opportunities. Soil and Water Conservation Society of Uganda Technical Report No. 2.

CURRICULUM VITAE

Godfrey Taulya was born on 27th October 1972. He graduated with a BSc. Agriculture (Soil Science Option) in October 2000. He was offered an Assistantship on the Rockefeller Foundation-funded Erosion Studies Project under the Department of Soil Science, Makerere University in 2001. Under the framework of this project, Godfrey pursued his MSc. Soil Science at Makerere University, graduating in October 2005. He started teaching undergraduate soil science classes during this Assistantship and has cumulative teaching and student supervision experience of 7 years at the public universities, Makerere and Gulu. He joined the International Institute of Tropical Agriculture (IITA) as a Research Assistant in April 2004 where he worked on banana agronomy research for 5 years before starting his PhD programme at Wageningen University in September 2009, in collaboration with IITA.

PE&RC Training and Education Certificate

With the training and education activities listed below the PhD candidate has complied with the 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)
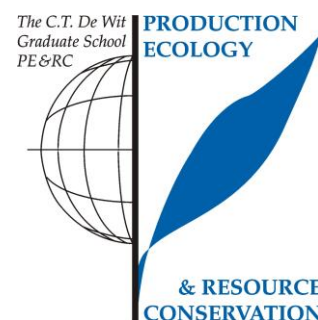
Review of literature (4.5 ECTS)
- Harnessing crop growth modelling for exploring horizons in biophysical constraints against East African Highland banana systems (2012)

Writing of project proposal (4.5 ECTS)
- Towards improved East African Highland banana productivity in the African great lakes region: field experiments and simulations (20120

Post-graduate courses (10.5 ECTS)
- Statistics and statistical computing course with SAS; IITA and NARO, Uganda (2009)
- Laboratory methods for soil and plant analysis in East Africa; IITA and National Agricultural Research Laboratories, Kawanda, Uganda (2009)
- Root ecology: drivers of foraging and interaction in a spatial context; University of Copenhagen and Wageningen University (2012)
- Multivariate analysis; Biometris and PE&RC (2012)

Invited review of (unpublished) journal manuscript (2 ECTS)
- Agricultural Ecosystems and Environment: evaluation of critical N and P concentration models maize under full and limited irrigation and rain-felt conditions (2015)
- Experimental Agriculture: sustainable banana production through integrated plant nutrition system

Deficiency, refresh, brush-up courses (3 ECTS)
- Quantitative analysis of cropping and grasslands systems (2009)
- Systems analysis, simulation and systems management (2009)
- Models for forest and nature conservation (2010)

Competence strengthening / skills courses (1.5 ECTS)
- Graduate seminars: scientific presentation skills; Makerere University (2010)

PE&RC Annual meetings, seminars and the PE&RC weekend (0.9 ECTS)
- PE&RC Weekend for candidates in their final years (2013)
- PE&RC Annual meeting/seminars (2013)

Discussion groups / local seminars / other scientific meetings (4.5 ECTS)
- Plant sciences seminars (2012)
- Wageningen centre for agro-ecology and systems analysis seminars (2013)
- IITA/NARO/Makerere University seminars; Uganda (2014)

International symposia, workshops and conferences (4.7 ECTS)
- Challenges and opportunities for agricultural intensification in the humid highland systems of sub-Saharan Africa; Kigali, Rwanda (2011)
- Integrated soil fertility management in Africa: from microbes to markets; Nairobi, Kenya (2012)

Lecturing / supervision of practical's / tutorials (1.5 ECTS)
- Models for ecological systems (2013)

Supervision of 1 MSc student
- Optimizing banana-coffee intercrop density for biological productivity in Uganda using the hyperbolic yield-density model

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