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The role of inter-specific competition for water in maize-legume intercropping systems in northern Tanzania

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HIGHLIGHTS

- Maize-legume intercropping is common in rain-fed smallholder production systems.
- Intercropping maize and legumes might aggravate dependency on annual precipitation.
- A parameter-sparse crop growth model revealed the role of inter-specific competition for water.
- The deep taproot makes legumes far less sensitive to drought than maize.
- Spatial complementarity in rooting systems safeguards productivity of maize-legume intercropping.

GRAPHICAL ABSTRACT
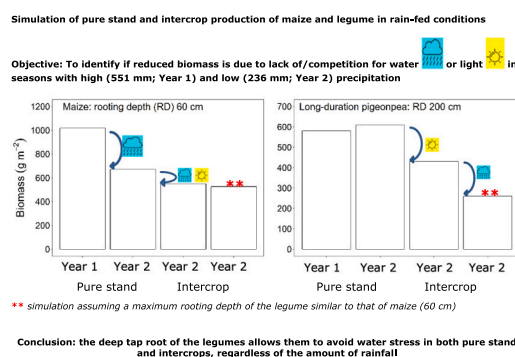
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ABSTRACT

CONTEXT: Maize-legume intercropping is common in sub-Saharan Africa. Effects of legumes on the companion maize crop are determined principally by choice of legume species and relative introduction time. Performance of intercrops is optimized when legumes' planting is timed such that their peak growth phase occurs after maize harvest, with legumes utilizing the residual soil moisture.
OBJECTIVE: We sought to understand the role of inter-specific competition for water in maize-pigeonpea and maize-lablab intercrops.
METHODS: We analysed experimentally determined shoot biomass of sole and intercropped maize, lablab, long and medium- duration pigeonpea. Experiments were conducted in northern Tanzania for two consecutive seasons. The second season was drier (236 mm) than the first (551 mm). We constructed a parameter-sparse growth model, calibrated based on sole crops data. The model calculates growth rate as radiation interception $\times$ radiation-use efficiency. When simulated actual soil moisture content fell below a species-specific critical level, the ratio between actual and potential transpiration for that species decreased, and crop growth rate was reduced proportional to this reduction.

RESULTS AND CONCLUSIONS: There was good agreement between simulated and observed shoot biomass of maize and the legumes. With rooting depth of 60 cm, maize was simulated to be sensitive to annual precipitation, resulting in 3.5 t ha^{-1} (34%) reduction in shoot dry matter production in the second season. By contrast, the legumes, with a rooting depth of 200 cm did not experience water shortage in either of the two seasons, resulting in nearly identical shoot dry matter production in both seasons. Explorative simulations assuming the legumes to have shallower rooting depth confirmed the importance of this trait for avoidance of water stress, with simulated reductions in dry matter production of 23–34% for the legumes when rooting depth was reduced from 200 to 60 cm. Maize in the intercrop was modestly influenced by the legumes due to light competition. In the low precipitation season, additional competition for water occurred and water shortage for maize was aggravated. Maize influenced the legumes only through competition for light, as a tap root allowed the legumes to utilize water stored in deeper soil layers. During the co-growth period, competition for light exerted by maize on the legumes was strong, but they partly compensated for this in the period after maize harvest.

SIGNIFICANCE: Our results emphasize the important role of the deep legume tap root for the success of maize-legume intercrops under rain-fed conditions.

1. Introduction

Cereal-legume intercropping is commonly practiced by smallholder farmers in sub-Saharan Africa (SSA) (Giller, 2001), to maximize factor productivity, secure food production, and avert production risks. Intercropping is defined as the cultivation of two or more crop species simultaneously in the same field (Vandermeer, 1989). Typically, cereal crops such as maize (*Zea mays*), pearl millet (*Pennisetum glaucum*) and sorghum (*Sorghum bicolor*) are the primary plant species, whereas legume crops such as pigeonpea (*Cajanus cajan*), dolichos lablab (*Lablab purpureus*), common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), groundnut (*Arachis hypogaea*), and soybean (*Glycine max*) are the secondary species (Kimaro et al., 2009; Mugi-Ngenga et al., 2021; Myaka et al., 2006). In intercrops, inter-specific competition is inevitable and counterbalances the benefits of potential improved total productivity and biological nitrogen fixation by the legumes. Competitive interactions and the potential for complementarity between the component species determine the performance of intercropping systems (Lithourgidis et al., 2011). Consequently, to maximize the benefits of cereal and legume crops in intercrops, management to optimize the spatial and temporal complementarity between the two component crops is essential to minimize competition for resources (Vandermeer, 1989). When component crops are complementary in terms of their temporal growth pattern, above-ground canopy structure, rooting patterns and associated dynamics of resource acquisition, intercropping enables a more efficient utilization of available resources (e.g., sunlight, moisture and soil nutrients) (Willey, 1990). This has been widely shown to result in relatively greater yields than when crops are grown as pure stands (Li et al., 2020; Mucheru-Muna et al., 2010).

Considering the difficulties associated with clearly unravelling how component crop species in intercrops combine and compete for resources such as water and radiation, crop growth simulation modelling provides a useful complementary tool to experiments (Corre-Hellou et al., 2009). Simulation modelling of resource competition offers an opportunity to investigate the effects of environment on productivity of crops grown as sole or intercrops, as these appear important to determine suitability of component crops to a specific environment (Keatinge et al., 1998; Qi et al., 2000). Several intercrop models exist which simulate the competition between two intercropped species (Baumann et al., 2002; Brisson et al., 2004; Evers et al., 2019; Gou et al., 2017; Tsubo et al., 2005). However, the models usually require many parameters that are difficult to acquire from experiments conducted under smallholder farming conditions with limited experimental facilities. Obviously, there is need for models where parameter requirement is more aligned with field observations.

Determining the suitability of component crops to a specific environment is important not only during the period when the component crops are growing together, but also after harvest of the early maturing crop, when the later maturing crop is able to make use of the residual resources. Whereas the competition for radiation between component crops can be readily observed in the field, it is less evident how below-ground competition for water influences performance of the intercrop. The following questions emerge in the context of maize-legume intercrops: Does the presence of a legume species induce any water shortage during the first part of the growing season? Does water consumption by the maize crop in the intercrop affect the performance of the legume crop before or after maize harvest? And, how important is the deep rooting system of the legume crops for optimizing resources use? To address these questions, a simple radiation interception × radiation-use efficiency model was developed and extended with a soil water balance module. The model was parameterized based on pure stands of maize, pigeonpea and lablab that were simultaneously grown with the intercrops, at the same site. Rather than a predictive tool, this model was designed as an analytical tool to analyse the influence of water availability and utilization on productivity of the intercrops. Our main objective was to ascertain the extent to which productivity of maize- pigeonpea and maize- lablab systems in northern Tanzania is limited by water availability. The specific objectives were: (i) to develop a parameter-sparse model for analysis of productivity of intercrops of maize and pigeonpea or lablab under rain-fed conditions; (ii) to parameterize the model based on observations of the crops in pure stand; (iii) to determine if maize production in northern Tanzania was restricted by water availability; (iv) to assess whether rooting depth of pigeonpea and lablab is critical to their dry matter production, and; (v) to examine if the combination of maize and either pigeonpea or lablab in intercrop aggravates the water-limited yields. We hypothesize that maize production will be influenced by water availability while productivity of pigeonpea and lablab will be less sensitive to precipitation due to a deeper rooting system.

2. Materials and methods

2.1. Field experiments

Data collected during two seasons of field experiments (2017/2018 and 2018/2019) in Arri ward, Babati district, northern Tanzania were used to calibrate and test the intercrop model. Details on experimental design and field management are presented in Mugi-Ngenga et al. (2022). The site lies in 04° 21′S, 35° 56′E, at an elevation of 1601 m above sea level. Within the site, the trials were established on three farms. In each of the selected farms, fields were ploughed and plots measuring 10 m × 5 m delineated just before planting. Paths measuring 1 m wide were left in between adjacent plots. Test crops used included maize (*Zea mays* L.) Seed Co. 513 hybrid variety, dolichos lablab (*Lablab purpureus* (L.) Sweet) "Selian-Rongai" variety, and pigeonpea (*Cajanus cajan* (L.) Millsp.) long ICEAP 00040 and medium duration ICEAP 00557 varieties. Pure stands of maize, pigeonpea and lablab were planted at a spacing of 0.90 m × 0.50 m inter- and intra-row, respectively. Maize-legume intercrops followed an additive design, with the legumes planted in the maize rows, in-between maize hills, maintaining the same

plant population for each crop in sole and intercrops (Mugi-Ngenga et al., 2022). Trials were planted with three seeds per hill for both maize and the legumes and later thinned to two plants, two weeks after emergence. Remaining plant populations of approximately 44,444 plants ha^{-1} were maintained in pure stands, whereas intercrops contained twice this density as they were laid out in additive design. Pigeonpea (both long and medium duration varieties) were planted simultaneously with maize, whilst lablab was relay-planted one month later. Maize was harvested 5–6 months after its emergence. Long-duration pigeonpea was harvested 3–4 month after maize harvest, whereas the additional growth period was 2–3 months for medium-duration pigeonpea and two months for lablab (Appendix 1). Fertilizer was applied in three treatments: no fertilizer; 40 kg P ha^{-1}; and 90 kg N ha^{-1} + 40 kg P ha^{-1}. Whereas P fertilizer was applied on maize and the legumes, the N fertilizer was spot applied only on maize, thus the NP fertilizer treatment was not applied in pure stands of pigeonpea and lablab. For the current analyses, observations on maize and the legumes were averaged over the fertilizer treatments.

2.2. Above-ground dry matter, plant height and maize leaf area

Above-ground dry matter was assessed through monthly destructive sampling across the two growing seasons. Within the 50 m^2 plot area, the data were obtained from 1 m^2 sub-plots, except for the determination of yield at physiological maturity, for which 9 m^2 was reserved. The plants from 1 m^2 sub-plots were cut at ground level, chopped and both the total and sub-sample fresh weights taken in the field. Sub-samples, 400–500 g in fresh weight, were taken to the laboratory at TARI-Selian, Tanzania for drying to constant weight. During the first season, sub-plots measuring 1 m × 1 m were demarcated in the net plot on all plots containing a legume and wire-mesh litter trap placed on the ground to capture fallen leaves from the legumes. The litter traps were stolen before the first sampling could be done. Consequently, fallen leaves were not quantified in the first season. In the second season, we installed similar sub-plots in all plots (1 m × 1 m), with no wire mesh. Every two weeks we collected the leaves from the ground to minimize decomposition, weighed and included them in the final determination of biomass yield.

The development of plant height and leaf area index (LAI) of maize was monitored in the 9 m^2 net plot through monthly non-destructive allometric leaf measurements throughout the growing seasons. Plant height of four plants, randomly selected within the net plot, was measured, and the average value determined. The plants were marked for subsequent measurements during the season. LAI of maize was estimated using a non-destructive method based on leaf length, leaf width and number of leaves. LAI of pigeonpea and lablab was not determined, due to the complex nature of the leaves. Number of leaves was determined by counting the total number from each of the plants used in determining plant height. Leaf length (m) and width (m) were measured on four representative leaves per plant, avoiding dry leaves as these are not photosynthetic. LAI for maize in pure stands and intercrops was then estimated using an allometric relation for area of a single leaf (LA; m^2/leaf):

$$LA = 0.78 \times leaf\ length \times leaf\ width \tag{1}$$

where 0.78 is a crop-specific coefficient for maize (Cunha et al., 2018).

Based on LA, the LAI of maize was estimated as:

$$LAI = LA \times \frac{n}{4} \times N \tag{2}$$

where n is the total number of leaves on the four sampled plants, and N is a maize plant population count from a 1 m^2 sub-plot within the 9 m^2 net plot area.

2.3. Radiation interception determination and calculations

Radiation interception (RI) was estimated through monthly measurements of photosynthetically active radiation (PAR) in each plot above and below the crop canopy, up to the time of final harvest. These observations were made at the same date as the destructive samplings. Measurements were taken using an AccuPAR LP-80 Ceptometer (Decagon Devices, Inc.; Northeast Hopkins Court, Pullman, USA). We avoided taking measurements when the sun was strong and near the horizon and focused on taking measurements within two hours either side of solar noon. To allow for a good representation of the overall area, measurements of PAR were taken at 14 positions in each plot: eight perpendicular to the rows and six parallel to the rows. The study used the mean of those two sets of observations as the basis for calculating the fraction of radiation intercepted (fRI):

$$fRI = 1 - \frac{I_{bottom}}{I_0} \tag{3}$$

where I_{bottom} is the measured PAR below the canopy and I_0 is the incident PAR above the canopy, both expressed in μmol m^{-2} s^{-1}.

Further, daily intercepted amount of radiation (RI; MJ m^{-2}d^{-1}) of pure stands and intercrops was estimated as:

$$RI = fRI \times I_{global} \times 0.5 \tag{4}$$

in which I_{global} is the daily global incoming radiation in MJ m^{-2} d^{-1} sourced from NASA power (https://power.larc.nasa.gov/data-access-viewer/), using GPS coordinates of the site, and 0.5 is the factor to convert global radiation to PAR (Sinclair and Muchow, 1999). Daily values of fRI were obtained by linearly interpolating between consecutive measurements.

2.4. Radiation-use efficiency (RUE) and extinction coefficient (k)

Radiation-use efficiency (RUE; g MJ^{-1} PAR) was obtained as the slope of the linear regression of above-ground dry-matter production on cumulative radiation intercepted by sole crops. For this analysis, the data set used for maize and the legumes covered the duration until the time of maize harvest.

The radiation extinction coefficient (k) of maize, which is an indicator of the efficiency at which the canopy absorbs radiation, was derived from LAI and radiation interception measurements in sole maize, by fitting Beer's law (Monsi and Saeki, 2005) as follows;

$$k = \frac{-ln\ (I_{bottom}/I_0\ )}{LAI} \tag{5}$$

Since LAI of pigeonpea and lablab was difficult to determine, an alternative procedure was developed to estimate the contribution of radiation interception of the legumes in the intercrops during the combined growth period of maize and legume. Following the principles of Spitters and Aerts (1983), total radiation interception of the two component species, as well as the distribution of intercepted radiation over the component species, was related to the product of LAI and k. For the legumes, the fraction of radiation intercepted in pure stands was used to determine the product of LAI and k, using Beer's law:

$$fRI = \left(1. - e^{-k \times LAI}\right) \rightarrow k \times LAI = -ln(1. - fRI) \tag{6}$$

The product $k \times$ LAI was then related to the dry weight of the legumes obtained at the corresponding sampling date. Only observations in the first half of the growing season, before leaf fall set in, were used to derive this relationship. Non-linear regression in R, using a quadratic function, was used to describe the relationship between shoot dry weight and $k \times$ LAI for each of the legume species.

2.5. Rooting depth measurements

To determine the rooting depths of maize, pigeonpea and lablab, two soil pits were manually dug using hand hoes and spades in one farm within the study site. Four more pits were dug at other locations where similar crop combinations were grown following similar treatments as in the study site. The pits were dug on the paths between two adjacent plots, to minimize destruction of the crops which were at 150 days post-emergence. The two adjacent plots consisted of maize-pigeonpea inter-crop, and sole lablab. The pits were more than 100 cm wide and digging stopped at 200 cm depth, as digging beyond that depth became problematic. Maize roots reached a depth of about 60 cm, whereas the tap root of each of the legumes extended below 200 cm.

2.6. Model description

A simple radiation interception × radiation utilization model for crop production, extended with a water balance following the tipping bucket principle, was constructed using Fortran Simulation Translator (FST) software (freely available at: https://models.pps.wur.nl/). The model operates with a time step of one day. The daily amount of intercepted radiation (RI; MJ m^{-2}d^{-1}) was obtained by multiplying fRI with daily incoming radiation (Eq. (4)). The fRI was derived through linear interpolation between the monthly field observations of light interception. Multiplication of RI with the species-specific RUE results in the potential daily shoot growth rate. A species-specific transpiration coefficient of 200 L kg^{-1} biomass for maize (Mudenda et al., 2017) and 300 L kg^{-1} biomass for pigeonpea and lablab (Siddique et al., 2001) was used to obtain the transpiration requirement (potential transpiration rate; mm d^{-1}). A soil water balance was included in the model. The maximum available amount of water in the rooting zone is calculated based on rooting depth and the volumetric water content at field capacity. Similarly, the volumetric water content at wilting point was used to calculate the minimum amount of soil water at which plants are still able to retrieve water from the profile. The volumetric water content at field capacity and wilting point were set at 0.21 and 0.13 corresponding to the values for a sandy-loam soil, following Ngetich (2012). Based on measurements obtained from profile pits dug in the field, rooting depth was set to 60 cm for maize and 200 cm for pigeonpea and lablab. Rainfall, which was recorded on-site, was used as input to the soil water balance, whereas water is lost through transpiration of the crop and percolation, which occurs if the actual amount of soil water in the rooting zone exceeds the maximum amount. Run-off was not observed, and therefore not included in the model. When actual soil moisture content falls below the critical level, the ratio between actual and potential transpiration decreases linearly from 1. at the critical level, to 0. at wilting point (Doorenbos and Kassam, 1979). The soil moisture depletion factor (p) depicts the critical soil water content below which the ratio between actual and potential transpiration rate drops below 1. This factor is positioned between field capacity (corresponding to $p = 0.$) and wilting point (corresponding to $p = 1.$), and was set to 0.8 for maize (Ngetich, 2012) and 0.65 for the legume species (Webber et al., 2006). In the model, the reduction in crop growth rate was set equal to the reduction in transpiration rate (van Keulen, 1975). Actual daily shoot growth rate was thus obtained by multiplying the earlier-obtained potential shoot growth rate with the ratio between actual and potential transpiration. Daily actual crop growth rate was accumulated over time until maturity of the crop, to arrive at the total shoot dry matter production. Maturity of both maize and the legumes was based on field observations.

For the simulation of the mixed systems, the model was extended. All crop growth and transpiration algorithms were included twice, with one set of algorithms assigned to the maize and the other set assigned to the legume. For both crops, a homogenous leaf area distribution in both the horizontal and the vertical plane, ranging from maximum plant height to zero at the soil surface, was assumed. Plant height of both species as measured in the field was used as input to the model. The canopy was dissected in a top (t) and a bottom (b) layer, with the top layer ranging from the maximum height of the shortest species to the maximum height of the tallest species, and the bottom layer ranging from soil level to the maximum height of the shortest species. Light interception in the top layer of the canopy ($I_{a,t}$) was calculated using Beer's law, using the product of light extinction coefficient (k) and the LAI of the tallest species (s_1) in the top layer ($LAI_{t,s1}$) and by accounting for a canopy reflection (ρ) of 7%.

$$I_{a,t,s1} = (1. - \rho) \, I_0 \left(1. - e^{-k_{s1} LAI_{t,s1}} \right) \tag{7}$$

The radiation transmitted through the top-layer (I_b) was used as incoming radiation for the bottom layer:

$$I_b = (1. - \rho) \, I_0 \, e^{-k_{s1} LAI_{t,s1}} \tag{8}$$

For the bottom layer, a two-step approach for light interception and distribution over the two competing species was used, following Spitters and Aerts (1983). First, total radiation interception of the bottom layer ($I_{a,b}$) was calculated using Beer's law, using the sum of the products of k and LAI for both species (s_1 and s_2, the shortest species).

$$I_{a,b} = I_b \left(1 - e^{\left(-k_{s1} LAI_{b,s1} - k_{s2} LAI_{s2} \right)} \right) \tag{9}$$

In a second step, this amount of absorbed radiation was distributed over the two species based on the share of each species in the sum of the product of k and LAI.

$$I_{a,b,s1} = \frac{k_{s1} LAI_{b,s1}}{\left(k_{s1} LAI_{b,s1} + k_{s2} LAI_{s2} \right)} \, I_{a,b} \tag{10}$$

$$I_{a,s2} = \frac{k_{s2} LAI_{s2}}{\left(k_{s1} LAI_{b,s1} + k_{s2} LAI_{s2} \right)} \, I_{a,b} \tag{11}$$

The daily amount of radiation intercepted by the tallest species was then obtained through summation of its radiation interception in the top and bottom layer.

$$I_{a,s1} = I_{a,t,s1} + I_{a,b,s1} \tag{12}$$

For the shortest species, radiation interception comprises only of the amount intercepted in the bottom layer.

For maize, both k and LAI are introduced as forcing functions, corresponding to field observations (LAI), or as derived based on field observations (k). For pigeonpea and lablab, the product of k and LAI was derived using the earlier determined species-specific relation between k × LAI and observed shoot dry weight. In the period after harvest of the maize crop, radiation interception for the legume, as the only remaining species, was directly calculated based on observed fRI following the procedure used in the sole crop models.

Next to a distinction in two canopy layers, the model for simulating intercrop productivity included two rooting zones. The upper layer ranged from soil surface to the maximum rooting depth of the maize (60 cm), and the lower layer covered the maximum rooting depth (60–200 cm). If rain is such that soil water in the upper layer exceeds the amount corresponding to that at field capacity, the excess water flows to the deeper layer. If the amount of water in the deeper layer exceeds the storage capacity of the second layer, the amount of water in excess percolates further to deeper layers, out of reach for the crops. For intercropped maize, the calculation of the ratio actual/potential transpiration rate followed the same procedure as in the sole crop model: If the actual water content of the upper soil layer is above the critical level, potential transpiration can be assumed, corresponding to a ratio actual/ potential transpiration of one. The effect of competition for water between maize and the intercropped legume is thus delayed. Both species retrieve water from the upper layer, thereby lowering the actual water content and influencing the moment in time when the actual soil moisture content drops below the critical level. It is only in this manner that both species influence the water uptake of the other species. For the

legume, the potential transpiration demand was divided proportionally to the depth of each layer. If the actual water content in the top layer was insufficient to meet the potential transpiration demand attributed to that layer, the difference was added to the potential demand credited to the second layer. Actual transpiration rate of pigeonpea and lablab in both layers was calculated similarly. Actual transpiration rate of the legumes from the first and the second layer were added and compared with the potential transpiration rate. This ratio represents the multiplication factor for obtaining the actual shoot growth rate based on potential shoot growth rate. Since transpiration during the early growth stages is not that large, it was assumed that pigeonpea and lablab have access to the second layer from the start of the simulation.

2.7. Simulations

The model analysis started with simulations of pure stands for both growing seasons. At the start of these simulations, the soil was assumed to be at field capacity. The simulated time course of shoot dry matter production was compared with field observations to evaluate the accuracy of the model. Additionally, the time course of the amount of soil water was investigated to check whether, at any point in time, the soil water content fell below the critical level. For each of the simulations, a soil water balance was composed as a check and to establish the fate of the water. Finally, the simulated shoot dry weight under the prevailing precipitation was compared with the result of a simulation in which the ratio actual/potential transpiration was fixed to one. The difference in shoot dry weight between both simulations provides insight into the degree to which water, as a growth limiting factor, influenced biomass production. A model exploration was made to gain insight into the importance of rooting depth for shoot dry matter production of pigeonpea and lablab. Simulations with reduced rooting depth were made, whereby in consecutive runs rooting depth was reduced by steps of 35 cm, from the original setting of 200 cm to a rooting depth of 60 cm, like that of maize.

Simulations of maize-pigeonpea and maize-lablab intercrops in the first season did not show a major increase in water shortage for either the maize or the legumes. Focus was therefore put on the second season, when precipitation (236 mm) was considerably less than in the first season (551 mm). The objective was to investigate whether, under conditions of low water supply and compared with pure stands, the combination of maize and pigeonpea or lablab in an intercropping system would aggravate the dependence of the system on water availability. The time course of shoot dry matter production for both maize and the accompanying legume were compared with field observations to determine the accuracy of the model. Root mean square error (RMSE) and mean absolute error (MAE) were used to estimate the accuracy of simulations as compared to observations, as shown below:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{N} (Sim_i - Obs_i)^2}{N}} \qquad (13)$$

$$MAE = \frac{\sum_{i=1}^{N} (Sim_i - Obs_i)}{N} \qquad (14)$$

where Sim_i is simulated value, Obs_i is observed value and N is the number of observations.

Soil water changes in the upper and lower-level soil depths were inspected to check whether, throughout the growing season, soil water content had dropped below the critical level of maize or the legume. Additional explorative simulations were run for maize in intercrop with pigeonpea or lablab, with a restricted rooting depth of the legumes of 60 cm. Finally, shoot dry matter production of maize and the legume species were compared for pure stands in the first season (high amount of precipitation), pure stands in the second season (low amount of precipitation), and intercrops in the second season with pigeonpea and lablab rooting depths of 200 and 60 cm. The comparisons among these simulation outcomes were used to establish the importance of precipitation for maize, pigeonpea and lablab shoot dry matter production, and to determine the degree of competition between maize and legume under conditions of scarce water supply.

3. Results

3.1. Field observations and parameter estimation

3.1.1. Radiation interception

For sole crops, maize reached its maximum radiation interception earlier than pigeonpea and lablab. This was at about 90 days after emergence (DAE) (Fig. 1a), while for the legume species the maximum radiation interception was attained at around 150 DAE across the two seasons (Fig. 1b, c, d). For intercrops, the time to reach maximum radiation interception was dependent on the legume species intercropped with maize. Here, the time of maximum radiation interception ranged from 120 to 180 DAE (Fig. 1e, f, g). Notably, the largest maximum radiation interception was in sole and intercropped lablab in the first season, where more than 90% of the radiation was intercepted (Fig. 1d, g). Though the fraction of radiation intercepted (fRI) and its pattern over the growing season was almost identical over the two years of experimentation for sole and intercropped pigeonpea, this was not the case for sole maize, and lablab (sole and intercropped). For those two crops, the intercepted radiation was markedly less in the second season than in the first season.

A comparison of radiation interception by crops in pure stand and in intercrop clearly showed the advantage of intercropping over pure stands. In case of the intercrop, radiation interception in the early growth stages matched that of the maize crop and was markedly greater than that of pigeonpea and lablab. The peak radiation interception in the maize crop observed close to the middle of the maize growing season, was markedly delayed in the intercrop. Here, overall radiation interception was still rising due to the presence of the legume. Also, after harvesting of the maize crop, radiation interception continued; initially at a slightly lower level than that of the pure stand of the two legume species, but at a nearly identical level during the last part of the legume growing season. Consequently, total radiation interception of the intercrop exceeded that of the sole crops of maize, pigeonpea and lablab.

3.1.2. Relation between biomass and $k \times LAI$

For pigeonpea and lablab, we found a strong relationship ($r^2 = 0.87$–0.98) between shoot dry weight and the product of $k \times LAI$ (Fig. 2). For long-duration and medium-duration pigeonpea, the relationship was nearly identical, showing that the radiation intercepting ability represented by $k \times LAI$ as a function of shoot biomass developed in an almost identical manner. Evidently, lablab was more efficient in intercepting radiation when compared at the same shoot biomass than pigeonpea. This greater capacity to intercept radiation might also explain the greater competitiveness of lablab, for which reason it was only introduced one month after maize. At the same time, the relation obtained for lablab was marked by a greater level of uncertainty ($R^2 = 0.873$ compared to 0.978 and 0.976 for long and medium- duration pigeonpea, respectively). This could be related to differences in development of lablab over the two seasons, with the poor establishment of the crop in the second season resulting in delayed canopy growth and reduced radiation interception (Fig. 1d, g).

3.1.3. Radiation-use efficiency (RUE)

Radiation-use efficiency (RUE) calculated based on biomass and cumulative photosynthetic- active-radiation interception was relatively stable across seasons for the two pigeonpea varieties and more variable for maize and lablab. Maize was more efficient in converting intercepted radiation into biomass in the first (RUE = 1.435 g MJ^{-1}) than in the second (RUE = 1.067 g MJ^{-1}) season. (Fig. 3a). The smaller value for the second season was associated with the lower precipitation. For the
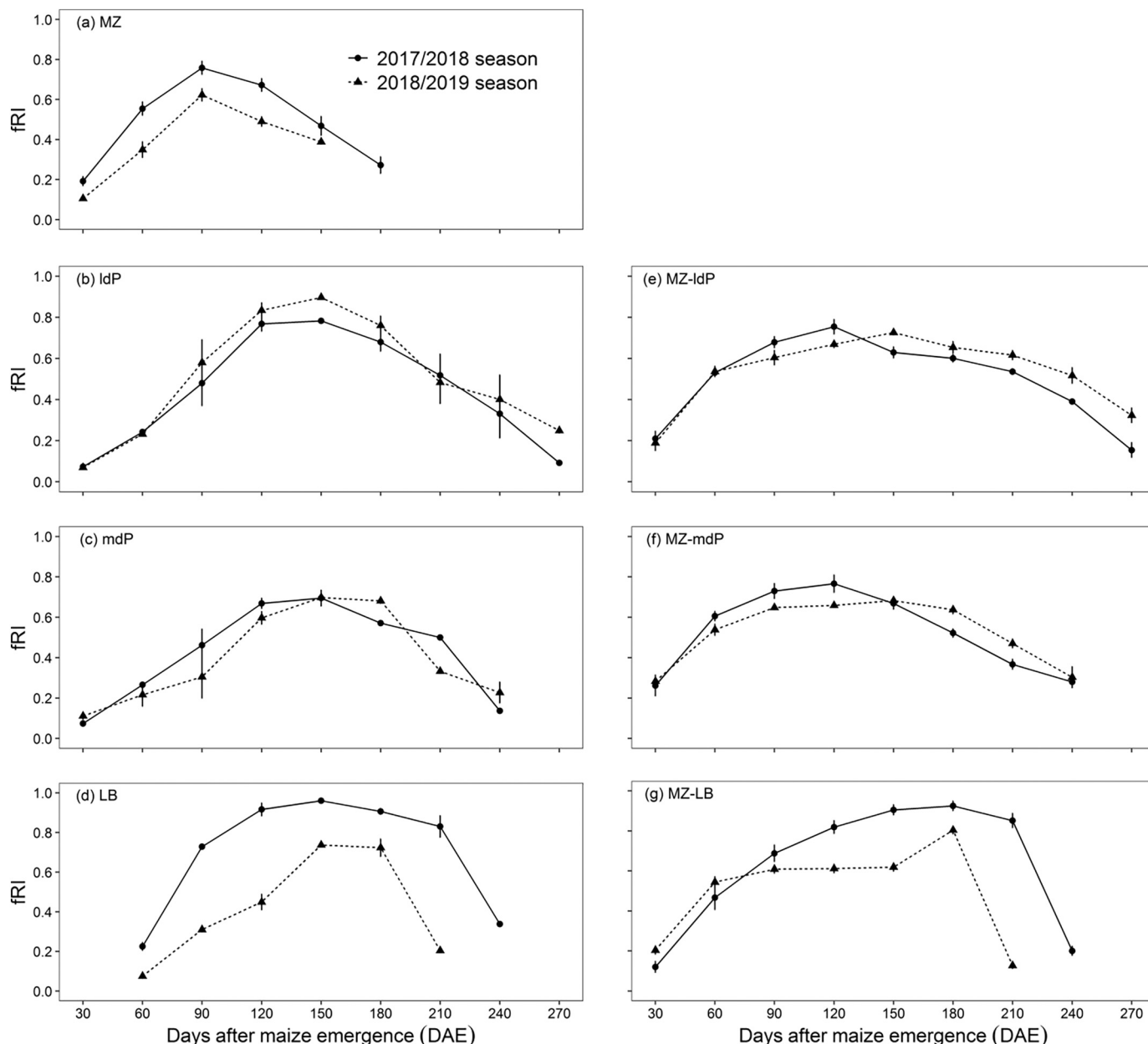
Fig. 1. Fraction of radiation intercepted (fRI) in sole crops of (a) maize (MZ), (b) long-duration pigeonpea (ldP), (c) medium-duration pigeonpea (mdP), (d) lablab (LB), and in intercrops of maize with (e) long-duration pigeonpea (MZ-ldP), (f) medium-duration pigeonpea (MZ-mdP), (g) lablab (MZ-LB) in the 2017/2018 and 2018/2019 seasons in Babati, northern Tanzania. Error bars represent the standard deviation.

legumes, RUE ranged between 0.487 and 0.737 g MJ^{-1} (Fig. 3b-d).

3.1.4. Plant height development

In sole crops, height development across the two seasons was largely identical, except for lablab where height development in the second season was severely delayed, related to the dry conditions at the time of sowing (lablab was always sown 30 days after the other crops) (Appendix 2). Maize and pigeonpea exhibited an upright architecture for which plant height was easy to determine. Lablab, on the other hand, exhibited a creeping, bushy, or twining growth habit. As such, the height of sole lablab was measured by stretching the stem vertically upwards during measurements. In the intercrop, plant height of lablab represents the actual height of the canopy, as lablab climbed on the accompanying maize crop. In the intercrops, maize consistently recorded greater or similar height than the accompanying legume across the two seasons, throughout the co-growth period.

3.1.5. Rooting studies

An inspection of root profiles in our study showed that maize root extended to about 60 cm in depth, while both pigeonpea and lablab had a deep taproot which extended beyond 200 cm depth (Appendix 3). For maize and the legume species, roots in the top 60 cm depth spread out horizontally and vertically, while beyond 60 cm the single taproot of the legumes extended vertically and became finer with depth.

3.2. Simulations of sole crops

The simulated biomass was compared with the observed data from sequential harvests (Fig. 4). For maize, the RUE of the first season was used, as there were strong indications that the lower RUE in the second season was the result of water shortage. In the model, such a reduction in RUE is included based on the water balance. There was a good agreement between simulated and observed shoot biomass of maize,
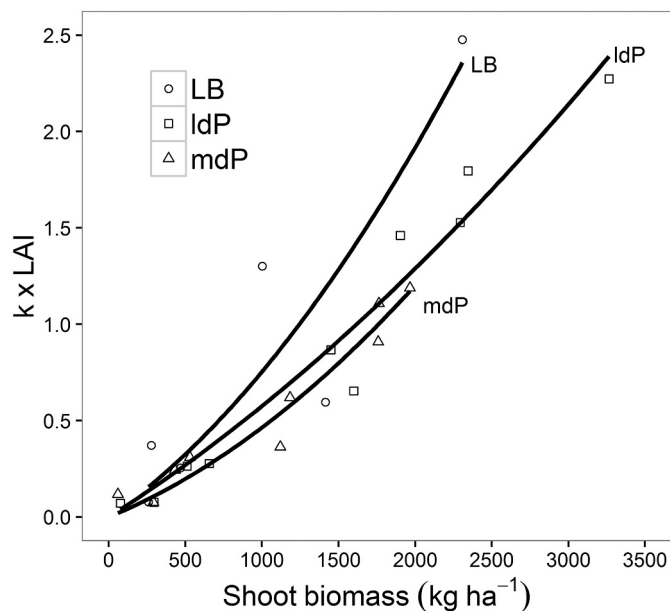
Fig. 2. Relationship between shoot biomass in sole crops of lablab (LB), long-duration pigeonpea (ldP), medium-duration pigeonpea (mdP), and the product of radiation extinction coefficient (k) and leaf area index (LAI) in Babati, northern Tanzania. (LB: y = $2.05 \times 10^{-7} \times^2 + 0.0005\times$; $R^2 = 0.873$; ldP: y = $0.69 \times 10^{-7} \times^2 + 0.0005\times$; $R^2 = 0.978$; mdP: y = $1.37 \times 10^{-7} \times^2 + 0.0003\times$; $R^2 = 0.976$, where x = shoot biomass in kg ha^{-1}).

pigeonpea and lablab, except for the final stages of legume growth in the first (2017/2018) season (Fig. 4c, e, g). This is because in the first season, leaf fall was not accounted for, as the litter traps placed to determine leaf fall were stolen. However, it can be noted that the gap for leaf fall in the first season (Fig. 4c, e, g) is in line with the gap observed in the second season (Fig. 4d, f, h). Here, the open dots indicate observed biomass with exclusion of leaf fall.

With a water balance included in the model and considering the amount of water in the soil from soil surface to maximum rooting depth for maize (60 cm) and the legume species (200 cm), it was observed that maize encountered water stress in the second season. Simulations showed that the amount of soil water fell below the critical soil moisture level (Fig. 5a). With an actual soil moisture below the critical level, the ratio between actual and potential transpiration rate (RATIOActPot) fell below 1 (Fig. 5b). Water shortage was observed starting 80 days after emergence, and lasted for 19 days, after which a rain shower replenished the soil up to an amount above the critical level. During the period of water shortage, the RATIOActPot of transpiration rapidly dropped and reached a minimum value of 0.06. The accompanying reduction in dry matter production amounted to 115 g m^{-2}.

In contrast, water stress was not encountered by the legumes throughout the growing period in either of the two growing seasons. This is illustrated, taking long-duration pigeonpea as an example, by the actual amount of soil water which remained above the critical soil moisture level (Fig. 5e). Consequently, the RATIOActPot of transpiration remained one (blue line in Fig. 5f). Evidently, the legumes had access to a larger part of the water stored in the soil, as their maximum rooting depth was set to 200 cm. To explore the importance of rooting depth for pigeonpea and lablab, rooting depth of the legumes was shortened from 200 cm to 60 cm. With an assumed rooting depth of 60 cm for long-duration pigeonpea, the implication for the second season is illustrated in Fig. 5 (c, d). After the last rainfall event at 144 days after emergence, the soil water steadily decreased, and at 185 days after emergence, the actual soil water content fell below the critical soil moisture level (Fig. 5c). From then on, RATIOActPot of transpiration dropped below one (Fig. 5d). This ratio steadily dropped, until, at the

end of the season, it was nearly zero. With less severe reductions in rooting depth (165, 130 and 95 cm), the same pattern was observed, but here the reduction started at a later moment in time and ultimately reached a less severe deficit (simulation results not shown).

In sole maize, from the initial amount of soil water and water supplied by the rain (551 mm), about two thirds (63.8%) percolated, while about a third (34.9%) was transpired, with a negligible amount of water remaining at the end of the first season (Appendix 4). In the second season (rainfall amount: 236 mm), there was much less percolation which represented about a third (37.5%) of the available water, while transpiration was nearly half (47.6%). Surprisingly, in the second season, more water remained in the soil at the end of the growing season (14.9%) (Appendix 4). For the legumes, 67% of the water was percolated under each legume, 21–27% was used for transpiration, while 7–12% was left in the system at the end of the first season. As with maize, a much smaller percentage (37–42%) of water percolated in the second season, while transpiration was 36–46%, and 17–22% remained in the soil profile at the end of the season (Appendix 4).

The implication of the differences in water supply on the final shoot biomass production of sole maize and the legumes is depicted in Fig. 6. Maize production in the second season was considerably smaller than in the first season (Fig. 6a). From the gap between simulated production in presence and absence of water shortage (115 g m^{-2}), it is evident that water shortage strongly affected maize growth. For the legumes, no difference was observed in either of the two seasons between the simulations with the actual water balance and the reference simulations where the ratio between actual and potential transpiration was fixed at one. Reducing the rooting depth of pigeonpea and lablab from 200 to 60 cm led to a decrease in shoot biomass production. With an assumed rooting depth of 60 cm, biomass was predicted to decline by up to 26%, 18% and 19% for long-duration pigeonpea, medium-duration pigeonpea and lablab, respectively, relative to the values for 200 cm (Fig. 6b-d). This illustrates the importance of the deep rooting system for adequate water access of the legumes under study.

For long and medium- duration pigeonpea, the ample water supply at a rooting depth of 200 cm also coincided with nearly identical shoot dry matter productions in both seasons (Fig. 6b, c). For lablab, this was not the case, as shoot dry matter production in the second season was 149 g m^{-2} less, than in the first season (Fig. 6d). This is likely related to the poor establishment of lablab in the second season.

3.3. Simulations of intercrops

The simulation model was used to analyse biomass production in intercrops of maize and long-duration pigeonpea, medium-duration pigeonpea and lablab in the 2018/2019 season. Simulated shoot biomass in intercrops was compared with the observed data from periodic harvests (Fig. 7). The black dots are observations, while the black lines are the simulation results. For pigeonpea and lablab, a species and season-specific RUE, determined from sole crops, was used. For maize, RUE of sole crop of the first season was used. There was a good agreement between simulated and observed shoot biomass of intercropped maize (Fig. 7a, b, c). Growth of the legumes was initially slightly underestimated during the co-growth period. Whereas this underestimation remained for long-duration pigeonpea, it turned into an overestimation in the final part of the growing season for medium-duration pigeonpea and lablab (Fig. 7d, e, f).

Simulations showed that with a rooting depth of 60 and 200 cm for intercropped maize and legume, respectively, maize, comparable to its pure stand, encountered water shortage. In intercrop with long-duration pigeonpea, the amount of soil water in the upper layer fell below the critical soil moisture level for maize (Fig. 8a). This resulted in the ratio between actual and potential transpiration rate (RATIOActPot) dropping below 1 (black line in Fig. 8b) and reaching a minimum value of 0.01. The intercropped maize experienced water shortage starting 71 days after emergence, which lasted for 28 days, after which a rain
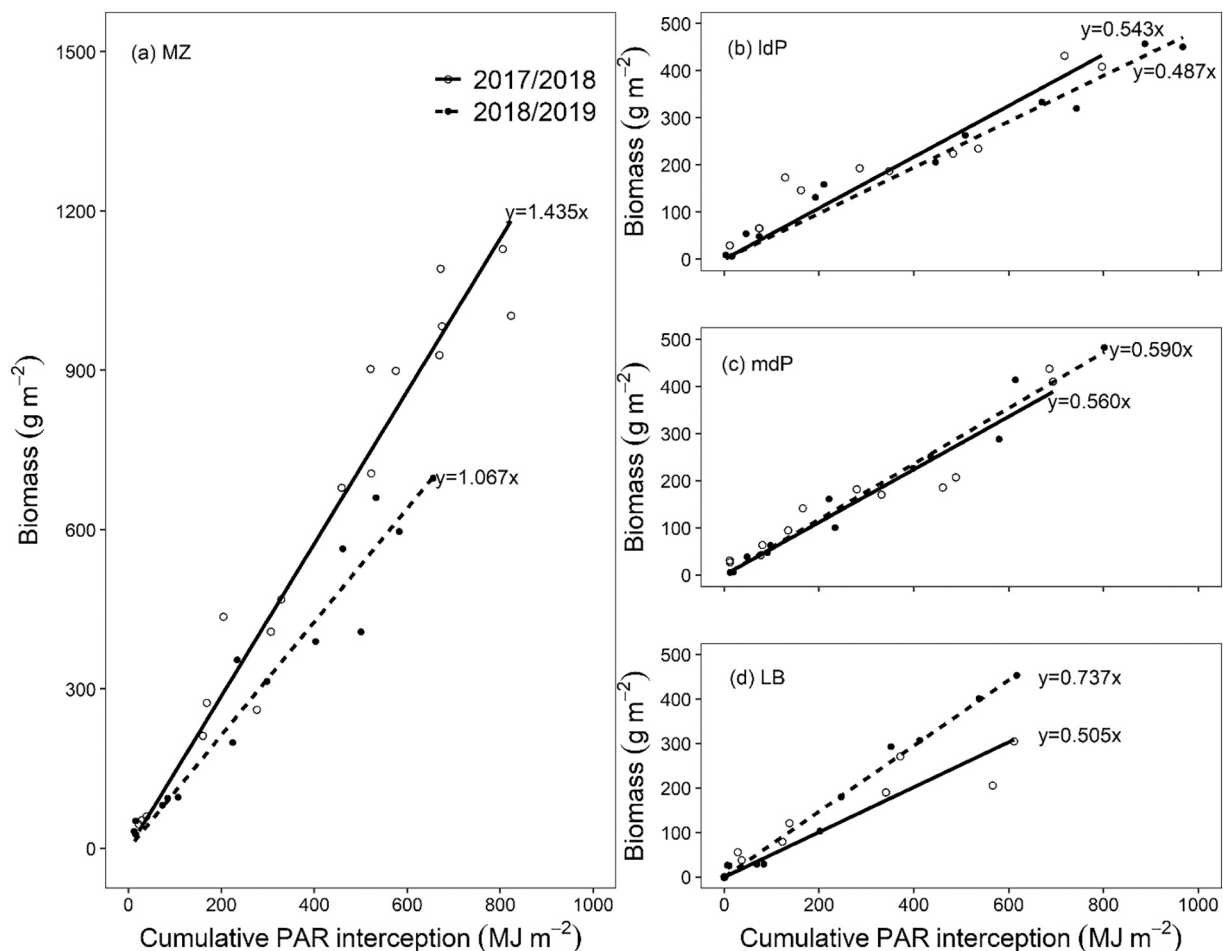
Fig. 3. Relationship between above-ground total biomass of pure stands of maize (MZ), long-duration pigeonpea (ldP), medium-duration pigeonpea (mdP), lablab (LB), and cumulative photosynthetic active radiation (PAR) interception in the 2017/2018 and 2018/2019 seasons. The slope of this relationship is radiation-use efficiency (RUE) (g MJ^{-1}).

shower replenished the soil up to an amount above the critical level.

In contrast, throughout the growing period, water stress was not encountered by any of the legumes. Water shortage in the upper layer, where pigeonpea and lablab ($p = 0.65$) would suffer earlier than maize ($p = 0.8$), was compensated for by a sufficiently high water-storage in the lower soil layer. This is illustrated by the actual amount of soil water which remained above the critical soil moisture level in the deeper layer (Fig. 8a). Consequently, the RATIOActPot of transpiration remained 1 (blue line in Fig. 8b). Presented results are for long-duration pigeonpea, but simulations of intercrops with the other legumes showed a similar result.

When assuming a rooting depth of long-duration pigeonpea similar to that of maize (60 cm), both maize and long-duration pigeonpea suffered from water stress earlier on, as illustrated by the actual soil water content below the critical soil moisture levels (Fig. 8c). From that point onwards, parameter RATIOActPot dropped below the value of 1 for both crop species (Fig. 8d). Due to its lower soil depletion factor, long-duration pigeonpea started to experience water constraints a few days earlier than maize. The shallower rooting depth of the legume also had implications for water availability after maize harvest. Like the simulations with sole legumes, a shallower rooting depth implied a lower amount of stored water, resulting in a situation where available soil water continued to decrease after the last rain and was nearly completely exhausted about one month after maize harvest.

Simulated shoot biomass yields in the intercrops are presented for maize and the three legume species (Fig. 6). The last two bars are the results of the simulations in intercrops, all for the second season, and

with an assumed rooting depth of the legumes of 200 and 60 cm. The presence of pigeonpea caused a further reduction in maize production, resulting from competition for water and radiation (Fig. 6a). Light interception of maize intercropped with pigeonpea was reduced (average 18%), whereas no such reduction was observed in the intercrop with the relay planted lablab. Due to the greater rooting depth of pigeonpea and lablab, these species hardly affected shoot dry matter production of maize.

While maize was modestly affected by presence of pigeonpea, the legumes were strongly affected by presence of maize (Fig. 6b-d). The simulations revealed that the reduction in legume yield was not due to insufficient water, as soil water content remained above the critical level throughout the growing season, as illustrated for long-duration pigeonpea (Fig. 8a, b). Light interception during the co-growth period with maize was however severely reduced, with reductions of over 40% for pigeonpea and over 60% for lablab. These reductions were partly compensated in the period after maize harvest, such that the overall reductions in light interception for pigeonpea was just over 20% and 44% for lablab. With the rooting depth assumed to be like that of maize, the shoot dry matter production of the legumes was further reduced (Fig. 6b-d). This further reduction could be solely attributed to water shortage, as illustrated for long-duration pigeonpea (Fig. 8c, d), but equally valid for medium-duration pigeonpea and lablab. This underscores the importance of the deep rooting system for the legumes under study.
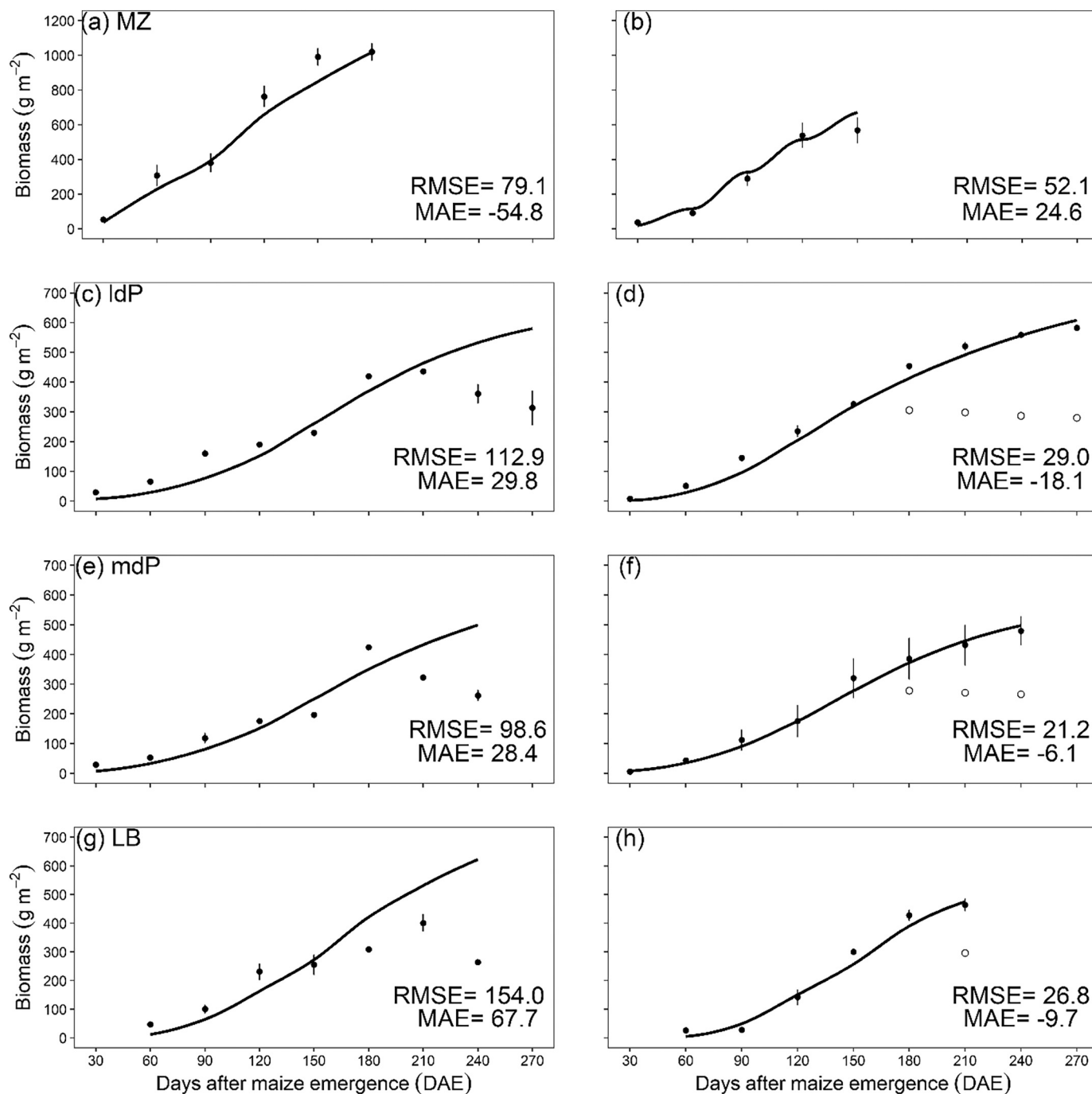
Fig. 4. Simulation results for shoot biomass in sole crops of maize (MZ) (a, b), long-duration pigeonpea (ldP) (c, d), medium-duration pigeonpea (mdP) (e, f) and lablab (LB) (g, h) in the 2017/2018 (a,c,e,g) and 2018/2019 season (b,d,f,h) in Babati, northern Tanzania. The closed points are observations. For legumes (c-h), observations in the 2017/2018 season do not include leaf fall, while this is included in the 2018/2019 season. The black lines are simulation results using an effective rooting depth of 60 cm (maize) and 200 cm (legumes). The open points in 2018/2019 season represent observations for shoot biomass of legumes excluding leaf fall. RMSE = Root Mean Square Error; MAE = Mean Absolute Error.

4. Discussion

4.1. Importance of water availability and competition for water in sole crops and intercrops of maize and legumes

Simulations showed that in the second season, maize production was water limited for 19 days (Fig. 5a, b). This was related to the limited soil-water storage capacity, determined by its relatively shallow root system (depth ∼ 60 cm), and a narrow gap in volumetric water content between field capacity (0.21) and wilting point (0.13) of the sandy loam soil at

our study site. This corresponds to a storage capacity of 0.8 mm per cm soil profile and a maximum stock of 48 mm. In the first season, precipitation was higher but less uniformly distributed, with the majority falling in a few intense rain events. This resulted in a high fraction of the water being percolated. In the second season when there was less precipitation, the fraction percolated was much less, and even more water remained in the soil at the end of the growing season as compared with the first season (Appendix 4). This confirms that in addition to the amount of precipitation, its distribution over the growing season is important. Percolated water is not of use to the crop species grown in
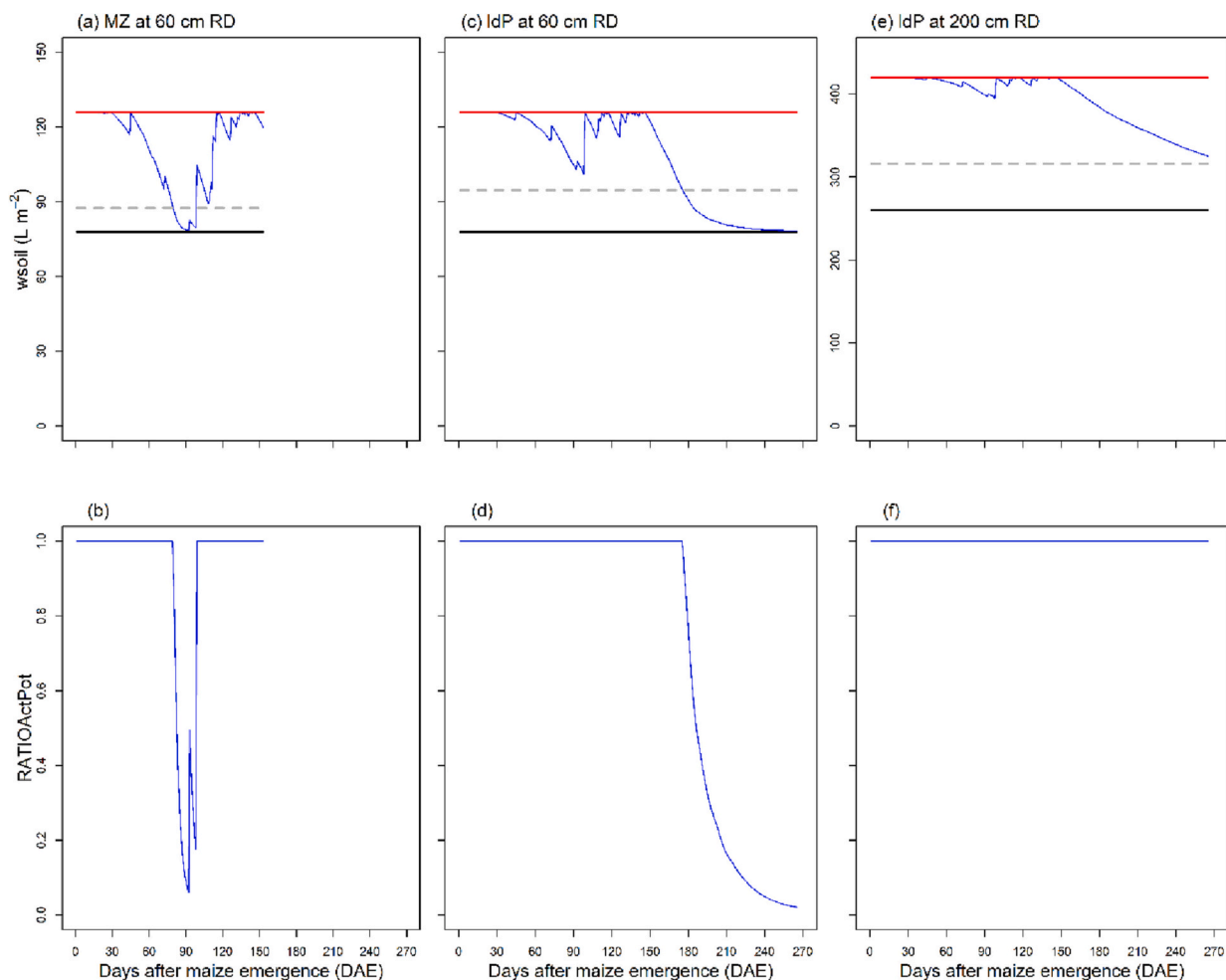
Fig. 5. Simulation of the amount of water in the soil from soil surface to maximum rooting depth (wsoil; Lm^{-2} = mm) (a, c, e), and the ratio between actual and potential transpiration rates (RATIOActPot) (b,d,f) in the 2018/2019 season in Babati, northern Tanzania. Panels a, c, e represent the wsoil for sole crops of (a) maize (MZ) at its actual situation (rooting depth; RD of 60 cm), (c) long-duration pigeonpea (ldP) assuming a rooting depth (RD) of 60 cm, and (e) long-duration pigeonpea (ldP) at its actual situation (rooting depth; RD of 200 cm). In Panels a, c, e, the blue, red and black solid lines represent actual amount of soil water and amount of water at field capacity, and wilting point, respectively, while the grey dashed lines represent the critical amount of soil water based on a soil depletion factor of 0.8 for maize and 0.65 for long-duration pigeonpea. Panels b, d, f represent the RATIOActPot of transpiration in sole crops of (b) maize (MZ) (rooting depth of 60 cm), (d) long-duration pigeonpea (ldP) assuming a rooting depth of 60 cm and (f) long-duration pigeonpea (ldP) at rooting depth of 200 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that season, as only the water transpired by the crop can be considered acquired and used productively in crop growth (Stomph et al., 2020). Our results confirm past research, that one of the major limitations in stabilizing and increasing yields in rain-fed farming systems is crop water stress, caused by inefficient use of total available seasonal rainwater (McHugh et al., 2007). Additionally, the high spatial and temporal intra-seasonal rainfall variability is considered as one of the most important factors affecting agricultural productivity in SSA (Laux et al., 2010).

In the second season, the presence of pigeonpea caused a further decline in the productivity of maize. Next to the aggravation of water shortage, both pigeonpea varieties also competed for light with maize, resulting in an 18% reduction in light interception. Lablab, due to a later introduction and a poor initial establishment, did not affect maize. This translated into a simulated maize yield reduction ranging from 0.1 t ha^{-1} (lablab; 2%) to 1.8 t ha^{-1} (medium-duration pigeonpea; 27%). This competitive effect is substantial, though considerably less than that of the difference between seasons (around 3.5 t ha^{-1}). It contrasts with previous research on maize-legume systems, showing insignificant effects of pigeonpea on maize growth and yield (Kimaro et al., 2009; Myaka et al., 2006; Rusinamhodzi et al., 2012; Waddington et al., 2007).

The current analysis suggests that, for seasons with insufficient rainfall, transpiration by grain legumes may result in reduced maize productivity.

Pigeonpea proved to be far less sensitive to differences in annual precipitation. In both seasons, nearly identical production was observed, and water shortage did not occur in either of the two seasons. Despite the higher transpiration coefficient of the legumes, the lower transpiration need, following from their lower radiation-use efficiency, but particularly the deeper rooting ability was shown to be responsible for this. Simulations of pigeonpea productivity with reduced rooting depth showed that water stress and a reduced productivity would occur if pigeonpea was not able to exploit the deeper layers in the soil profile (Fig. 5). Indeed, increased root proliferation at depths where the water is available has been shown to be a water-stress avoidance mechanism by crops with a capacity to root deeply (Lopes et al., 2011). We further relate the absence of water stress to the fact that legumes are known to lose senesced leaves towards maturity, so as to compensate for an increased transpiration demand in rain-fed conditions and/or decreased water availability without severe yield losses (Sennhenn et al., 2017). Lablab differed from pigeonpea, with a lower shoot dry matter production in the second year. However, the simulations indicated that this
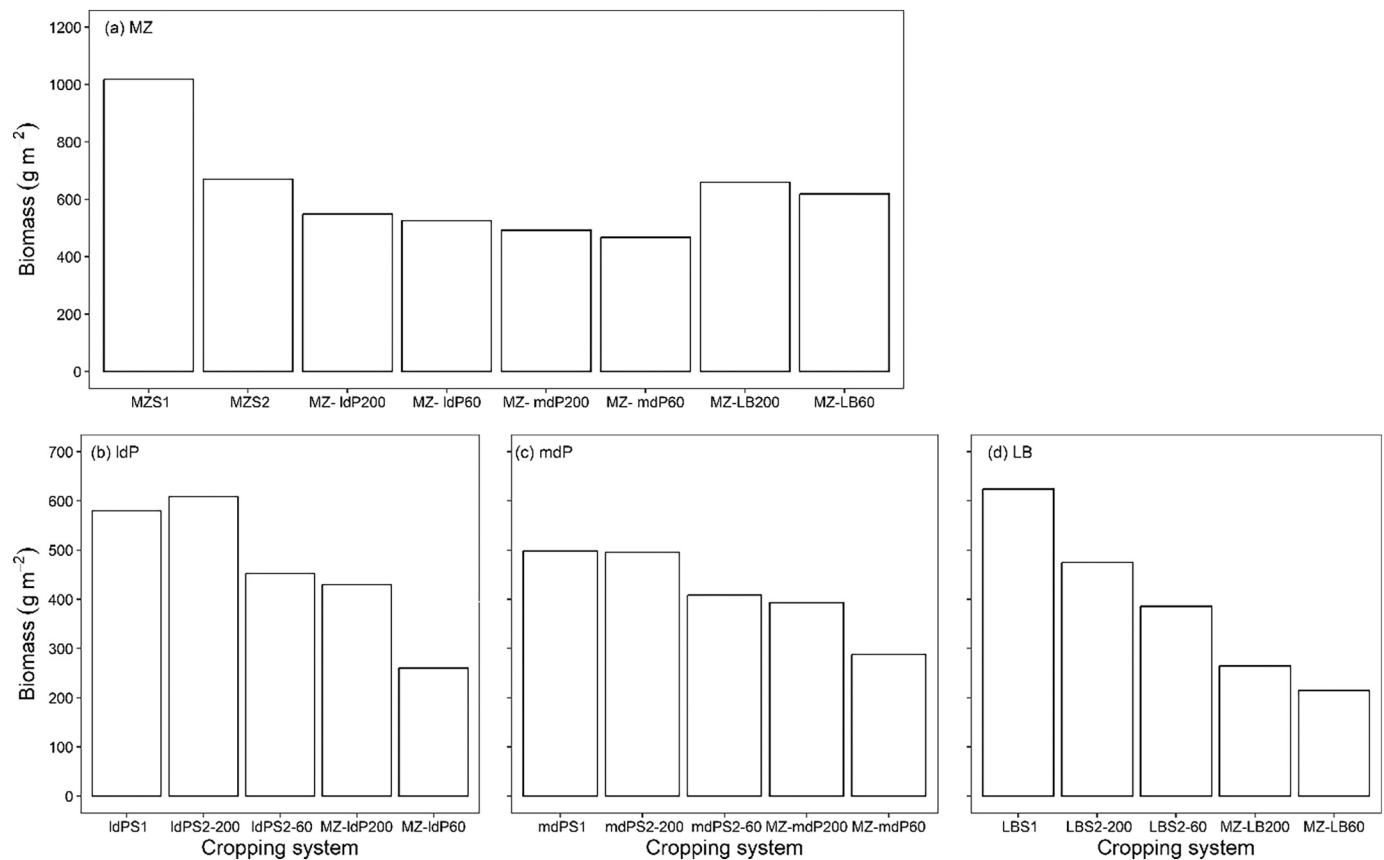
Fig. 6. Illustration of simulated biomass of (a) maize (MZ), (b) long-duration pigeonpea (ldP), (c) medium-duration pigeonpea (mdP), and (d) lablab (LB) under different cropping systems in Babati, northern Tanzania. Panel (a) shows maize biomass grown as sole crop in the first season (MZS1), sole crop in the second season (MZS2), maize intercropped in the second season with long-duration pigeonpea assuming a rooting depth of 200 cm (MZ-ldP200) and assuming a rooting depth of 60 cm (MZ-ldP60). The further bars in this panel represent maize intercropped with medium-duration pigeonpea and lablab assuming a rooting depth of 200 cm (MZ-mdP200 and MZ-LB200) and 60 cm (MZ-mdP60 and MZ-LB60). Panels (b, c, d) show biomass of the legumes, either as sole crop in the first season, sole crop in the second season assuming a rooting depth of 200 and 60 cm, and intercropped in the second season assuming a rooting depth of 200 and 60 cm.

was not a result of insufficient water for transpiration. Water shortage for germination and establishment before development of a tap root is more likely the case. Lablab was sown 30 days after maize, and in the second season this coincided with a dry spell. This shows the risk associated with delayed sowing of a legume, as this might lead to poor establishment. It further underscores the need for optimal timing of sowing dates, as this is considered as one of the agricultural management strategies, which is known to strongly affect crop production in rain-fed agriculture (Ati et al., 2002). This is even more relevant in many parts of semi-arid Africa, as the rainy season starts with some light showers followed by dry spells, which can cause poor crop emergence or desiccate a newly germinated crop (Makarau, 1995).

Simulations of intercropping systems showed that the presence of maize in pigeonpea and lablab systems caused a clear reduction in dry matter production of the legume, ranging from 1 to 2 t ha^{-1} (21–44%). However, the simulations revealed that this was not caused by competition for water, as also in presence of maize the legumes did not suffer from water stress. Competition for light was the dominant cause, with a reduced light capture during the co-growth period ranging from just over 40% for pigeonpea and an even stronger reduction for lablab (over 60%). When pigeonpea and lablab were assumed to have the same rooting depth as that of maize, the legume already suffered from water shortage during the co-growth period with maize, and this recurred later during its growing season, as the rooted soil profile dried out (Fig. 8c, d). The simulations in intercropping systems thus again point at the importance of the deeper rooting system of both legume species. In a scenario with equal rooting depths, the water stress in the upper layer is

a result of increased water acquisition in the intercrop, due to increased root density in the upper layers (Stomph et al., 2020). This implies that maize takes its share of water during the co-growth period, thus leading to an earlier depletion of water reserves in the soil (Morison and Gifford, 1984), at the expense of the legume which has a longer growth period. In relation to this, past research showed that under water limited conditions, water extraction by a crop is limited by root system depth, and by the rate of extraction (Robertson et al., 1993). The reduced transpiration of the legume with a rooting depth like that of maize translated into reduced productivity (Fig. 6b-d), as biomass production is closely linked to transpiration (Lopes et al., 2011).

4.2. Parameters derived for the model study

Model-parameterization required a closer look at some system traits that are interesting aspects on their own, such as radiation interception and radiation-use efficiency. Compared with sole cropping, intercropping was shown to have greater radiation capture potential (Fig. 1). We attribute this to the effect of combination of differing spatio-temporal use of radiation among component crops (Willey, 1990). Maize had a greater contribution to ground cover in the initial 90 days after emergence, eventually contributing greatly to radiation interception, while pigeonpea and lablab continued intercepting radiation after maize harvest.

Lablab was more efficient in intercepting radiation at a comparable shoot biomass (Fig. 3). This greater efficiency of lablab to intercept radiation might also explain the higher competitiveness of lablab, for
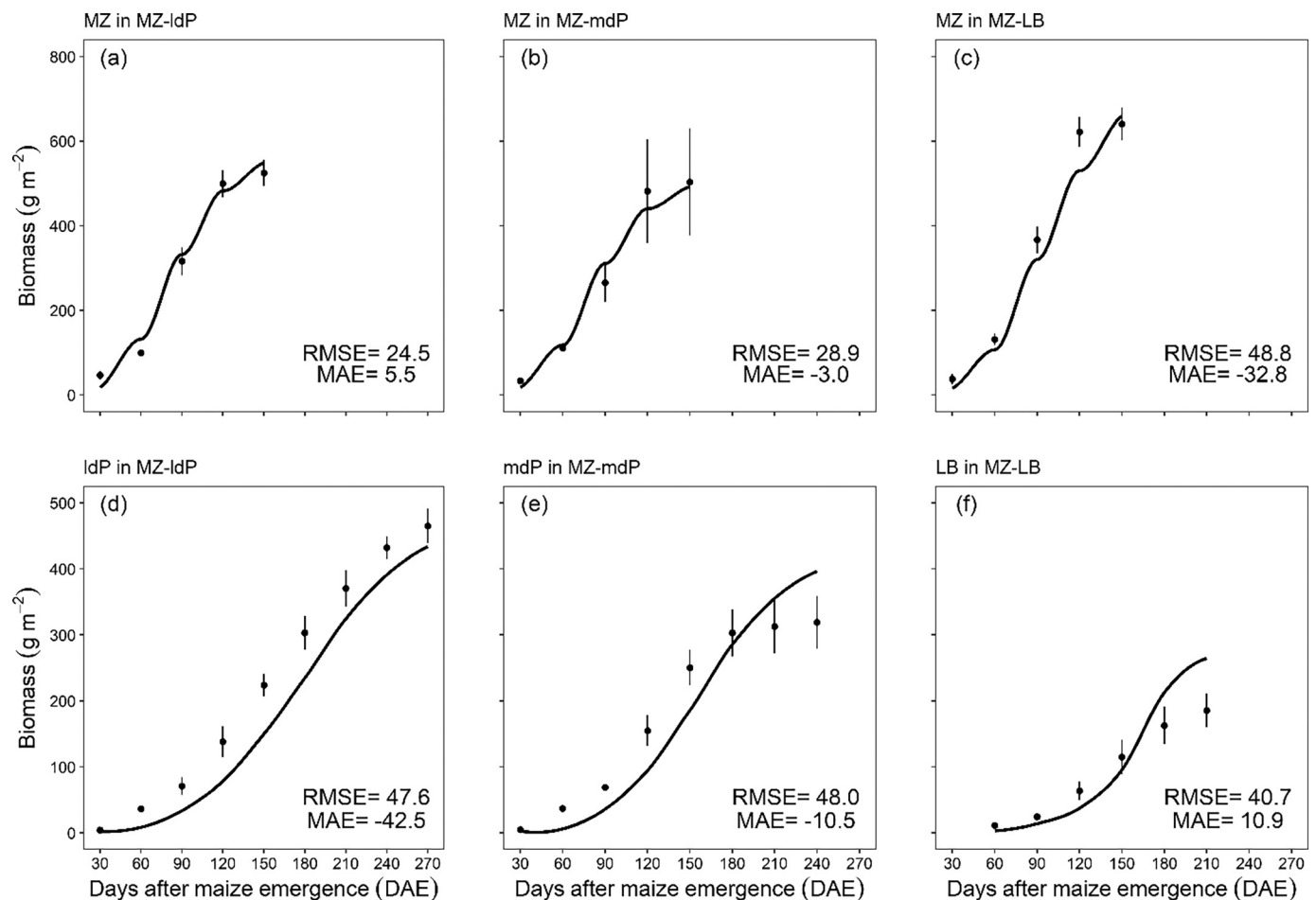
Fig. 7. Simulation results for shoot biomass of maize and the accompanying legume in intercrops of maize (MZ) with long-duration pigeonpea (MZ-ldP), medium-duration pigeonpea (MZ-mdP) and lablab (MZ-LB) in the 2018/2019 season in Babati, northern Tanzania. The points are observations. The black lines are simulation results for each crop in intercrop. RMSE = Root Mean Square Error; MAE = Mean Absolute Error.

which reason it was only introduced one month after maize and is possibly due to its inherently dense canopy (Cook et al., 2005). The procedure for distribution of total radiation interception of intercrops over component species, as described by Spitters and Aerts (1983), heavily relies on $k \times$ LAI. As these characteristics are not used in isolation, the direct determination of this product, which can be easily and accurately derived from radiation interception observations is a valid alternative for situations where determination of LAI is difficult or unreliable. However, exploration with the current data set showed that the relationship between shoot dry weight and $k \times$ LAI became far less stable once leaf fall sets in. This suggests the method to be particularly relevant during earlier stages of crop development.

Maize was more efficient in converting intercepted radiation into biomass, as indicated by its greater RUE relative to pigeonpea and lablab. Indeed, cereal crops have been shown to have greater RUE than legumes, though for all species the current values are smaller than what has been previously reported (Muchow et al., 1993; Sinclair and Muchow, 1999). The greater RUE for maize as compared with legumes has been linked to greater biomass production of maize (Elhakeem et al., 2021; Li et al., 2019). Simulations showed that the smaller RUE of maize recorded in the second season was attributable to water shortage. Using the RUE of the first season, where no water shortage was noted, combined with the assimilation routine that accounts for a reduced production following from water shortage, resulted in an adequate simulation of maize shoot dry matter. Related to this, soil water deficits have a major influence on leaf photosynthesis, and, consequently, RUE is also decreased under drought conditions (Sinclair and Muchow, 1999).

The RUE values for pigeonpea were relatively stable, which is in line with the model observations that water shortage was not encountered in either of the two seasons. Lablab was an exception, as irrespective of the absence of water stress, a greater RUE was obtained in the second season. It is unclear whether this result reflects the poor establishment that was observed in the second season.

4.3. Modelling approach

For the current analysis, a simple and parameter-sparse model was developed. Our approach follows the adage of C.T. de Wit 'no simulation without experimentation' and 'no experimentation without simulation' (see Silva and Giller, 2020). The model provides valuable additional insight in the functioning of maize and legumes, either grown as sole crop or intercrop. The model is largely driven by data directly observed in the field and was parameterized based on observations in sole crops. As such, the model should be regarded a valuable extension of experimental field observations enabling a better interpretation of collected data. The model is typically well suited for analysis and not for prediction purposes, as it is largely driven by observations. Although it might seem that our approach violates the rule that parameterization and validation of model performance should be based on independent datasets, we have no intention to extend the model for prediction purposes. The strength of the current approach is its transparency and underscores our belief in model simplicity. The model aligns with the observations and the level of detail with which observations were made in the field, ensuring that model-assumptions were reduced to a
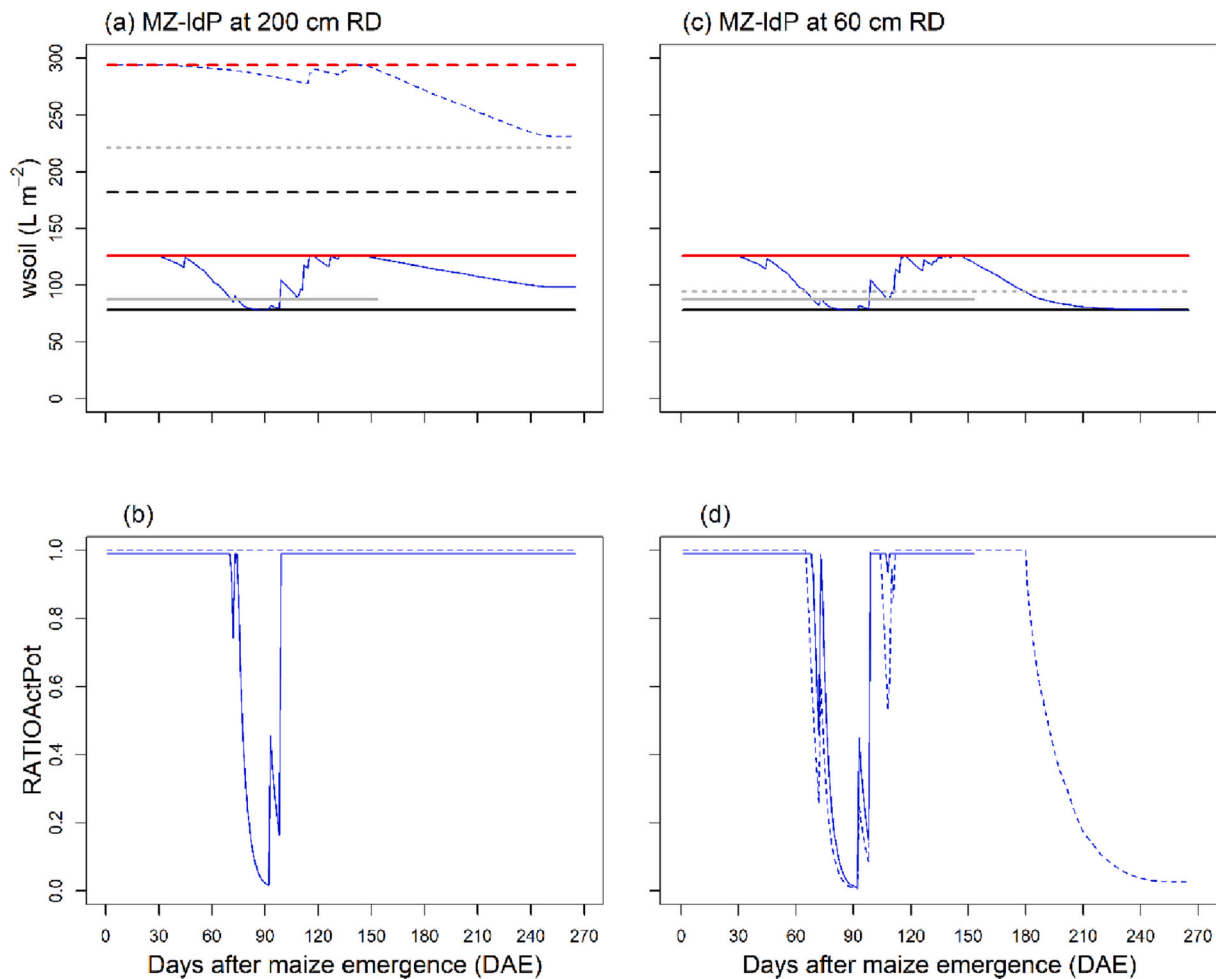
Fig. 8. Illustration of the amount of water in the soil from soil surface to maximum rooting depth (wsoil) (a c), and the ratio between actual and potential rates (RATIOActPot) of transpiration (b,d) in the 2018/ 2019 season in Babati, northern Tanzania. Panels a, c represent the wsoil for intercrops of maize and long-duration pigeonpea (MZ-ldP) assuming a rooting depth (RD) of 200 cm (a) and 60 cm (c) for the legume. In Panels a, c, the blue, red and black solid lines represent actual amount of soil water and the amount of water present at field capacity and wilting point, respectively in the upper layer (0–60 cm). The dashed lines represent the same for the deeper soil layer (60–200 cm). The solid and dotted grey lines represent the critical soil water amount for maize and long-duration pigeonpea, respectively. Panels b, d represent the RATIOActPot of transpiration in MZ-ldP intercrop for the maize crop (solid blue line) and the legume (dotted blue line) assuming a rooting depth for the legume of 200 (b) and 60 cm (d), respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

minimum. A few well-described principles and relations for radiation interception, radiation distribution over competing species, radiation-use efficiency, water use and water storage were included in the model, solely with the intention to increase the understanding of the functioning of maize-legume intercropping systems under rain-fed conditions.

To maintain model simplicity, evaporation was not included in the model and right from the start of a simulation-run, roots of each species were assumed to have access to the available water in the soil profile up to their final rooting depth. The reasoning behind both choices is that both issues will mainly be relevant during the first few months after maize sowing, and this coincided with the period in which the rainfall was concentrated. Drying of the top-soil layer during the early stages will therefore be evened out by early rainfall events. In the simulations, the absence of evaporation during these early stages will be compensated for by additional losses due to percolation. After the initial stages, evaporative losses will become marginal with further canopy development (Ritchie, 1972). Similarly, it is anticipated that the first few months will provide sufficient time to produce a well developed rooting system throughout the soil profile. Full rooting depth will thus be reached before scarcity of water becomes an issue. The only situation in

which these simplifications might have obscured the simulations is with the simulations of lablab in the second season. In that season, a relatively early dry spell coincided with the introduction of lablab. It cannot be excluded that the poor establishment of lablab might have been aggravated by a not fully developed root system encountering a dry upper soil. Here, the relatively coarse set-up of the model hinders a true evaluation of the role of water scarcity during these early growth stages.

Evidently a major omission in the current study is the absence of data regarding soil moisture content. This would have provided an important second pillar, next to data on shoot dry weight, for validation of the simulation results. Evidently, there is need for measuring soil-water attributes in the field for experiments involving intercrops, where competition for soil-water is probable.

5. Conclusion

The current model analysis showed that under rain fed conditions of northern Tanzania, productivity of pigeonpea is far less sensitive to differences in annual precipitation than maize, mainly because of the greater rooting depth of pigeonpea. For lablab, the greater rooting depth greatly helped in increasing its productivity, but an early dry spell in the

second season, around the time of relay planting, reduced productivity compared to the first season. Intercropping of maize with pigeonpea or lablab is a productive cropping system resulting in over- yielding (i.e., intercrops having greater yield than mean of the sole crops), partly due to temporal niche differentiation, which gives rise to enhanced light capture. Spatial and temporal niche differentiation, through the greater rooting depth of the legumes compared to the maize greatly enhances the success of the system. In the maize-pigeonpea intercropping system, maize was influenced by the legume through a mild competition for light. In the season with low precipitation, water shortage for maize was further aggravated through competition for water. It is plausible that during drought periods, farmers should consider reducing the planting density of the secondary crop (the legume) in additive intercrops, to minimize reduction of maize yields as a result of competition for moisture. Maize influenced pigeonpea only through competition for light, as the rooting system of the legume allowed it to utilize the water stored in deeper soil layers. Competition for light was however severe, with a reduction in amount of radiation intercepted by pigeonpea of over 40% during their co-growth period. This reduction was partly compensated in the period after maize harvest, resulting in an overall reduction in amount of intercepted radiation of around 20% at physiological maturity. Our analysis further confirmed the strong radiation capturing ability of lablab, expressed when the legume was grown in pure stand. Delayed introduction of lablab in intercrop with maize was sufficient in avoiding competitive stress for radiation of the legume on maize, but

also resulted in poor establishment of the legume in the second season. Consequently, simultaneous maize-pigeonpea intercropping seems a more stable option. Our analysis confirms the important role of the deep rooting system of the legume for the success of maize-legume inter-cropping systems under rain-fed conditions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.
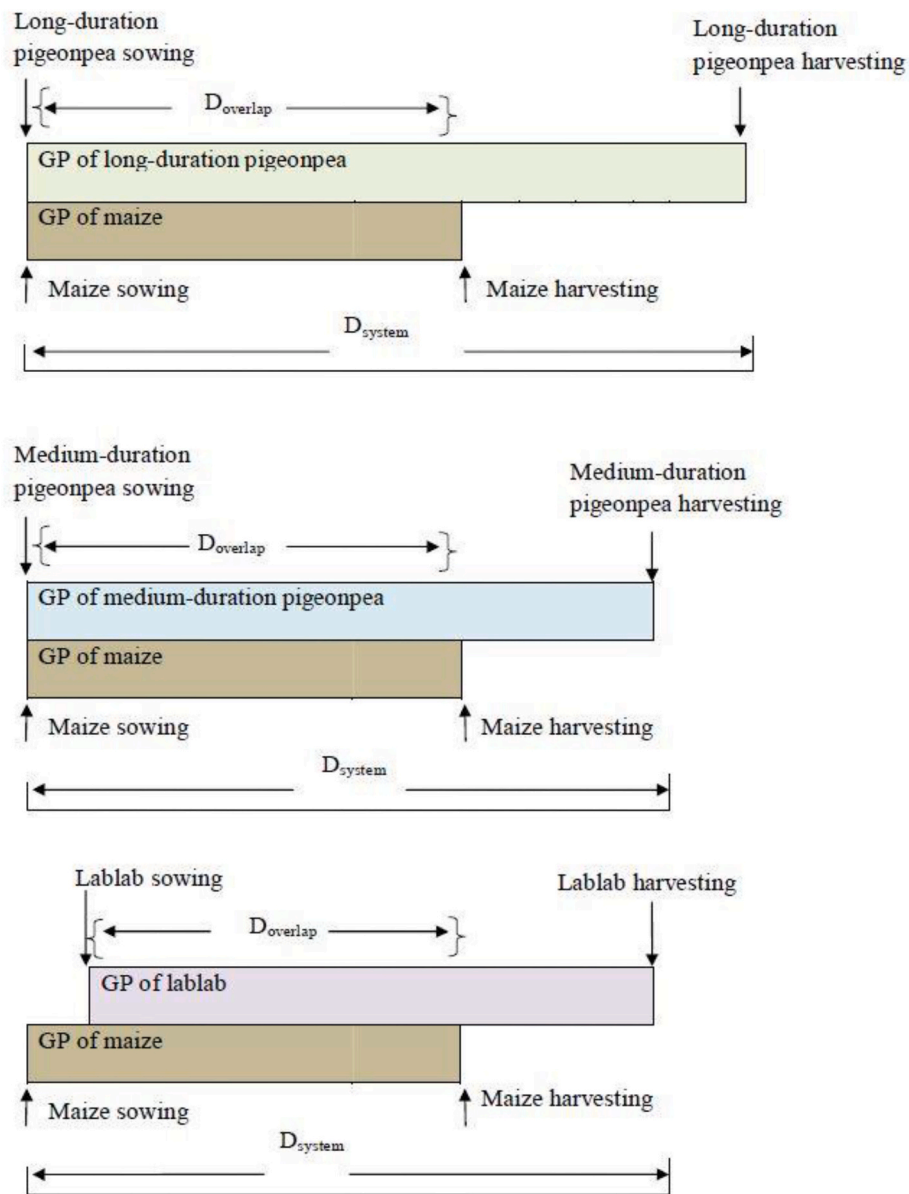
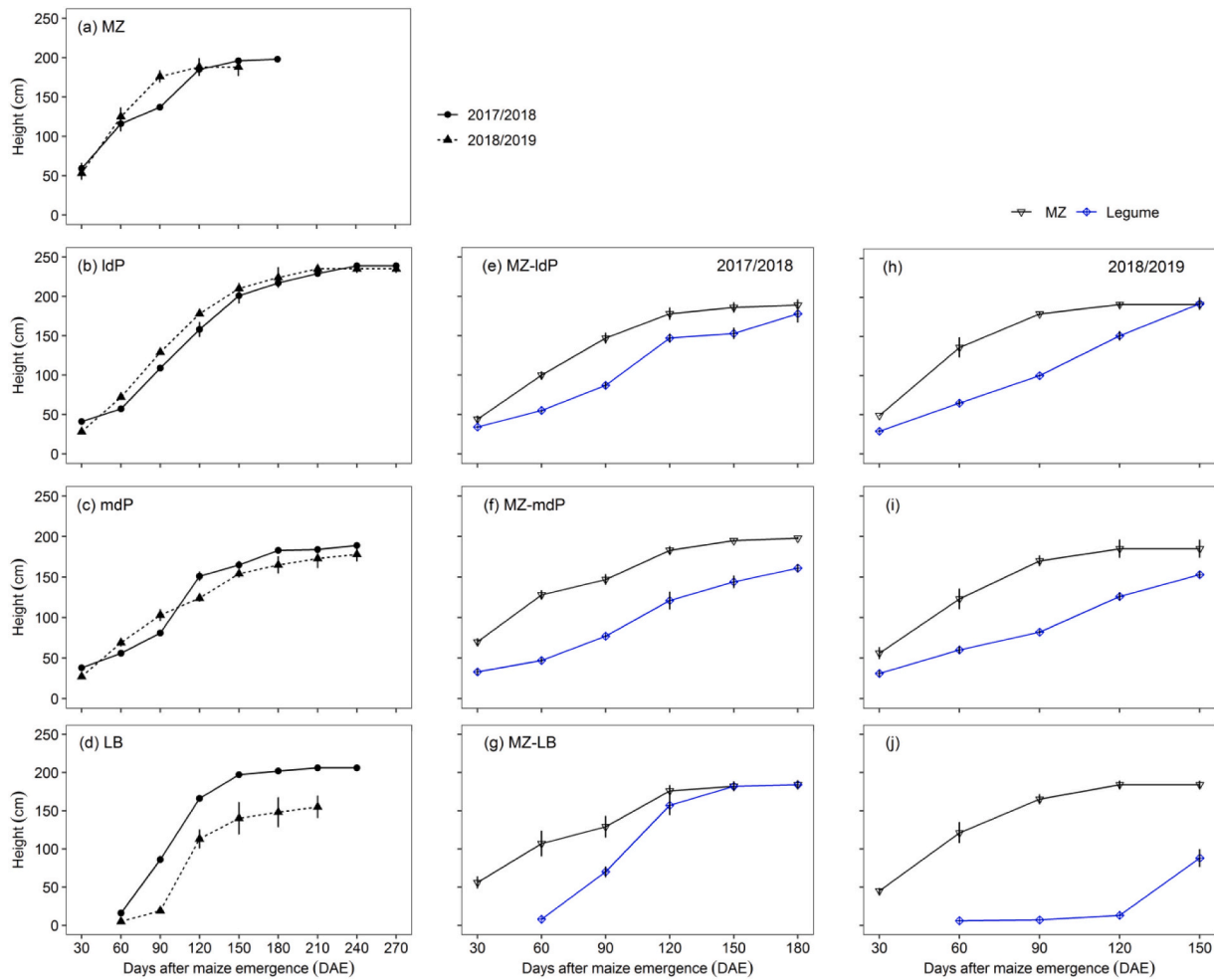**Data availability**

Data will be made available on request.

Appendix A. Appendices

Appendix 1. An illustration of temporal niche differentiation for maize-legume intercrops in Babati, northern Tanzania. GP = Growing period of the component crop; D_{system} = Total system duration; $D_{overlap}$ = Overlap duration (duration when the two crops were growing together).
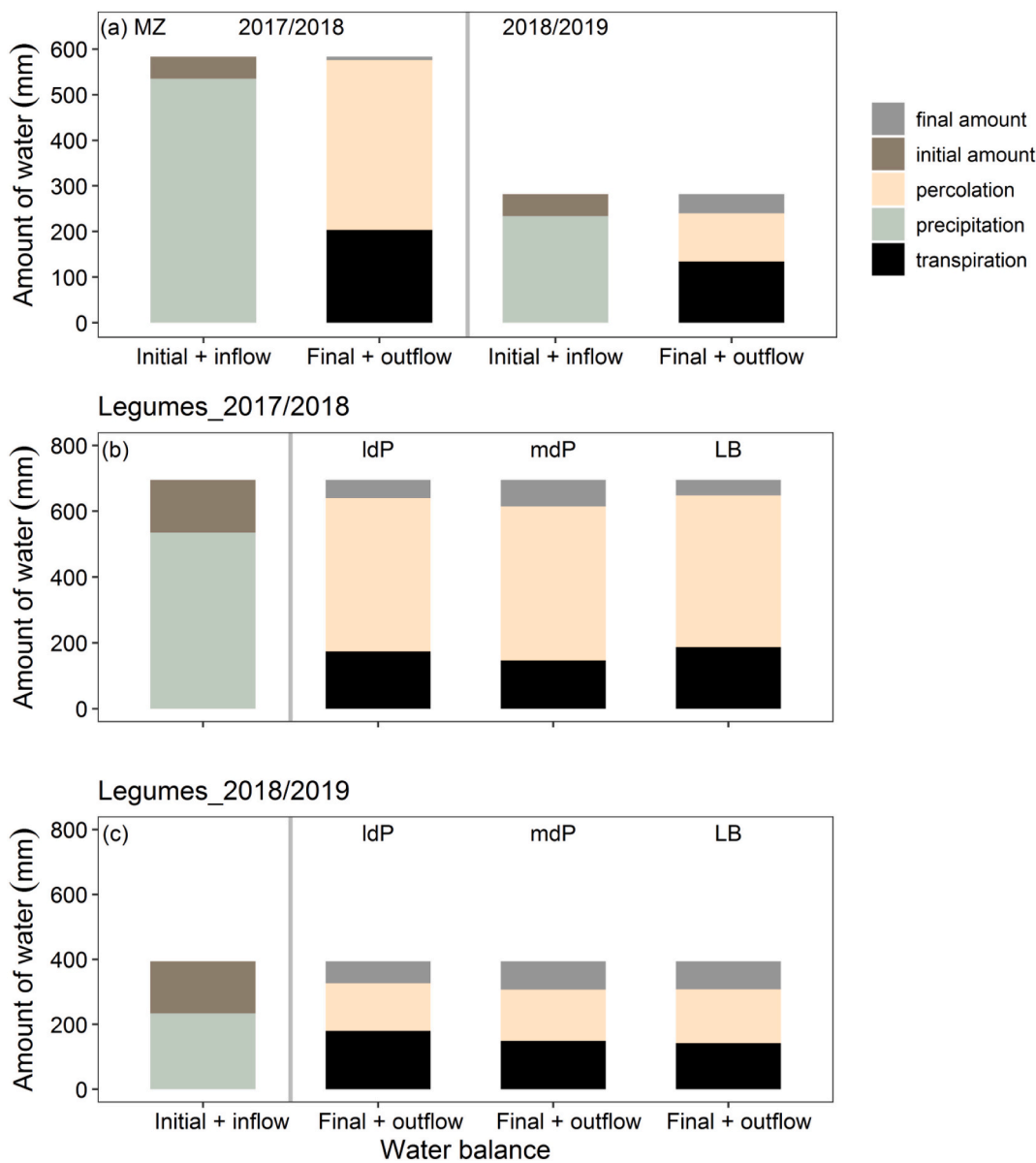
Appendix 2. Height development in sole crops of (a) maize (MZ), (b) long-duration pigeonpea (ldP), (c) medium-duration pigeonpea (mdP) and (d) lablab (LB) in the 2017/2018 and 2018/2019 season, and in intercrops of maize with long-duration pigeonpea (MZ-ldP), medium-duration pigeonpea (MZ-mdP) and lablab (MZ-LB) in the 2017/2018 (e-g) and 2018/2019 season (h-j) in Babati, northern Tanzania. In intercrops, height development is presented only for the duration when the two component crops were growing together.

Appendix 3. Illustration of the deep taproot of pigeonpea extending beyond 200 cm depth as monitored in Babati, northern Tanzania at 150 days after sowing of the crops.

Appendix 4. Simulation results for water balance in sole crops of (a) maize (MZ) in the 2017/2018 and 2018/2019 season, (b) long-duration pigeonpea (ldP), medium-duration pigeonpea (mdP) and lablab (LB) in the 2017/2018 season, and (c) the legumes in the 2018/2019 season in Babati, northern Tanzania. The input to the water balance comprises the initial amount of water in the soil (initial amount) and precipitation. The output includes transpiration, percolation, and the final amount of water that is left in the soil (final amount).

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