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Water and radiation use efficiencies explain the effect of potassium on the productivity of cassava

K.S. Ezui[a,b,*], A.C. Franke[b,c], P.A. Leffelaar[b], A. Mando[a], J. van Heerwaarden[b], J. Sanabria[d], J. Sogbedji[a,e], K.E. Giller[b]

[a] *International Fertiliser Development Centre (IFDC), North and West Africa Division, BP 4483 Lomé, Togo*
[b] *Plant Production Systems Group, Wageningen University, P.O. Box 430, 6700 AK Wageningen, The Netherlands*
[c] *Soil, Crop and Climate Sciences, University of the Free State, Bloemfontein 9300, South Africa*
[d] *International Fertiliser Development Centre (IFDC) – Headquarters, P.O. Box 2040, Muscle Shoals, Alabama 35662, USA*
[e] *School of Agronomy, University of Lomé, BP 1515 Lomé, Togo*

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ABSTRACT

We studied the effects of potassium (K) and its interactions with nitrogen (N), phosphorus (P) and harvest time on the productivity, water use efficiency (WUE) and radiation use efficiency (RUE) of cassava under rain-fed conditions. A field experiment was conducted during two consecutive years on K-deficient soils in Djakakope and on relatively K-rich soils in Sevekpota in Southern Togo, West Africa. Fifteen fertiliser combinations involving K and N rates of 0, 50 and 100 kg ha^{-1} each, and P rates of 0, 20 and 40 kg ha^{-1} were tested. Monthly measurements of leaf area index from 3 to 11 months after planting and daily weather data were used to estimate light interception, RUE, potential water transpiration and WUE of cassava. Overall WUE was 3.22 g dry matter kg^{-1} water transpired and RUE was 1.16 g dry matter MJ^{-1} intercepted photosynthetic active radiation (PAR). On the K-deficient soils, application of K increased WUE and RUE by 36–41% compared with 2.81 g dry matter kg^{-1} water transpired and 0.92 g dry matter MJ^{-1} intercepted PAR achieved without K, respectively. However, the effect of K on cassava growth depended on N availability. Applications of N had relatively weak effects on RUE and WUE, but induced a positive correlation between RUE/WUE and K mass fractions in the plant, and increased the cumulative amount of light intercepted by 11–51%, and the cumulative amount of water transpired through increased leaf area by 13–61%. No significant effect of P on WUE and RUE was observed. Increased cassava yields could be achieved under rain-fed conditions in West Africa through enhanced K management to increase RUE and WUE, along with sufficient N supply for improved light interception and water transpiration by the crop.

1. Introduction

Potassium is a key determinant of the productivity of root crops, including cassava (*Manihot esculenta*, Crantz). It plays many roles such as stimulating the photosynthetic activity of leaves, increasing the translocation of photosynthates to the storage roots (Hillocks et al., 2002), and regulating stomatal aperture and closure (Chérel et al., 2014), which helps to minimise water losses during drought. Potassium deficiency can lead to reduced yield and starch content of storage roots (Nair, 1986). A lack of K can also lead to an increased hydrogen cyanide (HCN) content of cassava roots, especially when N supplies are inadequate (Marschner and Marschner, 1995). High HCN content in storage roots constitutes a serious health hazard, since fresh cassava roots are popular food in West Africa.

Cassava productivity can be measured as function of the radiation use efficiency (RUE) and the amount of light intercepted (Pellet and El-Sharkawy, 1997). It can also be expressed as the product of water use efficiency (WUE) and the amount of water transpired (El-Sharkawy and Cock, 1986). Thus, a linear relationship is assumed under favourable conditions between biomass production and light interception, which defines RUE (Pellet and El-Sharkawy, 1997; Sinclair and Muchow, 1999; Veltkamp 1985), and between biomass production and water consumption by the crop, which determines WUE (Yao and Goué, 1992). The amount of water consumed by the crop can be calculated as the amount of rainfall received during the growing season (generally unreliable method, as it neglects

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[*] Corresponding author at: P.O. Box 430, 6700 AK, Wageningen, The Netherlands.
E-mail addresses: sezui@yahoo.com, guillaume.ezui@wur.nl (K.S. Ezui).

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drainage, run-off, and changes in soil moisture), or as the amount of water evapo-transpired, or transpired during the growing season. When WUE is based on water transpiration, it is also referred to as transpiration efficiency (Siahpoosh and Dehghanian 2012; Zhang et al., 1998). El-Sharkawy and Cock (1986) reported WUE value of 2.9 g total biomass DM per kg of water transpired for cassava. Reported values of WUE based on evapo-transpiration range from 0.4 to 4.8 g DM per kg water (Lemon (1969) as cited by Yao and Goué (1992)). Thus, it is important to define the units used to assess WUE. Pellet and El-Sharkawy (1997) obtained RUE values between 1.15 and 2.30 g DM per MJ intercepted light under a high rainfall regime of 1800 mm per year. Both light interception and water transpiration depend on the dynamics of the leaf area index (LAI) of the crop, highlighting the importance of LAI in assessing RUE and WUE. We are not aware of any studies to the RUE and WUE dynamics of cassava cultivars commonly promoted in West Africa such as TME 419 (highly promoted in the cassava belt in Nigeria, and referred to as “Gbazekoute” in Togo) and TMS 30572 (“Afisiafi” in Ghana, also grown in Nigeria). Assessing these parameters will inform cassava growth models simulating potential and water-limited yields of cassava in West Africa.

The application of K fertilisers increases cassava productivity on K-deficient soils (Ezui et al., 2016; Howeler 1991; Kang 1984; Sogbedji et al., 2015). It is however poorly documented how K affects the interaction between RUE, light interception and cassava productivity. Similarly, information on the effect of K on WUE and water transpiration by cassava productivity is scarce. It is unclear whether K is most active in light interception or in efficient use of light or in both. Moreover, the dynamics of K impacts on RUE and light interception as well as on WUE and water transpiration during cassava crop life as affected by the availability of N and P is poorly reported. This hinders our ability to improve K management in relation to N and P availability, needed to increase cassava productivity in West Africa. In this paper, we address these knowledge gaps.

This paper aims to assess the interaction between K and the availability of N and P on the RUE, light interception, WUE, transpiration, dry matter and harvest period of cassava under rain-fed conditions in West Africa. We hypothesised that: i) K increases either RUE or light interception through its interaction with N and P; ii) K increases WUE or water transpiration through its interaction with N and P.

2. Material and methods

2.1. Location, climate and soils

A field experiment was carried out at two locations in the Coastal Savannah agro-ecological zone of Southern Togo: Sevekpota (6.437^0N, 0.959^0E, with an elevation of 121 m above sea level − masl) and Djakakope (6.464^0N, 1.597^0E, 86 masl). This agro-ecological zone has a bi-modal rainfall distribution, which favours two growing seasons from mid-March through July and from September through mid-November. The experiment was conducted on Ferralsols (Ferrallitic soil with a depth over 200 cm) with a low exchangeable K capacity in Djakakope and on Acrisols (Ferruginous, shallow soils with a hard pan at about 50–80 cm depth) with a relatively better K supplying capacity in Sevekpota.

2.2. Experimental design

A randomised complete block design was used with three blocks of 15 NPK treatments defined to account for interactions among nutrients (Table 1). In total 45 plots of 5.6 × 8 m (44.8 m^2) were laid out at a planting density of 0.8 × 0.8 m (15,625 plants ha^{-1}) as recommended for cassava production in the area. Spacing was 1 m between plots and 2 m between blocks.

Table 1
N, P and K fertiliser rates in kg ha^{-1} in the experimental treatments.

Treatments	N	P	K
P1	0	0	0
P2	100	0	0
P3	0	0	100
P4	100	0	100
P5	0	40	0
P6	100	40	0
P7	100	40	100
P8	0	40	100
P9	0	20	50
P10	50	0	50
P11	50	20	0
P12	50	40	50
P13	50	20	100
P14	100	20	50
P15	50	20	50

2.3. Crop establishment and management

Gbazekoute (TME 419) was selected for this experiment as the main improved cultivar adopted by farmers in Southern Togo. It is generally grown for 10 to 12 months and yields on average 20–25 Mg ha^{-1} of fresh storage roots (30–40% dry matter content). This variety can produce 56 Mg ha^{-1} under optimal management (Odedina et al., 2009). Healthy cuttings were planted on May 22, 2012 (Year 1) and April 23, 2013 (Year 2) in Sevekpota, and May 25, 2012 and May 03, 2013 in Djakakope. Fertiliser was applied as urea (46% N), triple-super phosphate (TSP: 46% P_2O_5, 20% P) and muriate of potash (MOP: 60% K_2O, 50% K). Triple-super phosphate was given in one application at planting, whereas one-third of the urea and MOP were applied 21 days after planting (DAP). The remaining two-thirds were applied at 60 DAP just after weeding. Weeding was carried out four times during the growing season. Harvests in Sevekpota took place on the following dates: 127, 245 and 317 DAP in Year 1 and 139, 238 and 322 DAP in Year 2; in Djakakope the crop was harvested at 318 DAP in Year 1, and at 136, 231 and 322 DAP in Year 2.

2.4. Data collection

Soil samples were composed of five sub-samples per sampling depth before crop establishment on each site at the following depths: 0–20 cm, 20–40 cm and 40–60 cm. These samples were air-dried and ground to pass through a 2 mm mesh sieve. Particle size was determined using the hydrometer method, pH (H_2O, 1:2.5) using a glass electrode pH meter, organic carbon by the Walkley-Black method, total N using Kjeldahl digestion, and available P by the method of Bray 1. Exchangeable cations (K^+, Na^+, Ca^{2+} and Mg^{2+}) were extracted using a single extraction with dilute Silver-Thiourea (AgTU) solution (0.01 M Ag^+) and measured using an atomic absorption spectrophotometer for Ca^{2+} and Mg^{2+}, and a flame spectrophotometer for Na^+ and K^+. All analyses were conducted by the ICRISAT laboratory, Niamey, Niger.

Daily rainfall was measured on each site using manual rain gauges. Daily minimum and maximum temperatures, air humidity, and wind speed data were provided by the nearest weather station at Lomé (6.167^0N, 1.250^0E, 19.6 masl) for Sevekpota and Tabligbo weather station (6.583^0N, 1.500^0E, 40 masl) for Djakakope. Daily solar radiation was not measured in the area and therefore, satellite data provided by NASA were used (http://power.larc.nasa.gov/cgi-bin/cgiwrap/solar/agro.cgi?email=agroclim@larc.nasa.gov).

Canopy dimensions were measured monthly from 2 to 3 months after planting (MAP) to final harvest using measuring tapes. Light interception was assessed through measurements of the Photosynthetic Active Radiation (PAR) above and below the plant canopy from 3 to 11 MAP using Decagon's AccuPAR model LP-80 PAR/LAI Ceptometer. AccuPAR LP-80 measures PAR in the 400–700 nm waveband, and derives plant canopy leaf area index (LAI) from these readings. An external sensor was wired to it and held above the canopy with a stick, so that PAR above and below canopy are measured simultaneously. Measurements of PAR were taken at four locations in each plot. At each location, values of PAR below the canopy were measured in the space between two cassava plant stands at 40, 20 and 2 cm away from a selected plant stand. Thus, in total 12 PAR measurements were taken per plot and the average values (PAR above, PAR below) were retained. In addition, average values of the zenith angle of the sun (θ) and the beam fraction of the PAR above canopy (f_b) were provided by AccuPAR per plot assuming a default leaf angle distribution (x) value of 1, since no value of this parameter was provided for cassava. Assuming an ellipsoidal leaf angle distribution, we then used canopy dimension measurements to estimate x and used it to derive the light extinction coefficient (k_ext) and LAI of cassava following Norman (1979). Adjusting the x value to the range associated with the crop of interest and the growing conditions is important to ensure sound assessment of k_ext and LAI. The overall value of k_ext was determined by plotting ln (PAR below/PAR above canopy) versus LAI where the slope was calculated from the regression line following Kiniry et al. (2005). The method of determination of those parameters is described in Section 2.5.

At harvest, cassava storage root, stem and leaf weights were measured per plot. Each plot contained 10 rows with seven plants per row. Three successive harvests were made per plot. Each harvest concerned two consecutive rows, excluding border rows (10 plants harvested in total: five plants per row). From the harvested plants, three per plot were randomly selected for the following measurements: number of leaves, leaf weight, number of leaf scars, number of storage roots, storage root weight. Samples of storage roots, stems and leaves per harvested plot were oven dried at 68–70 °C until constant weight and analysed for their NPK content by ICRISAT. Dried plant organs were ground and digested in H_2SO_4–salicylic acid – H_2O_2–Selenium solution. Total N concentration was measured from this extract using a colorimetric method based on Berthelot's reaction (Sommer et al., 1992), total P concentration based on the method of the molybdo-phosphate complex with ascorbic acid as a reducing agent and K concentration by atomic absorption spectrophotometry using Perkin Elmer model Analyst 400 (Houba et al., 1995).

2.5. Parameters calculations

The dry matter (DM) of the total biomass, also referred to as biomass produced, was obtained by summing up DM yield of storage roots, stems, harvested leaves and fallen leaves for each treatment. Dry matter of fallen leaves was estimated at a given harvest time as:

$$\begin{aligned}&\mathit{Fallen\ leaves}(\mathrm{kg\,ha^{-1}}) = \mathit{average\ single\ leaf\ weight}[\mathrm{kg}] \times \\ &\quad \mathit{number\ of\ leaf\ scars}[\mathrm{ha^{-1}}] \qquad (1)\end{aligned}$$

$$\begin{aligned}&\mathit{Average\ single\ leaf\ weight}(\mathrm{kg}) = \mathit{harvested\ leaves\ weight}[\mathrm{kg\,ha^{-1}}] \\ &\quad /\mathit{number\ of\ harvested\ leaves}[\mathrm{ha^{-1}}] \qquad (2)\end{aligned}$$

Dry matter of storage roots, stems, and harvested leaves were calculated as follows:

$$\begin{aligned}&DM(\mathrm{kg\,ha^{-1}}) = (\mathit{DM\ per\ plot}[\mathrm{kg}]/\mathit{number\ of\ plants\ harvested\ per\ plot}) \\ &\quad \times \mathit{number\ of\ plants\ per\ hectare}[\mathrm{ha^{-1}}] \qquad (3)\end{aligned}$$

The calculation of light interception ($IPAR$ expressed in MJ PAR m^{-2}) was based on the assumptions that PAR exponentially decreases with depth, that $IPAR$ results from the difference between PAR above (incident radiation) and PAR below the canopy and that PAR above is about 50% of the daily total radiation (DTR):

$$IPAR = 0.5 \text{ x } DTR \text{ x } (1 - e^{-k\_ext \text{ x } LAI}) \qquad (4)$$

DTR is expressed in $\mathrm{MJ\,m^{-2}\,d^{-1}}$, 0.5 gives the ratio MJ PAR $\mathrm{MJ^{-1}}$ DTR, LAI is the leaf area index in m^2 leaf m^{-2} ground, and k_ext the light extinction coefficient. We calculated k_ext for each AccuPAR measurement using Eq. (5) assuming an ellipsoidal leaf angle distribution (Campbell, 1986):

$$k\_ext = \frac{\sqrt{x^2 + \tan\theta^2}}{x + 1.744(x + 1.182)^{-0.733}} \qquad (5)$$

θ is the zenith angle of the sun estimated by AccuPAR; x is the leaf angle distribution parameter, defined as the ratio of horizontal to vertical axes of ellipsoidal leaf distribution (Campbell, 1986). We calculated x based on cassava canopy dimensions measurement as:

$$x_i = \frac{CW1_i + CW2_i}{2CT} \qquad (6)$$

$CW1$ and $CW2$ (cm) are the largest and the smallest horizontal width of the canopy; CT (cm) is the vertical thickness of the canopy. $CW1$, $CW2$ and CT were measured on each plot on the same day that PAR measurements took place.

With the measured x and the resulting k_ext values, LAI was determined using Eq. (7) derived from the model for canopy light transmission by Norman and Jarvis (1975). The mechanism for retrieving LAI from this model while accounting for leaf angle distribution, canopy transmission and scattering is described in the operational guide of the AccuPAR ceptometer (Decagon Devices, 2004).

$$LAI = \frac{\left[\left(1 - \frac{1}{2k\_ext}\right) f_b - 1\right] ln\tau}{A(1 - 0.47f_b)} \qquad (7)$$

f_b is the beam fraction of the incident radiation, τ the ratio PAR below/PAR above canopy. Values of f_b, PAR below and PAR above canopy are measured by AccuPAR. Since the variables of Eq. (7) were measured, we refer to the calculated LAI values as "measured LAI" throughout the paper. A is a term for primary and secondary canopy absorption, that is empirically related to the leaf absorptivity in the PAR band:

$$A = 0.283 + 0.785a - 0.159a^2 \qquad (8)$$

The leaf absorptivity is denoted as a. We used an a value of 0.85 (Sinclair and Muchow, 1999).

For the calculation of RUE, cumulative light interception (cumulative $IPAR$, MJ PAR m^{-2}) was derived by numerical integration of $IPAR$ over time with measured LAI values (Eq. (9)). A Fortran Simulation Translator (FST) program was developed to facilitate the implementation of this calculation.

$$\mathit{Cumulative\ IPAR} = \int_0^t (0.5 \text{ x } DTR(t) \text{ x } (1 - e^{-k\_ext \text{ x } LAI(t)}))dt \qquad (9)$$

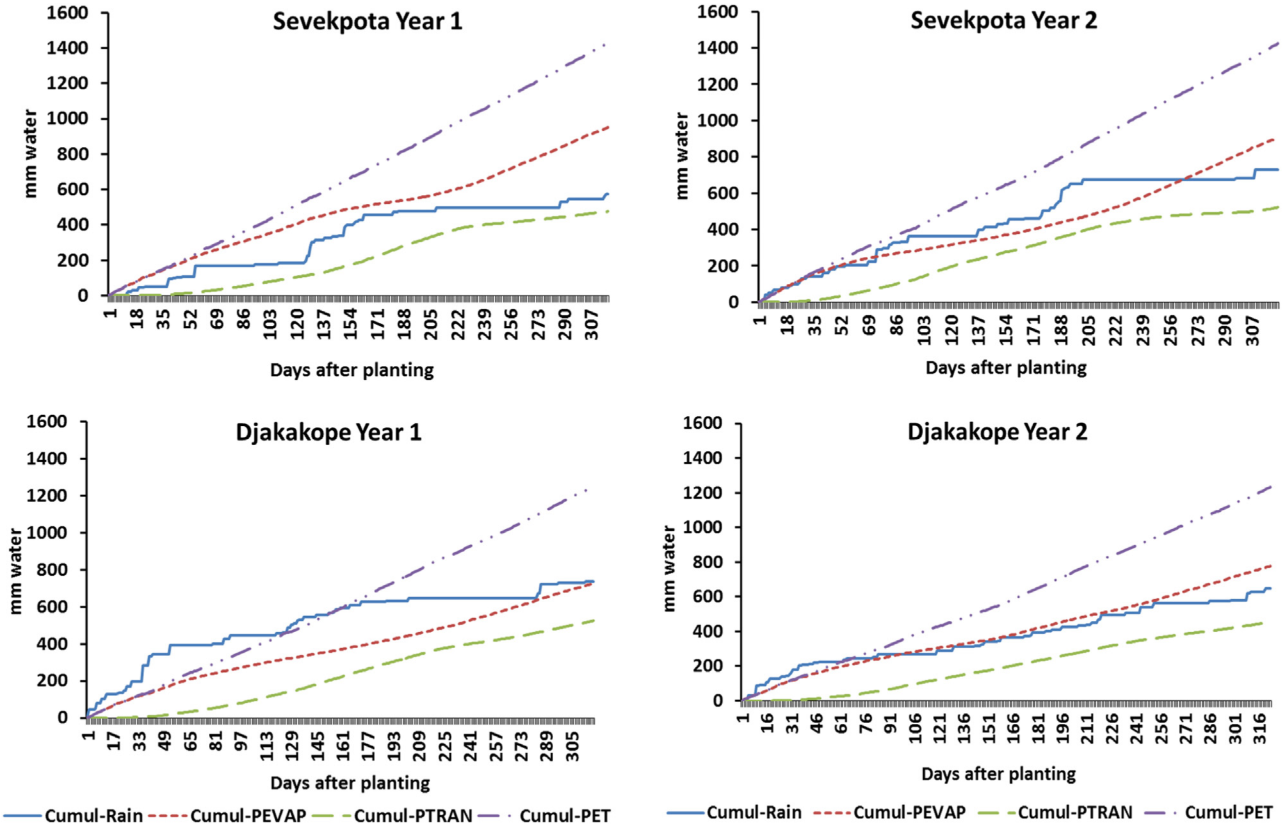

Fig. 1. Cumulative rainfall (Cumul-Rain), potential evaporation (PEVAP), potential transpiration (PTRAN) and potential evapotranspiration (PET) from planting to final harvest in Sevekpota and Djakakope in two years.

Since the LAI(t) values are measured only at certain points in time (monthly from 3 to 11 MAP), LAI(t) in between these points were estimated by linear interpolation.

Cumulative *IPAR* calculated on a daily basis from planting to a specific harvest was plotted against the associated amount of biomass produced (leaves + stems + storage roots + fallen leaves). Here, we combined all treatments. The slope of the linear regression was used to estimate RUE (g DM MJ^{-1} IPAR) for the whole cropping season (Pellet and El-Sharkawy, 1997; Sinclair and Muchow, 1999; Veltkamp, 1985). The intercept of this regression line was set to zero given there is no cassava biomass production without light interception. To assess the dynamics of RUE between two consecutive harvests, changes in RUE were estimated by dividing the difference in biomass by the difference in cumulative *IPAR* between the two harvests. To investigate the effect of fertiliser and harvest time, RUE was also calculated for individual treatments at a given harvest by dividing biomass by accumulated *IPAR*.

Water use efficiency (g DM kg^{-1} water) was estimated at each harvest as the weight of the biomass produced from planting over the cumulative amount of water transpired from planting. We limited the calculation of WUE to potential water transpiration since actual transpiration was not measured. This is likely to result in smaller WUE compared with WUE based on actual transpiration, especially under drought conditions. Potential transpiration (*PTRAN*) as well as potential evaporation (*PEVAP*) were based on the Penman equation (Penman, 1948) using daily LAI values (Appendix A). Cumulative *PTRAN* and cumulative *PEVAP* were obtained by integrating *PTRAN* and *PEVAP* over time from planting to the different harvests. We assumed LAI to be zero at emergence at about 15 days after planting. The cumulative *PTRAN* at each harvest was plotted against the amount of biomass produced at that harvest. The slope of the regression line of this graph is taken as the WUE for cassava. As in the case of RUE, WUE was also calculated for individual treatments at a given harvest by dividing the accumulated biomass by the accumulated *PTRAN*. The sum of *PTRAN* and *PEVAP* was denoted as potential evapotranspiration (*PET*).

2.6. Statistical analyses

Genstat statistical package (version 17) was used for analysis of variance and regression using mixed models. The analyses were done for each experimental year and site separately, since site and year were confounded and only one final harvest was done in Djakakope Year 1. Hence, a mixed linear model was used to analyse the data from Djakakope in Year 1 using N, P, K, and their interactions as fixed factors and block as random factor. For Year 2 in Djakakope and Year 1 and Year 2 in Sevekpota where three consecutive harvests were done, we used repeated measurements with plots nested in blocks as subject, harvest time expressed in MAP as time points and harvest time x (N, P, K, and their interactions) as fixed factors. These models were fitted for correlation within subjects across time using antedependence model order 1 (Kenward, 1987), which accounts for heterogeneity in time. Pearson correlation analyses were conducted to assess the significance of the relationship between RUE, WUE and K mass fractions of cassava total biomass.

3. Results

3.1. Cassava growing conditions and LAI dynamics

3.1.1. Water availability and soil characteristics

In Sevekpota in Year 1, less rain was received than in Year 2 (574 and 731 mm rain water), unlike in Djakakope where Year 1

Table 2
Soil physical and chemical characteristics before crop establishment on the fields in Sevekpota and Djakakope at 0–20, 20–40 and 40–60 cm depth.

	Sevekpota						Djakakope					
	2012, Field 1			2013, Field 2			2012, Field 1			2013, Field 2		
	0–20	20–40	40–60	0–20	20–40	40–60	0–20	20–40	40–60	0–20	20–40	40–60
SOC, g kg^{-1}	11.5	9.2	6.4	12.2	7.3	6.7	6.2	3.6	2.7	4.7	3.1	2.7
SON, g kg^{-1}	0.9	0.6	0.5	0.8	0.5	0.5	0.4	0.3	0.3	0.3	0.2	0.2
Na^+, mmol kg^{-1}	1.15	1.04	0.50	0.40	0.41	0.44	0.09	0.09	0.09	0.14	0.10	0.11
K^+, mmol kg^{-1}	3.52	2.19	1.12	1.35	0.98	1.43	0.38	0.28	0.26	0.66	0.21	0.15
Ca^{2+}, mmol kg^{-1}	18.1	14.5	16.0	13.6	14.3	15.7	18.2	13.6	14.4	17.3	14.9	15.7
Mg^{2+}, mmol kg^{-1}	5.32	3.51	5.43	4.47	5.84	4.86	7.1	6.8	7.7	7.0	4.8	6.5
Sand, g kg^{-1}	536	399	306	680	565	499	835	745	622	858	767	704
Silt, g kg^{-1}	163	147	152	150	101	95	52	46	43	45	37	32
Clay, g kg^{-1}	301	454	542	170	334	406	113	209	335	97	196	264
pH H_2O, 1:2.5	6.5	6.3	6.2	6.5	6.3	6.2	6.5	6.1	6.0	6.5	6.0	5.8
P-Bray-I, mg kg^{-1}	1.9	1.0	0.7	3.2	1.0	0.7	4.5	2.7	1.9	10.4	3.1	1.7
P-total, mg kg^{-1}	189	143	116	202	177	176	155	160	194	194	204	202

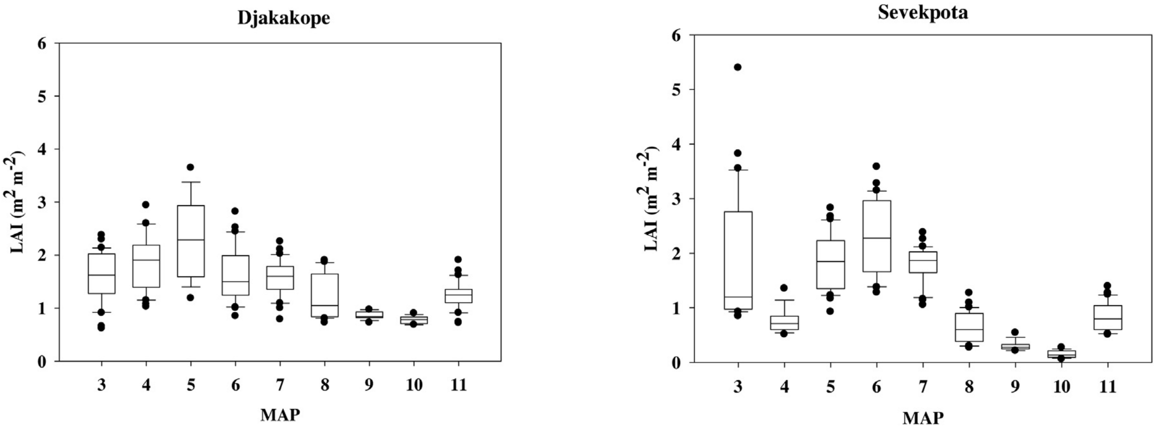

Fig. 2. Leaf Area Index (LAI) dynamics at Djakakope and Sevekpota (averages for years and for treatments). Whiskers indicate 10th and 90th percentiles. The black dots indicate outliers.

was wetter than Year 2 (736 and 649 mm rain water) (Fig. 1). Accumulated rainfall was above potential evapotranspiration (PET) at the beginning of the cropping season in Djakakope, especially in Year 1. This indicates a sufficient supply of water during the early phase of vegetative growth. In Sevekpota, the rainfall curve was continuously below the PET curve, especially in Year 1, probably resulting in water stress. Potential evaporation (PEVAP) was greater than potential transpiration (PTRAN) on both sites. The overall ratio of PTRAN over PET varied between 0.17 and 0.60, and averaged 0.35, thereby indicating about 65% soil water evaporation across the growing season.

Soil chemical characteristics show large differences between the two sites (Table 2). Sevekpota site had larger soil organic carbon (SOC) and exchangeable K and Na contents but less available P and exchangeable Mg than in Djakakope. Soil Mg, Ca and Na contents are medium on both sites (Howeler, 2002). The pH was slightly below 7 at both sites. Soil textures were sandy clay loam to sandy loam in Sevekpota, and loamy sand to sandy in Djakakope.

3.1.2. *LAI dynamics*

The determination of LAI required the prime assessment of light extinction coefficient (*k_ext*, Eq. (5)), which dependent on leaf angle distribution parameter (x). Estimated x values ranged from 1.3 to 4.0 (Table 3), hence larger than 1, which was the default value of AccuPAR. These values of x were quite similar from 2 to 5 or 6 MAP with an average value of 1.6 (1–6 MAP), but tremendously increased from 7 to 8 MAP with an overall average of 2.1. We used an x value of 1.6 for the estimation of *k_ext* and LAI since canopy establishment of cassava takes place during the first 6 MAP (Alves, 2002). Calculated *k_ext* values range of 0.66–0.77 for different treatments with an overall value of 0.66. A comparable range of k values of 0.50–0.78 for cassava was reported earlier (Pellet and El-Sharkawy, 1997).

Table 3
Estimated cassava leaf angle distribution (x) values from 2 to 8 MAP (averages over years and treatments).

MAP	mean	STDEV
2	1.6	0.29
3	1.3	0.28
4	1.4	0.31
5	1.8	0.64
6	2.1	0.96
7	2.6	1.03
8	4.0	2.11
average 2–8 MAP	2.1	0.80
average 2–6 MAP	1.6	0.50

Calculated LAI values spread from 0.62 to 3.64 m^2 m^{-2} in Djakakope, against 0.06 to 3.82 m^2 m^{-2} in Sevekpota. Peak LAI values were reached around 5 MAP in Djakakope and 6 MAP in Sevekpota (Fig. 2). The development of LAI over time is related to the dynamics of the cassava canopy in response to water availability. The months with low LAI values around 4 MAP in Sevekpota and from 8 to 10 MAP at both sites (Fig. 2) coincided with dry seasons in August and December to February. The canopy suffered more from LAI reduction at 4 MAP in Sevekpota than in Djakakope, probably because the soil in Sevekpota is shallow with an impervious pan at about 60 cm depth. The soil in Djakakope is deeper (>200 cm), offering the crop the possibility to explore deeper soil layers to access

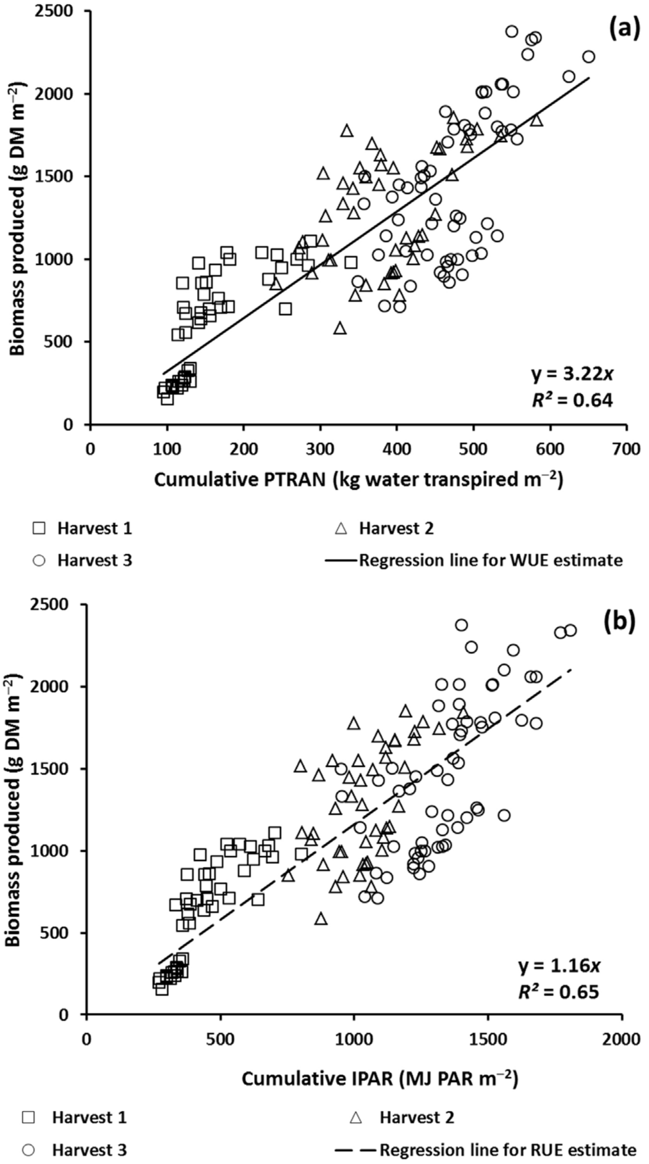

Fig. 3. Relationship between the cumulative cassava biomass produced and the cumulative amounts of (a) PTRAN and (b) IPAR for different harvest times, and the regression lines indicating WUE (slopes of the lines). Each point corresponds to the average of a treatment at a given site, harvest, time and year.

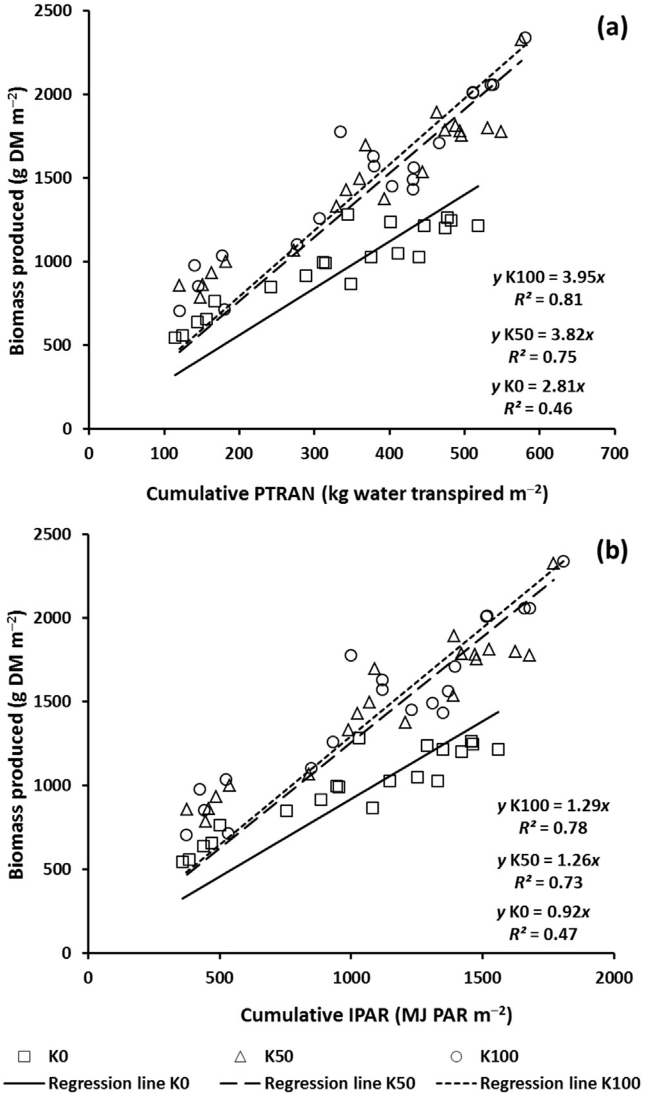

Fig. 4. Response of cassava biomass production to (a) PTRAN and (b) IPAR accumulation as affected by K rates in Djakakope, and the related (a) WUE and (b) RUE as indicated by the slopes of the regression lines. Each point corresponds to the average of a fertiliser treatment at a given harvest, time and year.

water during drought. In Djakakope, LAI in the dry season (8–10 MAP) did not drop as strongly as in Sevekpota. At both sites, LAI rose between 10 and 11 MAP because rain resumed before harvest at 11 MAP. It is common practice in the Coastal Savanna zone of West Africa to perform the final harvest after rain has resumed to ensure the soil is sufficiently wet to harvest and prevent the storage roots from breaking.

The responses of LAI to fertiliser applications were stronger with N than with K. Nitrogen applications significantly increased LAI at both sites (data not shown, $P = 0.030$ and <0.001 in Years 1 and 2 in Djakakope, and $P = 0.010$ and <0.001 in Years 1 and 2 in Sevekpota). Potassium also significantly increased LAI (data not shown), but only in Year 2 in Djakakope ($P = 0.001$). No significant effect of P on LAI was observed.

3.2. Effect of N, P and K on WUE, PTRAN and PET

Water use efficiency was estimated from the response of cassava biomass DM to cumulative PTRAN by the crop (Fig. 3a). This resulted in a WUE of 3.22 g biomass DM produced per kg water transpired over the cropping season, with a coefficient of determination (R^2) of 0.64. WUE was 3.58 and 2.99 g DM per kg water in Djakakope ($R^2 = 0.64$) and Sevekpota ($R^2 = 0.68$), respectively. In Years 1 and 2, WUE values were 3.39 ($R^2 = 0.56$) and 3.71 ($R^2 = 0.59$) in Djakakope, and 2.20 ($R^2 = 0.92$) and 3.61 ($R^2 = 0.86$) g DM per kg water in Sevekpota (data not shown). Water use efficiency obtained at each harvest for individual treatments varied from 1.54 to 7.12 g DM per kg water transpired (Fig. 3a). The variability in WUE within sites can be ascribed to the effect of harvest time since WUE appeared to vary across the cropping season. Greater overall WUE was obtained (graphically) at Harvest 1, decreasing to smaller values at Harvests 2 and 3 (3.89, 3.31 and 3.11 g DM kg^{-1} water transpired at Harvest 1, 2 and 3 ($P < 0.001$) (data not shown). The decline in WUE was also observed between consecutive harvests (Table 4). Water use efficiency was larger between planting and Harvest 1, than between Harvests 1 and 2, and between Harvests 2 and 3 in Year 2 in Djakakope and Sevekpota. The opposite trend was observed from planting to Harvest 2 in Sevekpota during Year 1, whereas the lack of increase in biomass between Harvests 2 and 3 negatively

Table 4
Change in storage roots and total biomass produced (Mg DM ha^{-1}), accumulated potential transpiration (PTRAN, kg water, m^{-2}), potential evaporation (PEVAP, kg water, m^{-2}), water use efficiency (WUE, g biomass DM kg^{-1} water transpired), accumulated light (IPAR, MJ PAR intercepted m^{-2}) and radiation use efficiency (, g biomass DM MJ^{-1} IPAR) between consecutive harvests and the overall cropping season. H1-3 stand for Harvest 1–3, PL indicates time of planting.

Site/Year	Period	Storage roots	Biomass	PTRAN	PEVAP	WUE	IPAR	RUE
Djakakope								
1	PL-H3	7.8	16.5	491	768	3.33	1518	1.07
2	PL-H1	4.4	7.9	149	332	5.36	450	1.77
2	H1-H2	3.2	5.0	175	205	2.80	524	0.94
2	H2-H3	0.6	2.2	127	246	1.67	384	0.55
2	PL-H3	8.2	15.1	451	783	3.32	1357	1.10
	P value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Sevekpota								
1	PL-H1	1.1	2.5	115	434	2.18	319	0.79
1	H1-H2	4.5	7.1	283	256	2.49	731	0.96
1	H2-H3	−1.2	−0.2	68	271	−0.27	187	−0.10
1	PL-H3	4.5	9.4	466	961	2.01	1237	0.76
	P value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
2	PL-H1	4.7	8.7	226	363	4.00	569	1.57
2	H1-H2	5.0	7.4	209	240	3.57	531	1.40
2	H2-H3	4.2	9.1	272	567	3.29	705	1.27
2	PL-H3	8.9	17.8	498	930	3.57	1274	1.39
	P value	<0.001	<0.001	<0.001	<0.001	0.027	<0.001	0.009

Table 5
Accumulated potential transpiration (PTRAN, kg water m^{-2}), potential evapotranspiration (PET, kg water m^{-2}) and WUE (g biomass DM kg^{-1} water transpired) as affected by N, P and K fertiliser applications and their significant interactions with harvest time in Djakakope and Sevekpota. For each fertiliser rate of a given nutrient, all rates of the two other nutrients are included.

Main effects/Year	Factor levels	Djakakope			Sevekpota		
		PTRAN	PET	WUE	PTRAN	PET	WUE
N effects							
1	0N	417	1271	3.26	297	1026	2.07
1	50N	529	1251	3.48	335	1021	2.15
1	100N	525	1252	3.31	347	1018	2. 37
	P value	<0.001	<0.001	0.338	0.906	0.907	0.539
2	0N	267	865	3.73	290	1033	3.99
2	50N	318	856	4.11	401	1016	3.70
2	100N	339	853	3.81	468	1005	3.44
	P value	<0.001	<0.001	0.051	<0.001	<0.001	0.021
P effects							
1	0P	477	1261	3. 44	331	1021	2.23
1	20P	524	1252	3.40	326	1022	2.13
1	40P	471	1262	3.22	323	1022	2.24
	P value	0.479	0.492	0.823	0.193	0.281	0.577
2	0P	300	859	3.73	391	1017	3.68
2	20P	308	858	4.13	403	1015	3.49
2	40P	315	857	3.83	365	1021	3.85
	P value	0.788	0.813	0.296	0.029	0.020	0.277
K effects							
1	0 K	451	1266	2.66	323	1022	2.14
1	50 K	517	1253	3.58	327	1022	2.18
1	100 K	503	1256	3.76	330	1021	2.28
	P value	0.181	0.156	<0.001	0.765	0.703	0.373
2	0 K	288	862	3.14	368	1021	3.74
2	50 K	317	856	4.22	411	1014	3.77
2	100 K	318	856	4.26	379	1019	3.51
	P value	0.301	0.297	<0.001	0.730	0.822	0.162
Significant interactions (*P* value)							
2	Harvest x N	0.001	0.002				0.092
2	Harvest x N x K			0.024			
2	P x K						0.062

affected WUE. The variability in WUE can also be attributed to the response of the crop to different fertiliser rates (Table 5).

Nitrogen applications did not significantly affect WUE in Year 1, but led to decreased WUE in Sevekpota in Year 2 (Table 5). In Year 2, PTRAN increased and PET declined in response to N applications. Phosphate fertiliser did not have any significant effect on WUE of cassava at either site. Phosphate fertiliser did not affect PTRAN and PET, except for Year 2 in Sevekpota, where 20 kg P ha^{-1} improved PTRAN and reduced PET in contrast to 0 and 40 kg P ha^{-1}. Potassium addition improved WUE over the cropping season in Djakakope in both years (Fig. 4a; Table 5). The slope of the WUE regression lines was larger at 50 and 100 kg K ha^{-1} than without K (K0). Potassium

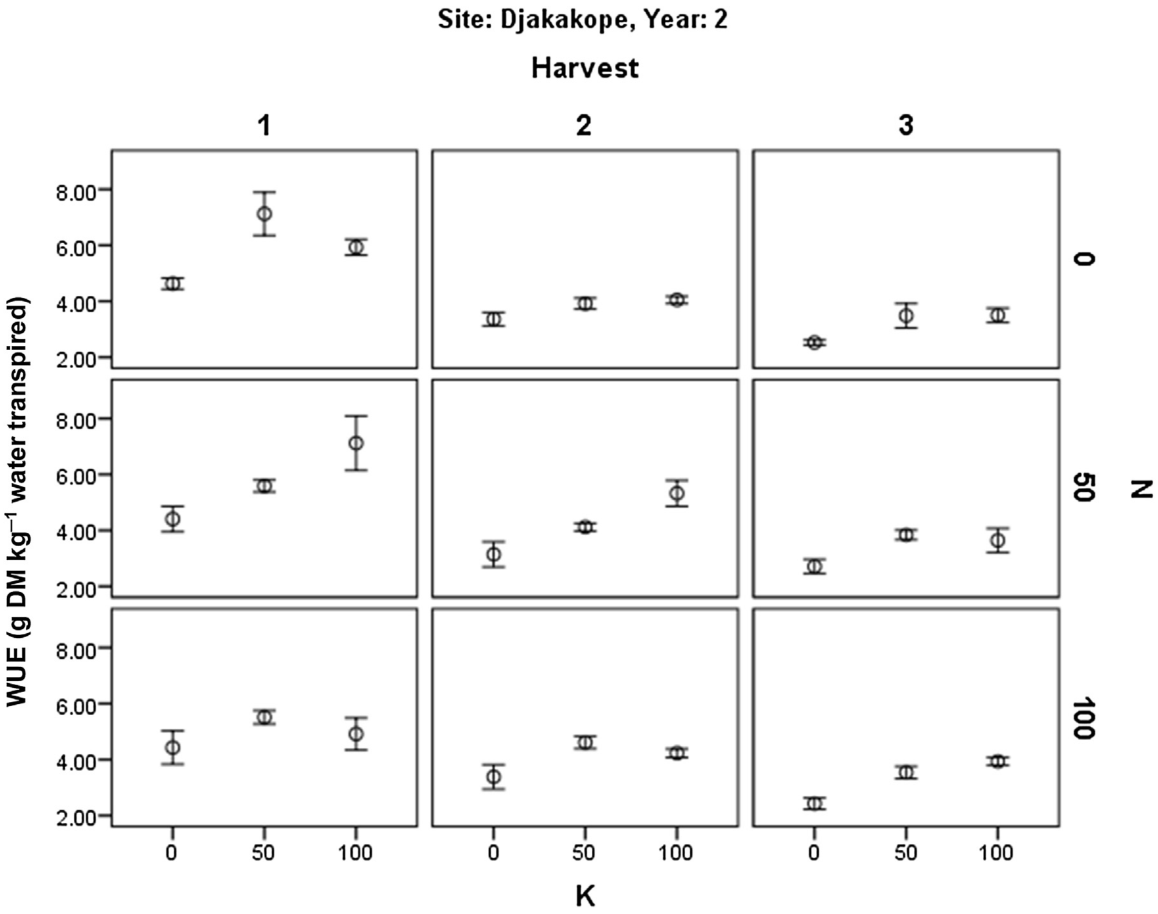

Fig. 5. WUE as affected by interactions between K and N rates (kg ha^{-1}) and different harvest times in Djakakope in Year 2. Each point corresponds to the mean WUE value at a given K and N rate at a specific harvest time. The bars around the means represent the SEM.

fertiliser application did not affect WUE in Sevekpota, and had no significant effect on PTRAN and PET.

There were no significant interactions of N, P and K on WUE, except between N, K and harvest time in Djakakope in Year 2 (Table 5, Fig. 5). Nitrogen application and harvest time influenced the effect of K on WUE. Without added N, the largest WUE was attained at 50 kg K ha^{-1}, irrespective of harvest time (Fig. 5). With the application of 50 kg N ha^{-1}, the largest WUE was observed at 100 kg K ha^{-1} at Harvest 1 and 2, and at 50 kg K ha^{-1} at Harvest 3. When 100 kg N ha^{-1} was applied, the largest WUE was obtained at 50 kg K ha^{-1}.

3.3. *Effects of N, P and K on RUE, IPAR, biomass and storage roots production*

A RUE of 1.16 g DM per MJ PAR intercepted was derived graphically for the cropping season on both sites ($R^2 = 0.61$) (Fig. 3b). Site-specific RUE values were 1.17 ($R^2 = 0.63$) in Djakakope and 1.15 g DM per MJ ($R^2 = 0.64$) in Sevekpota. RUEs for individual treatments were variable and ranged from 0.55 to 2.30 g DM per MJ IPAR (Fig. 3b). The small RUEs emanated from poor biomass production, especially in Sevekpota in Year 1, during the period of planting to Harvest 1 and from Harvest 2 to Harvest 3 (Table 4). Like in the case of WUE, RUE declined between consecutive harvests (Table 4). RUE declined from Harvests 1 to 3, respectively as: 1.47, 1.24 and 1.10 g DM biomass MJ^{-1} IPAR ($P < 0.000$, data not shown).

The effects of N fertiliser on RUE were not significant, except for Year 2 in Djakakope, where the largest RUE was attained with the application of 50 kg N ha^{-1} (Table 6). Nitrogen additions did increase storage roots DM, biomass DM and IPAR in both years in Djakakope and in Year 2 in Sevekpota. There was no significant effect of P fertiliser on RUE, nor on storage roots DM, biomass DM and IPAR in Djakakope. This was also the case in Sevekpota, except for IPAR in Year 2, where the application of 20 kg P ha^{-1} generated the largest average IPAR. Potassium fertiliser increased RUE, as well as storage roots and biomass DM in Djakakope. The smallest values of RUE were found in treatments without fertiliser, especially in Djakakope, where RUE was 0.92 g DM MJ^{-1} IPAR without K application, and 1.26 and 1.29 with the application of 50 and 100 kg K ha^{-1}, respectively (Fig. 4b). However, K did not significantly affect IPAR at this site. Likewise, K applications did not influence IPAR and RUE in Sevekpota. K application did increase storage roots and biomass production at this site.

Most nutrient interaction effects on RUE were observed in Year 2. In Djakakope the interaction between K, N and harvest time on RUE was significant. The strongest responses of RUE to K were obtained at Harvest 1 at smaller N rates (0 and 50 kg ha^{-1}) (Data not shown since the trends were comparable to Fig. 5). At the same site, interaction effects between harvest time and N were significant for biomass production and IPAR, and so was the interaction between harvest time and K on storage roots and biomass production. In Sevekpota, the only significant interaction effect on RUE was observed between P and K.

3.4. *Relationship between cassava tissue K mass fractions and WUE and RUE*

The relationship between cassava tissue K and WUE and RUE followed a polynomial curve (Fig. 6). Water use efficiency and RUE increased as plant tissue K increased, and reached their maxi-

Table 6
Storage roots and total biomass produced (Mg DM ha^{-1}), IPAR (MJ PAR intercepted m^{-2}) and RUE (g DM MJ^{-1} IPAR) as affected by N, P and K fertiliser applications and their significant interactions with harvest time in Djakakope and Sevekpota. For each fertiliser rate of a given nutrient, all rates of the two other nutrients are included.

Main effects/Year	Factor level	Djakakope				Sevekpota			
		Storage roots	Biomass produced	IPAR	RUE	Storage roots	Biomass produced	IPAR	RUE
N effects									
1	0N	6.33	13.60	1308	1.04	3.24	6.16	799	0.77
1	50N	8.82	18.43	1628	1.13	3.85	7.19	889	0.81
1	100N	8.15	17.38	1617	1.07	4.18	8.21	916	0.90
	P value	<0.001	0.004	<0.001	0.175	0.826	0.573	0.913	0.511
2	0N	5.59	9.97	818	1.22	6.70	11.58	765	1.51
2	50N	7.45	13.08	954	1.37	8.23	14.84	1021	1.45
2	100N	7.28	12.90	1009	1.28	8.39	16.11	1157	1.39
	P value	0.006	0.010	<0.001	0.030	<0.001	<0.001	<0.001	0.156
P effects									
1	0P	7.57	16.40	1491	1.10	3.75	7.37	879	0.84
1	20P	8.28	17.84	1611	1.11	3.67	6.93	868	0.80
1	40P	7.44	15.17	1451	1.05	3.86	7.25	858	0.84
	P value	0.899	0.495	0.467	0.881	0.354	0.473	0.173	0.565
2	0P	6.30	11.18	906	1.23	7.63	14.40	994	1.45
2	20P	7.34	12.72	927	1.37	7.65	14.06	1018	1.38
2	40P	6.68	12.05	948	1.27	8.03	14.07	931	1.51
	P value	0.089	0.101	0.715	0.319	0.094	0.372	0.043	0.271
K effects									
1	0 K	5.58	11.99	1382	0.87	3.60	6.92	860	0.80
1	50 K	8.71	18.51	1598	1.16	3.75	7.13	870	0.82
1	100 K	9.01	18.92	1573	1.20	3.92	7.51	875	0.86
	P value	<0.001	<0.001	0.074	<0.001	0.033	0.030	0.780	0.297
2	0 K	4.87	9.04	877	1.03	7.71	13.76	939	1.47
2	50 K	7.74	13.37	952	1.40	8.56	15.48	1038	1.49
2	100 K	7.71	13.54	952	1.42	7.05	13.29	966	1.38
	P value	<0.001	<0.001	0.301	<0.001	0.048	0.020	0.553	0.101
Significant interactions (*P* value)									
2	P × K								0.049
2	Harvest × N		0.007	<0.001					
2	Harvest × K	<0.001	<0.001						
2	Harvest × N × K				0.024				

Table 7
Pearson correlation analysis results between RUE and K mass fractions of the plant for different N and K fertiliser application rates at two sites.

Location	Treatment	*r*	*P*	*n*[a]
Djakakope	0 N	0.335	0.149	60
	50 N	0.606	0.005	60
	100 N	0.644	0.002	60
	0 K	0.516	0.020	60
	50 K	0.520	0.019	60
	100 K	0.089	0.709	60
Sevekpota	0 N	−0.827	0.000	90
	50 N	−0.675	0.000	90
	100 N	−0.846	0.000	90
	0 K	−0.767	0.000	90
	50 K	−0.705	0.000	90
	100 K	−0.854	0.000	90

[a] *n* represents the number of observations.

mum values within a range of plant tissue K values, then declined beyond this range. The greatest values of WUE and RUE (above 75th percentile) were achieved within K mass fractions values of 3.9 to 11.9 g kg^{-1}. Increasing WUEs and RUEs with increasing K concentrations were mainly observed in Djakakope, where the soil was poor in K, whereas the reverse relationship was observed in Sevekpota. Pearson correlation analysis between RUE and K mass fractions (Table 7) indicated that without N application in Djakakope, there was no significant relationship between K mass fractions and RUE. When N fertiliser application was applied, RUE values rose with increasing K mass fractions. On this site, RUE and K mass fractions were positively correlated without K and with the application of 50 kg K ha^{-1}. No significant correlation was obtained when 100 kg K ha^{-1} was applied. In Sevekpota, RUE declined with increasing K mass fractions in the plant, regardless N application rates (0, 50 and 100 kg N ha^{-1}). The correlations between RUE and K mass fractions were also negative, irrespective of K application rates (0, 50 and 100 kg K ha^{-1}). The correlation analysis between WUE and K mass fractions indicated similar trends to those of RUE (not shown).

4. Discussion

The prime objective of this study was to assess how K availability interacting with N, P and harvest time affect cassava yield, WUE, transpiration, RUE and light interception under rain-fed conditions in West Africa. Differences in cassava performance between sites and seasons were clear. Stronger responses of WUE, water transpiration, RUE, light interception, biomass and storage root production to fertiliser applications were obtained at Djakakope, which had soils that were more deficient in N and K than Sevekpota. Water stress restricted crop growth at Sevekpota in Year 1 (Fig. 1), especially early in the vegetative stage. Water availability to cassava from 1 to 5 MAP is crucially important for determining yield of storage roots (Connor et al., 1981).

The effect of N applications on WUE was not significant in most cases, but N application increased PTRAN and reduced PET. The increase in PTRAN indicates a rise in plant photosynthetic activity (El-Sharkawy and Cock, 1986) due to the positive effect of N on leaf area development (Section 3.2). By extending leaf area, N application accelerates and increases soil coverage by the plant canopy, which leads to reduced evaporation from the soil (Mihara 1961; Pellet and El-Sharkawy, 1997). Unlike N, addition of K improved WUE in Djakakope (Fig. 4a), but not in Sevekpota. This shows that K fertiliser can increase WUE and cassava production on K deficient

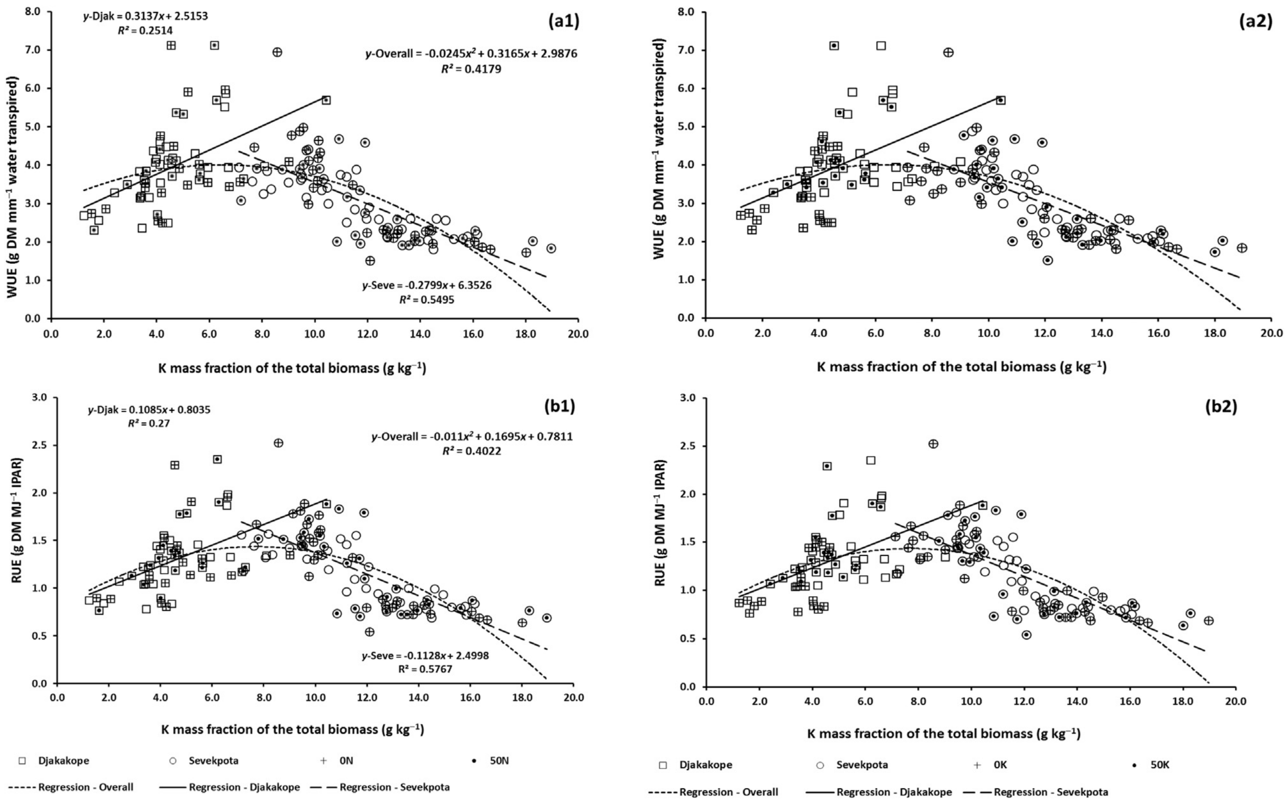

Fig. 6. Relationship between plant biomass K mass fraction and (a) WUE, and (b) RUE at two sites with highlight of applied N (a1, b1) and K (a2, b2) quantities in kg ha^{-1}. The blank symbols indicate 100 kg N ha^{-1} in a1 et b1, 100 kg K ha^{-1} in a2 et b2. Djak and Seve in the regression equations stand for the sites Djakakope and Sevekpota. A polynomial regression line was fitted for all data, linear lines were fitted for data from the individual sites.

soils under rain-fed conditions. A similar influence of K availability on crop productivity under rain-fed conditions was found for banana production in Uganda (Taulya, 2013). The positive effect of K on WUE could be associated with the ability of K to regulate stomatal aperture and closure (Chérel et al., 2014), given the high sensitivity of cassava to leaf-to-air vapour pressure deficit. This mechanism allows the crop to consume the limited amount of available water slowly during the dry season, resulting in greater dry matter gain over the stress period and larger WUE over the cropping season (El-Sharkawy, 2004). However, in our study, K effects on WUE can be ascribed to the effect of K on the total biomass produced, since WUE was expressed relatively to the potential water transpiration, which likely masks the effect of stomata regulation by the crop on transpiration. Nevertheless, we assumed that the effects of stomata regulation on the cassava plant's performance are reflected in the total biomass measured in the field experiments.

The availability of K was not a major determinant of PTRAN and PET, for which N was more important. The effect of K on WUE was influenced by N application and harvest time (Fig. 5). Along with increasing rates of K, optimal N supply was required at different crop ages for greater WUE of cassava. The greatest responses were obtained at Harvest 1 around 4 MAP at 50 kg K ha^{-1} without N application, and at 100 kg K ha^{-1} with the application of 50 kg N ha^{-1}. These results suggest a need for a balanced nutrition by adjusting K application rates to match the availability of N. However, too much N appeared to impede the positive effect of K on WUE, since the value of WUE achieved at 50 kg N ha^{-1} was greater than that obtained at 100 kg N ha^{-1} with the application of 100 kg K ha^{-1} in Djakakope, especially at 4 MAP (Fig. 5). Too much N relative to K supply can induce an unbalanced nutrition (Ezui et al., 2016), which can reduce the WUE by the crop.

No significant effect of P application on WUE was observed. This implies that the P supplying capacity of the soil was sufficient to reach WUE values comparable with those obtained at P fertiliser rates of 20 and 40 kg ha^{-1}, even though soil available P concentrations were small, especially at Sevekpota (Table 2). Cassava forms strong mycorrhizal associations, which makes it efficient in extracting P from the soil (Sieverding and Leihner, 1984).

It is noteworthy that the overall WUE was probably slightly overestimated, especially during drought periods for two main reasons. The effect of leaf litter on reducing evaporation and increasing the availability of water for transpiration was not accounted for in the estimation of potential evaporation and transpiration. Moreover, we did not consider the impact of a dry soil surface crust reducing evaporation. We did not have appropriate data to implement such corrections. However, the estimated range for WUE of 1.54–7.12 g DM per kg of water transpired, which corresponds to 0.5–2.5 g DM per kg water evapo-transpired for an average PTRAN/PET ratio of 0.35 obtained on the study sites, falls within the interval of 0.4–4.8 g DM per kg water evapo-transpired reported by Lemon (1969) as cited by Yao and Goué (1992). Furthermore, the overall WUE of 3.22 g biomass DM per kg water transpired is comparable to that reported by El-Sharkawy and Cock (1986) of 2.9 g total biomass DM per kg of water transpired for cassava. Our WUE is also comparable to 3.1 g total biomass DM per kg of water transpired reported for sorghum (El-Sharkawy and Cock, 1986), and falls within the range obtained for wheat: 2.5–6.3 g biomass kg^{-1} water transpired (Siahpoosh and Dehghanian 2012; Zhang et al., 1998). The WUE we obtained for cassava is much larger than that of other C_3 plants such as bean with 1.7 g total biomass DM kg^{-1} water transpired (El-Sharkawy and Cock, 1986), indicating a high drought tolerance of cassava.

A RUE of 1.16 g DM per MJ PAR intercepted across the cropping season (Fig. 3b) falls within the lower part of the range of 1.15–2.30 g DM per MJ IPAR obtained by Pellet and El-Sharkawy (1997). This could be attributed to the fact that the latter range was achieved under high rainfall regime amounting 1800 mm per year, whereas only 574–736 mm rain was recorded across the growing season on our study sites. Radiation use efficiency and total biomass production were differently affected by fertiliser applications. Potassium applications increased RUE, storage roots and total biomass production in Djakakope, but did not significantly affect IPAR. The reported beneficial effects of K on plant growth include CO_2 assimilation for photosynthesis, enzyme activation or stimulation and protein synthesis (Chérel et al., 2014). Potassium application increases leaf K^+ concentration, especially cytosolic K^+ and chloroplast K^+, which enhances the photosynthetic rate of a specific leaf area (Marschner and Marschner, 1995). Plant tissue K^+ concentration is related to soil K availability. Hence, the poor availability of soil K at Djakakope contributed to the response of cassava storage roots and biomass to K applications. The soil exchangeable K of 0.38 and 0.66 mmol kg^{-1} in Years 1 and 2 at this site were below the critical range of 0.8–1.8 mmol kg^{-1} soil exchangeable K for cassava production (Howeler, 2002). The response to K in terms of cassava biomass and storage roots in Year 2 in Sevekpota with a soil exchangeable K value of 1.35 mmol kg^{-1}, implies that the critical K requirement for cassava production on this site is above 1.35 mmol kg^{-1}. However, the positive responses of biomass and storage roots to K in Year 1 in Sevekpota were unexpected since exchangeable K content of the soil was high (3.5 mmol kg^{-1}). This may be explained by the fact that under drought conditions, chloroplasts loose a large amount of their K^+, resulting in decreased photosynthesis, which can be overcome through external K supply (Marschner and Marschner, 1995). It could also be explained by the large leaf K requirements under drought conditions to maintain high stomatal K^+ concentrations and thus optimal rates of photosynthesis (Marschner and Marschner, 1995).

The improvement of RUE by K application without a substantial effect on IPAR in Djakakope suggests that K affects more the efficiency of converting light into photosynthates than the amount of light intercepted. This conversion of light energy into photosynthates is driven by the enhancement of photosynthesis by K applications (Marschner and Marschner, 1995), involving the activation of many enzymes and the production of adenosine triphosphate (ATP).

The lack of increase of RUE in response to K applications in Sevekpota, especially in Year 2 when K concentration was small (1.35 mmol kg^{-1}) may be explained by the fact that RUE without K application at this site (1.47 g DM MJ^{-1} PAR) was close to optimum, since a comparable RUE was achieved with K applications in Djakakope (1.40–1.42 g DM MJ^{-1} PAR) in Year 2 (Table 6). This suggests that plant tissue K concentration is more limiting for RUE than soil exchangeable K. Under K deprived conditions, optimum crop growth can be maintained as long as the cytosolic K^+ concentration is above a critical value, despite the depletion of vacuolar K^+ concentrations (Chérel et al., 2014). However, excess K did not generate higher RUE (Fig. 6b, Table 7). The largest RUEs were achieved with a total biomass K mass fraction range of 3.9–11.9 g K kg^{-1} biomass DM. Below and beyond this range, RUE of cassava was smaller. Weak RUEs with low K concentration were obtained in Djakakope (Fig. 6b), because soil K was highly deficient at this site, which likely caused a lower cytosol K^+ concentration, leading to the poor RUE. By contrast, in Sevekpota poor RUE was observed with large concentrations of K (Fig. 6b), and RUE declined with increasing K concentrations, with or without K fertiliser application. This can result from the fact that the indigenous K supply on this site was generally above critical requirements for cassava response to K applications. However, this may also imply an overriding impact of another limiting factor, which may be drought as shown in Fig. 1. These findings suggest that the large RUE of cassava can be achieved under optimum plant tissue K concentrations.

Nitrogen applications did not significantly influence RUE, but led to increased production of storage roots and biomass, and improved light interception of cassava (Table 6). Thus, the fact that N applications increased light interception and biomass production did not imply increased RUE. In response to N applications, both biomass (numerator) and IPAR (denominator of RUE) changed in a similar way, without yielding any significant change in RUE. For this reason, one should look to both RUE (and WUE) and their component variables (biomass and IPAR for RUE; and biomass and PTRAN for WUE), for an enhanced understanding of the effect of nutrients on crop productivity. The positive response of IPAR and the lack of response of RUE to N applications together suggest that N is more important in determining radiation interception than in RUE of cassava. However, Sinclair and Horie (1989) showed that addition of N can increase RUE at low leaf N content for maize, rice and soybean. Possibly in our case, indigenous soil N supply provided sufficient leaf N for optimal RUE of cassava. However, N applications induced positive correlations between RUE and K concentrations in Djakakope (Table 7), where soil N and K were low (Table 2). Thus, N application can enhance K uptake, and therefore contribute to an increased RUE on N and K deficient soils.

Both WUE and RUE were larger when estimated at 4 MAP (Harvest 1) than at 8 and 11 MAP (Harvest 2 and 3) in Djakakope and Sevekpota in Year 2 (Table 4). These results may be attributed to greater water and light energy demands during the first 6 MAP, which comprises a period of strong vegetative growth of cassava, generally from 3 to 6 MAP (Alves, 2002). Beyond this period (7–10 MAP), the rate of shoot growth is reduced in favour of carbohydrate translocation to the roots (Alves, 2002). Veltkamp (1985) also obtained higher RUE values of 1.34–1.40 g biomass DM MJ^{-1} IPAR during the first 6 MAP for four different cultivars and reported a decreased RUE beyond 6 MAP. Since the variations in RUE and WUE seem to be physiologically imposed, it might be erroneous to use their values estimated at one specific stage of the crop alone to predict cassava productivity for the whole crop cycle.

Water-use efficiency and RUE explained the effect of K on cassava biomass and storage root production. Hence, improved K management can increase WUE and RUE of cassava. High WUE is important, especially in rain-fed production systems in SSA to optimise the use of water during droughts. A high RUE increases the productivity of the crop. Cassava cultivars selection for K deficient soils should favour cultivars with high K use efficiency (El-Sharkawy and Cadavid, 2000) that can optimise the use of available K and response to K fertilisers. Enhancing K management implies improving soil K supply, which involves applying the right rate of K when the plant needs it most on soils where K availability falls below the critical requirement for the plant. Potassium requirements of cassava varied from site to site, from harvest to harvest, and depended on N availability. Thus, improving K supply must be matched with a balanced supply of other nutrients, especially N. These findings demonstrate that the food insecurity threat of nutrient mining in smallholder farming systems in SSA is compounded by reductions in the efficiency of water use. This study also provides quantitative values of RUE for water-limited yield predictions, and values of WUE that can be indicative in irrigation planning to estimate cassava water needs and distributions over the season for a given target yield.

5. Conclusion

We showed that the effect of K on the productivity of cassava was largely due to the positive effect of K on RUE and WUE rather than on light interception and water transpiration. Light interception and water transpiration of cassava were more influenced by the availability of N than of K, stressing the leading role of N in photosynthesis. These results highlight the important and complementary roles of N and K in achieving high RUE and WUE of cassava under rain-fed conditions in West Africa. Cassava response to K is mainly noticeable when soil K is below the required critical level. The best responses of cassava to K applications were observed during the vegetative stage of the crop, suggesting a timely application of required nutrients and timely planting to make the best use of the rainfall to achieve high yields. Enhanced K management is key to improving WUE and RUE for increased cassava production under rain-fed conditions in West Africa.

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Appendix A. Formulas for calculating PTRAN, PEVAP and PET based on Penman equations as used in the LINTUL model.

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PEVAP = EXP(−0.5*LAI) * (PENMRS + PENMD)/LHVAP.
PTRAN = (1.-EXP(−0.5*LAI)) * (PENMRC + PENMD)/LHVAP.
PTRAN = MAX(0., PTRAN − 0.5*RNINTC).
DTRJM2 = DTR * 1.E6.
BOLTZM = 5.668E-8.
LHVAP = 2.4E6.
PSYCH = 0.067.
BBRAD = BOLTZM * (DAVTMP+273.)**4 * 86400.
SVP = 0.611 * EXP(17.4 * DAVTMP/(DAVTMP + 239.)).
SLOPE = 4158.6 * SVP/(DAVTMP + 239.)**2.
RLWN = BBRAD * MAX(0.,0.55*(1.-VP/SVP)).
NRADS = DTRJM2 * (1.−0.15) − RLWN.
NRADC = DTRJM2 * (1.−0.25) − RLWN.
PENMRS = NRADS * SLOPE/(SLOPE+PSYCH).
PENMRC = NRADC * SLOPE/(SLOPE+PSYCH).
WDF = 2.63 * (1.0 + 0.54 * WN).
PENMD = LHVAP * WDF * (SVP-VP) * PSYCH/(SLOPE + PSYCH).
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