



Dynamics of N-P-K demand and uptake in cassava

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Accepted: 22 October 2020
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Abstract

Fertilizers are required to improve productivity of cassava and meet the increasing demand for cassava as food, feed, or raw material for processing industries. Our objective was to develop nutrition indices for N, P, and K to provide quantitative insight in the dynamics of nutrient demand and uptake of cassava. On-farm experiments were conducted at six locations in Nigeria from 2016 to 2018, across the major cassava growing agro-ecologies of West Africa. Nitrogen, P, and K were applied at different rates. Uptake of nutrients was measured in leaves, stems, and storage roots at 4, 8, and 12 or 14 months after planting (MAP) and used to construct NPK dilution curves and nutrition indices. About 67, 61, and 52% of total N, P, and K were taken up at 4 MAP, with a maximum uptake rate of 0.21, 0.03, and 0.12 g/m²/d for N, P, and K, respectively. Nutrient concentrations in stems and storage roots declined gradually, in contrast to concentrations in the leaves that fluctuated within narrow ranges. Dilution curves and nutrition indices for N, P, and K were established for the first time in cassava. Dilution curves of N, P, and K in the crop for the highest NPK application treatment were described as $N_c = 82DM^{-0.61}$, $P_c = 7.4DM^{-0.54}$, and $K_c = 43DM^{-0.54}$, when total biomass was between 5 and 57 t/ha dry matter (DM). The nutrition indices were linearly related to relative crop biomass. Insight into the nutrient uptake and dilution patterns during the growth cycle can help to understand the temporal nutrient demands of cassava and identify sustainable management practices. Initial ample supply of N and P and moderate K, with extra K top-dress during the second growth phase, will benefit cassava growth and yield. Furthermore, such information provides a basis to develop a dynamic model to simulate nutrient-limited growth of cassava.

Keywords *Manihot esculenta* Crantz · Nutrient dynamics · Nutrition indices · NNI · PNI · KNI · Dilution curves

1 Introduction

Cassava (*Manihot esculenta* Crantz) is an important food crop in West Africa with a high yield potential of over 90 t/ha of fresh storage roots (32 t/ha dry matter—DM) in a year and high nutrient use efficiency (Howeler 2017; Adiele et al. 2020). Cassava contributes greatly to food security and as raw material for industrial processing. Cassava chips are

effective energy substitutes for cereals in pig and poultry diets, while cassava starch is a high-quality resource for the paper and textile industries (FAO 2018). It is also used as feedstock for ethanol production (Dai et al. 2006). The increasing demand for cassava offers farmers the opportunity to intensify production, earn higher incomes, and boost their food supply (FAO 2018). Therefore, the use of inorganic fertilizers, following the 4R nutrient stewardship (right amount, right time, right place, and right source), is required to improve productivity sustainably in the future (Oliveira et al. 2017). Cassava can grow under a wide range of environmental conditions, but growth rates are strongly affected by biophysical conditions and management (Howeler 2012). Cassava is a perennial plant where vegetative and storage root growth occurs simultaneously, from the onset of storage root initiation, with dry matter partitioned between the shoot and storage roots (El-Sharkawy 2007). Typically, assimilates are partitioned mostly to the shoot during canopy establishment, and partitioning to storage organs strongly increases from about 4 months after planting (MAP) onwards. In West Africa, a reduction in leaf growth rates usually occurs during a dry season and leaf

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growth resumes when rainfall returns. During this stage, the crop allocates most of the assimilates to the storage roots (Howeler and Cadavid 1983). The bi-modal growth pattern of leaves poses a challenge for crop management in terms of optimizing nutrient application and uptake to allow optimum development of leaf area index (LAI) for adequate light interception and maximum growth, while regulating shoot growth to avoid lodging.

Nitrogen (N), phosphorus (P), and potassium (K) uptake and partitioning in cassava have been documented in Latin America (Howeler and Cadavid 1983). Howeler and Cadavid (1983) reported that uptake of N, P, and K was limited during the first 2 months of cassava growth, peaked during the third and fourth months, before slowing again. Until six MAP, N accumulated mainly in the leaves, after which N in leaves declined due to leaf fall, but continued to increase in stems and remained constant in roots (Howeler 2012). Phosphorus and especially K accumulated mainly in the roots, followed by stems and leaves (Howeler 2012). The uptake and partitioning of nutrients in cassava is further influenced by demand in response to climatic conditions, soil water availability, soil fertility, and plant age. Climate variability contributes to differences in plant growth rates and production potential (Alva et al. 2002). Howeler (2012) reported that in both irrigated and non-irrigated plots, the concentration of N, P, and K in the plant decreased remarkably during dry months and increased with the onset of rains. In cassava, there is usually a distinct decrease in nutrient uptake during the dry season, with or without adequate soil water (Fukai and Hammer 1987; Howeler 2012). This may be due to stomatal closing during day time and decreased transpiration in response to low relative humidity.

Several studies have shown that nutrient concentration of plants decreases during the growth cycle, even when nutrient supply is sufficient. Howeler (2012) found that concentrations of N, P, and K decreased with increasing age of cassava in all plant parts. This has been attributed to dilution as the plant ages (Justes et al. 1994; Lemaire 2012), directly related to increase in the proportion of structural and storage tissues (Greenwood et al. 1991). The minimum nutrient concentration required by the crop to reach its maximum growth rate at a given amount of biomass accumulation, time, and field situation is referred to as critical value of the mineral nutrient. With the critical nutrient dilution curves, it becomes possible to determine Nutrition Indices (NI), as ratio between actual and critical nutrient concentration of a plant at different growth stages. The concepts of critical nutrient concentration and nutrition index have been widely used as a diagnostic tool for crop nutrient sufficiency, and to simulate crop demand for nutrients (Justes et al. 1994; Lemaire 2012; Gómez et al. 2018). The N critical dilution curve based on aboveground biomass has been established for various crops, e.g., wheat (Justes et al. 1994), corn (Plénet and Lemaire 1999), and rice

(He et al. 2017). Furthermore, the concepts of a critical dilution curve and a nitrogen nutrition index have been extended successfully to other crops, including tuber and root crops such as fodder beet (Chakwizira et al. 2016), Irish potato (Zamuner et al. 2016; Gómez et al. 2018) and sweet potato (Zunfu et al. 2020). For these root and tuber crops, nutrition indices were based on plant biomass including leaves, stems, and storage roots, while the observed nutrient dilution patterns were similar to cereals. However, we are unaware of any published reports on dilution curves and the nutrition indices of N, P, and K in cassava, especially on poor soils where soil N, P, and K limit crop growth.

Understanding the nutrient uptake and dilution pattern during the growth cycle can help to understand the temporal nutritional demands of cassava and to identify management practices to prevent nutrient deficiency as well as excess. Such information can also be used to improve simulation models to predict cassava growth and storage root yield production under nutrient-limited conditions. Our objectives were to: (1) quantify the dynamics of nutrient uptake of cassava in the season as affected by fertilizer application; (2) quantify the biomass and amounts of N, P, and K in plant parts across the crop growth cycle, to gain insights in the distribution of nutrients over plant organs and (3) establish nutrient dilution curves and nutrition indices for cassava. We hypothesize that these nutrition indices can explain the observed relative amounts of biomass and hence crop growth rates for nutrient-limited situations.

2 Materials and methods

2.1 Study area

On-farm experiments were conducted from 2016 to 2018. The six selected experimental fields were located in three agro-ecological zones (Rainforest—Cross River; Transition Rainforest—Edo; and Guinea Savanna—Benue), covering the major cassava producing regions in Nigeria. Each year, three field trials were established, one in each zone. The fields in Edo were located at 7.05° N, 6.13° E in 2016 and 6.80° N, 6.13° E in 2017. For Cross River, field locations were at 7.27° N, 8.18° E in 2016 and 5.96° N, 8.77° E in 2017. In Benue, fields were located 6.76° N, 8.69° E in 2016 and 7.27° N, 8.19° E in 2017. The growing season begins with the onset of rains in the south from April (Cross River), gradually moving north, with first rains in Edo by early May and June in Benue. The dry season with intermittent or no rainfall runs from November to early April–May.

The experiment locations (Cross River and Edo) fall within the Niger delta, which contains deep deposits of relatively young material, rich in clay, resulting in mostly Nitisols or Ferralsols, while Benue is located within the rift basin, with

Acrisols or Lixisols as dominant soil types. Observed rooting depths of cassava were more than 3.2 m depth in Edo, providing large volumes of soil water that were available for the crop. Measured growth rates remained high throughout the period without rainfall, strongly suggesting that growth of the cassava crop was not limited by water (Adiele et al., 2020). Rooting depths were about 1.5 m in Benue where rooting was restricted by a dense clay layer causing soil water saturation at depth after periods of heavy rainfall. Weather data were obtained from nearby weather stations at distances of approximately 2.5, 60, and 0.5 km (as the crow flies), with mean annual rainfall of about 2300, 2200, and 1400 mm for Cross River, Edo, and Benue respectively (Ukhurebor and Abiodun 2018).

2.2 Experiment design, crop establishment, and management

The larger experiment, fully described in Adiele et al. (2020), included 12 treatments from which 4 treatments were selected for this study. Each experiment contained three blocks to account for any gradient present in the field with fertilizer treatments randomized within these blocks. The N, P, and K rates applied in the selected treatments are provided in Table 1. The plot size was 10 m by 8 m. Planting was done at the onset of rains each year, except at Benue in 2016, where planting was done approximately 2 months later (mid-season). Dates of planting were May 24, June 16, and August 16, in 2016 and May 12, June 3, and June 15, in 2017 for Edo, Cross River, and Benue respectively. Stem cuttings of 25 cm long from cassava cv. TME 419 were planted at a distance of 1.0 by 0.8 m, resulting in the recommended planting density of 12,500 plants per hectare. The selected TME 419 cultivar has a high storage root DM and starch contents, and is characterized by erect stems with minimal branching, which facilitates intercropping as well as higher planting densities (Ezui et al. 2016). Phosphorus was applied by placement close to the cuttings at planting, while N and K were also spot-applied near the plant base in three splits at 1, 2.5, and 3.5 MAP. The N, P, and K fertilizers used were urea, triple super phosphate (TSP), and muriate of potash (MOP). The experimental

plots were well managed and weeded regularly, especially before each fertilizer application Fig 1.

2.3 Data collection

At the start of the experiment, just before land preparation, soil samples were collected from five points in a “W” pattern from 0 to 30 cm depth in each plot, bulked together before a composite sample was taken. The samples were air dried and sieved through a 2 mm mesh sieve. The pH was measured in water using a 2.5:1 dilution. The hydrometer method was used to determine the particle size. Soil organic carbon was obtained by the combustion method and N by Kjeldahl digestion. The Mehlich-3 extraction was used for Ca, Mg, and K, while available P was determined in Olsen extracts. All soil analyses were done at the IITA laboratory, Ibadan, Nigeria.

2.4 Yield assessment and plant nutrient content measurements

At 4, 8, and final harvest (FH) at 12 or 14 MAP, a net plot of 6.4 m² (eight plants) was harvested in each experimental plot. Plants were separated into leaves, stems, and storage roots and weights of each harvested plant part (leaf with petiole, stem, and storage root) were recorded for each plot. Subsamples of about 400 g fresh weight were collected in the field using a digital field scale, and oven dried at 60 °C until constant weight and weighed to allow dry matter (DM) yield determination. Dried subsamples from leaves with petioles, stems, and storage roots were analyzed for total N, P, and K concentration. Total N in the tissue was analyzed by Dumas combustion using a Carlo Erba EA1108 elemental analyzer. Total P and K concentrations were measured with inductively coupled plasma (ICP) (iCAP 7400, Thermo Fisher Scientific, USA). Subsamples collected at 4 MAP in Benue in 2016, and in Cross River in 2017, were not analyzed.

2.5 Calculations and data analysis

The N, P, and K uptake in each crop component were calculated by multiplying nutrient content by the plant biomass dry matter (g/m²) (Ciampitti et al. 2013). Nitrogen, P, and K uptake rates (g/m²/d) at 4 and 8 MAP and at FH were calculated as the difference between plant uptake at 8 minus 4 MAP or final harvest minus 8 MAP divided by the number of days between the growth intervals, following the approach used by Bista et al. (2018). Temperature sum (Tsum) was calculated using Eq. 1, at a T_{base} of 15 °C.

$$Tsum = \sum_1^d \max \left(\frac{(T_{max,d} - T_{min,d})}{2} - T_{base}, 0 \right) \quad (1)$$

Table 1 Nutrient application rates per treatment, (f) represents full rate of the nutrient (N = 300, P = 100, and K = 300 kg/ha)

Treatment	Nitrogen (N) kg/ha	Phosphorus (P)	Potassium (K)
1. Control	0	0	0
2. N150P40K180	150	40	180
3. NfPfK180	300	100	180
4. NfPfKf	300	100	300

where T_{\max} and T_{\min} are the daily maximum and minimum temperatures ($^{\circ}\text{C}$). T_{base} is the base temperature below which the crop no longer develops.

2.6 Establishment of nutrient dilution curves

For this objective, only data points from Edo and Cross River were used, so as to capture the more ideal cassava growing environment considering soil conditions. The nutrient dilution curve describing the relationship between nutrient concentration and total or shoot biomass across locations and years, was generated by fitting a simple negative power function (eq. 2), following (Gómez et al. 2018).

$$C_{(N,P,K)} = a_{(N,P,K)} (DM)^{-b_{(N,P,K)}} \quad (2)$$

where DM is total biomass (the sum of aboveground and storage roots biomass (t/ha DM), excluding fibrous roots) or shoot biomass only; C (g/kg) is the total concentration of N, P, or K in the plant biomass. Coefficient a (g/kg) represents the concentration of N, P, or K when the DM is exactly 1 t/ha. Thus, it is related to the level of nutrient supply and the intrinsic ability of the crop to take up the nutrient during early growth stages (Lemaire et al. 2007). Parameter b represents a “dilution coefficient,” which describes the reduction in nutrient concentration associated with the increment in biomass. It characterizes the pattern of decrease of the nutrient concentration with increase in DM. If b is zero, the nutrient concentration remains constant. If $b = 1$, there is an increase in biomass without any increase in N, P, or K concentration. Also, nutrient dilution curves at maximum growth rates were determined using Eq. 2. For this study, we described the nutrient dilution curves as function of shoot (leaves and stem) and plant biomass (including leaves, stems, and storage roots) following the procedures used by Zamuner et al. (2016) and Gómez et al. (2018) for

potato and Chakwizira et al. (2016) for fodder beet. This required identification of values by which the evaluated nutrients do not limit crop growth. Therefore, the full treatments with largest application rates for N, P, and K and highest yields across locations and years were selected to determine the parameters a and b for each nutrient for maximum growth rate.

Two envelope curves were defined for N, P, and K, describing the minimum and maximum concentrations (Eqs. 3 and 4) following the method of Justes et al. (1994) for N.

$$C_{(N,P,K),\max} = a_{(N,P,K),\max} (DM)^{-b_{(N,P,K)}} \quad (3)$$

$$C_{(N,P,K),\min} = a_{(N,P,K),\min} (DM)^{-b_{(N,P,K)}} \quad (4)$$

The C_{\max} curve represents the highest observed nutrient accumulation capacity of the plant and was assumed to correspond to maximum nutrient uptake rate (Justes et al. 1994; Lemaire 2012). The C_{\min} curve represents the minimum nutrient concentration and is assumed as the lower limit below which metabolism ceases. Note that C_{\min} is probably an overestimate of the true minimum limit at which cassava growth stops, because it could be less under other growth conditions. The fitted values for a were adjusted manually to find best values for the a_{\max} and a_{\min} parameters for each nutrient, such that they visually matched the dilution patterns of N, P, and K, whereas the b parameter was not adjusted. Following Greenwood et al. (1986), the nutrition indices (NI) were calculated as:

$$NI_{(N,P,K)}(DM) = \frac{C_{(N,P,K)}(DM) - C_{(N,P,K),\min}(DM)}{C_{(N,P,K),\max}(DM) - C_{(N,P,K),\min}(DM)} \quad (5)$$

where $C_{(N,P,K)}(DM)$ represents the nutrient concentration for N, P, or K for a given amount of dry matter. The relative biomass production was calculated as a ratio of the total

Fig. 1 Cassava plant in plots with PK fertilizer on left hand side and NPK treatments on right hand side and typical storage root growth underground. The photographs were taken from the experiment in Ekpoma, Edo state, Nigeria



biomass weight (DM, t/ha) obtained at each harvest period to the largest total biomass (Lemaire 2012). In the Benue experiment in 2016, the crop suffered from late planting and stagnating water in the lower soil profile that likely affected initial root growth and resulted in poor growth rates until about 8 MAP. Therefore, only data from the last harvest were included in the NI analysis.

2.7 Statistical analysis

Treatment effects on nutrient uptake rate were analyzed separately for each location and growth stage, using a linear mixed model with nutrient uptake rate as response variable and fertilizer treatment as explanatory factor, while years were considered random effects. The interactions of plant part nutrient uptake response with location and year or treatment were analyzed with a mixed linear regression model. A simple linear regression was used to assess the relationship between relative biomass and nutrition indices. Secondly, a mixed linear regression model was used to test if a combination of nutrition indices can explain observed differences in relative yield. NNI, PNI, KNI, and harvest number were included as fixed factors while site, a combination of location and year, was included as a random factor. Effects were analyzed with a type-III ANOVA using Satterthwaite's approximation method. Differences between treatment means were considered significant when probability ≤ 0.05 . R software (R Core 2019), version 3.5 with the lme4, lmerTest, and Predictmeans packages was used for statistical analysis.

3 Results and discussions

3.1 Dynamics of plant nutrient uptake and uptake rate

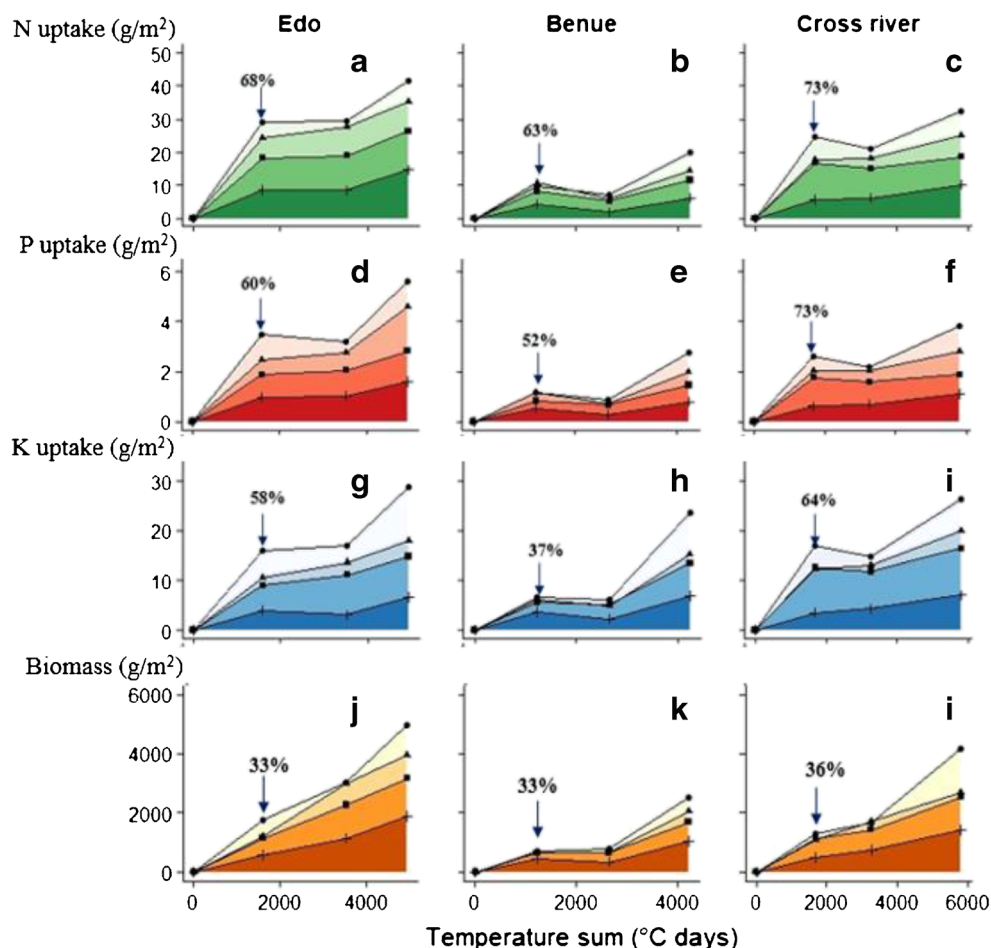
The proportion of nutrients taken up at 4 MAP in relation to the total uptake at final harvest, varied with locations and treatments. In Edo, there was no water deficiency and growth continued during the dry period between 4 and 8 MAP, while nutrient uptake during this period was minimal (Fig. 2a–j). Growth ceased completely in Benue and was strongly reduced in Cross River during this period, while some loss of N and P was observed, and to a lesser extent of K, due to leaf fall (Fig. 2). The proportional uptakes for the fertilized treatments were larger than the unfertilized treatments. At all locations, a larger proportion of N was taken up before the drought when compared to P and K (Fig. 2b–c). On average, cassava in Edo at 4 MAP took up 59, 60, and 60% of N, P, and K in the unfertilized treatment, compared to 70, 62, and 56% in the fertilized treatments. At Benue, cassava in the unfertilized treatment took up 70, 66, and 53% of N, P, and K at 4 MAP, compared

with, on average, 48, 41, and 35% uptake of N, P, and K in the fertilized treatments. At Cross River, these values were 56, 55, and 50% of N, P, and K at 4 MAP for the unfertilized treatment and 76, 73, and 65% for the fertilized treatments.

While nutrient uptake in cassava was mostly concentrated in the first 4 months, it continued after return of the rains. In the dry period, small amounts of nutrients were taken up or even lost, depending on the location. At 4 MAP, with only one-third of whole season total biomass produced, plants already took up on average 67, 61, and 52% of N, P, and K that was present in the plant (leaves, stems, and storage roots) at final harvest (Fig. 2). In Edo, at 8 MAP, the uptake of N, P, and K increased only by 4, 1.1, and 10% in the fertilized treatments from 4 MAP. In the unfertilized treatment, there was no difference in N and K uptake between 4 and 8 MAP, only P uptake increased by 3.5%. Nutrient uptakes strongly reduced in the drier part of the season, while biomass growth continued. The soil type in Edo allowed for deep rooting, and plants likely had access to deeper soil water while nutrients were not available for uptake in the top soil because this soil layer was too dry. It is possible that excess nutrient uptake in the first part of the season is needed to support growth during this period, with dilution as a result. This means that split fertilizer application, such as top dressing with N, P, and K after the dry season could benefit cassava and may strongly reduce nutrient loss, but may also reduce growth in the dry season for sites with deep soil water availability. From this, it is unclear what the best fertilizer strategy would be: split applications after drought or a large initial supply. Our results suggest that a substantial supply of nutrients is needed before the dry season for sites where the crop can access soil water at depth.

The fastest N uptake rate during the growing season was observed in Edo, at 4 MAP with the NfPfKf treatment (0.21 g/m²/d, compared with an average of 0.15 g/m²/d across the locations and years), (Table 2). The cumulative N uptake from 4 MAP to FH was significantly influenced by treatment and location, except at 8 MAP when there was no significant effect of treatment due to the dry season (Tables S1–3). Also, phosphorus uptake rate was at its peak at 4 MAP with a maximum value of 0.03 g/m²/d and an average of 0.02 g/m²/d (Table 2). Across locations and years, the average quantities of P taken up in the unfertilized and fertilized treatments were 0.7 and 1.2 g/m² and 1.9 and 3.2 g/m² at 4 MAP and FH, respectively. Similar to N and P, the maximum K uptake rate (0.12 g/m²/d, and average of 0.1 g/m²/d) was observed at 4 MAP in Cross River. The quantities of K taken up at 4 MAP and FH by unfertilized plants were 3.7 and 6.9 g/m², while the fertilized plants took up 10.7 and 20.1 g/m² at 4 MAP and FH stages, respectively. N, P, and K uptake rates strongly decreased during the dry season to 0.07, 0.004, and 0.03 g/m²/d on average. There was a rise in N, P, and K uptake rate to 0.1, 0.02, and 0.09 g/m²/d from 8 MAP to FH with the return of rainfall (Table 2). Nutrient uptake rates were much slower at Benue

Fig. 2 Cassava cumulative plant nutrient uptake for N (panels a, b, c), P (panels d, e, f), and K (panels g, h, i) and total biomass (panels j, k, l) as a function of cumulative temperature sum from planting through harvests at 4, 8 months after planting (MAP) and final harvest. Intervals between symbols indicate average values for harvests at 4, 8 MAP and final harvest across the 2 years. The symbols—solid circle, triangle, square, and cross—represent treatments NfPfKf, NfPfK180, N150P40K180, and Control respectively. The arrows indicate average percentages (for all treatments) of N, P, and K uptake and biomass production at 4 MAP compared with final harvest



from 0 to 4 and 4 to 8 MAP than for the other locations, while uptakes rates were comparable from 8 MAP to FH. This suggests that nutrient uptake was reduced due to soil water limitations in the first 8 MAP, resulting in much less total nutrient uptake.

The peak nutrient uptake rate occurred in the first 4 MAP. The fastest uptake rates of N and P were obtained in Edo, while the largest K uptake rate was obtained in Cross River with values of 2.1, 0.25, and 1.24 kg/ha/d for N, P, and K respectively. The high nutrient uptake rate observed in Edo is related to availability of these nutrients and deep rooting ability of cassava, as the soil in Edo is well-structured and permits deep rooting, with large amount of soil water available to plants even during dry periods (Adiele 2020). Potassium was the most limiting nutrient at Edo, while soils in Cross River had a higher K availability. The least nutrient uptake rate was recorded for Benue. This could be attributed to limitations in soil water availability resulting from shallow rooting due to some periodic water stagnation at depth due to a clay-rich layer resulting in lower soil moisture availability in the dry season and a large impact of the seasonal dry conditions (Adiele 2020).

3.2 Leaf/stem and storage root/shoot nutrient accumulation dynamics

The ratio of N, P, and K uptake for leaves and stem strongly differed among growth stages ($p < 0.001$). The leaf/stem uptake ratio was largest at 4 MAP (3.6 for N, 1.2 for P, and 2.0 for K), and reduced to 0.47, 0.2, and 0.2 for N, P, and K at 8 MAP, before increasing at final harvest (1.1, 0.6, and 0.4 for N, P, and K). Also, the storage root/shoot N, P, and K ratios differed only between growth stages ($p < 0.001$), with lowest values at 4 MAP (0.4, 0.6, and 1.17 for N, P, and K), increasing to 0.67, 1.23, and 2.0 for N, P, and K at final harvest. Storage root/shoot N ratio decreased with crop age, while P and K uptake ratios increased significantly with crop age and DM (calculated from Tables S1–3).

3.2.1 Nitrogen, P, and K in leaves, stems, and storage roots

Both unfertilized and fertilized treatments showed similar trends with the largest proportion of N (55% of the total N uptake by the plant) in the leaves at 4 MAP (Fig. 3). At 8 MAP, N partitioning to the leaves decreased but increased in

the stems. Shoot N uptake at FH in fertilized treatments was proportionally largest in the stem at 54%, in contrast to the unfertilized treatment where the proportion of stem N in the shoot was 38% (Fig. 3). There was no significant difference between the fertilized and the unfertilized treatments in the partitioning of N, P, and K at the different growth stages ($p < 0.05$). Proportional P content was largest in the storage roots (54%) at final harvest and was similar for fertilized and unfertilized treatments (Fig. 3). The storage roots also accumulated the largest proportion of K, increasing from 4 MAP to FH for both unfertilized and fertilized treatments, in all locations and years (Fig. 3 and Table S3). The proportions of K in storage roots across locations and years were on average 49, 60, and 60% in the fertilized compared with 60, 70, and 69% for unfertilized treatments at 4, 8 MAP, and FH, respectively.

The storage root was the primary sink for P and K, demonstrated by the high storage root/shoot ratios, while the shoot was the primary sink for N. The storage root/shoot ratios for P and K increased with crop age and DM. A major reallocation of nutrients during growth took place between the leaves and stems (Table S4). The relative nutrient uptake and allocation

to plant parts varied over time but was similar for fertilized and unfertilized plants although the fertilized plants absorbed nutrients in much greater quantities, concurring with Howeler (2012). Results from our study show that varied fertilizer rates and locational differences did not result in any changes or modifications of cassava physiology. At the first harvest at 4 MAP, N was mostly partitioned to the leaves. The partitioning to leaves for N significantly reduced at 8 MAP, while at the same time, N partitioning to the stems increased. The re-growth of new leaves with onset of rains resulted in a larger partitioning of N to leaves while partitioning to stems was smaller (Fig. 3) resulting in a strong dilution of N in the stems.

3.3 Nutrient concentration in leaves, stems, and storage roots

The pattern of seasonal change in the N, P, and K concentrations was similar for locations and years, with smaller concentrations in leaves at 8 MAP than at 4 MAP or FH. Nutrient concentrations differed by growth stage and between unfertilized and fertilized treatments ($p < 0.001$) with a smaller leaf N,

Table 2 Average cassava nutrient uptake rates from 0 to 4, 4–8 months after planting (MAP), and from 8 MAP to final harvest (FH) at Edo, Cross River, and Benue across the years

Treatment	N (g/m ² /d)			P (g/m ² /d)			K (g/m ² /d)		
	0–4 MAP	4–8 MAP	8 MAP-FH	0–4 MAP	4–8 MAP	8 MAP-FH	0–4 MAP	4–8 MAP	8 MAP-FH
Edo									
NfPfKf	0.210	0.075	0.098	0.025	0.004	0.019	0.114	0.029	0.079
NfPfK180	0.178	0.053	0.049	0.018	0.002	0.012	0.074	0.027	0.028
N150P40K180	0.132	0.023	0.039	0.014	−0.002	0.005	0.064	0.020	0.023
Control	0.062	0.001	0.034	0.007	0.001	0.003	0.029	−0.007	0.022
ANOVA									
Treatment	*** (0.005)	*(0.017)	** (0.007)	** (0.001)	ns	*(0.003)	** (0.007)	ns	*(0.015)
Cross River									
NfPfKf	0.181	0.034	0.086	0.019	0.004	0.014	0.124	0.025	0.093
NfPfK180	0.130	0.028	0.053	0.015	0.003	0.005	0.090	0.022	0.044
N150P40K180	0.120	0.025	0.031	0.013	0.003	0.004	0.093	0.019	0.032
Control	0.042	0.014	0.030	0.005	0.001	0.002	0.093	0.008	0.025
ANOVA									
Treatment	-	ns	*(0.016)	-	ns	*(0.001)	-	ns	*(0.012)
Benue									
NfPfKf	0.070	0.019	0.069	0.008	0.003	0.017	0.049	0.020	0.092
NfPfK180	0.077	0.005	0.036	0.009	0.002	0.006	0.045	0.017	0.058
N150P40K180	0.06	0.005	0.034	0.006	0.001	0.004	0.041	0.014	0.047
Control	0.032	−0.003	0.025	0.004	0.001	0.003	0.027	0.005	0.026
ANOVA									
Treatment	-	ns	ns	-	ns	*(0.004)	-	*(0.003)	ns

*Significant at $P < 0.05$

**Significant at $P < 0.01$

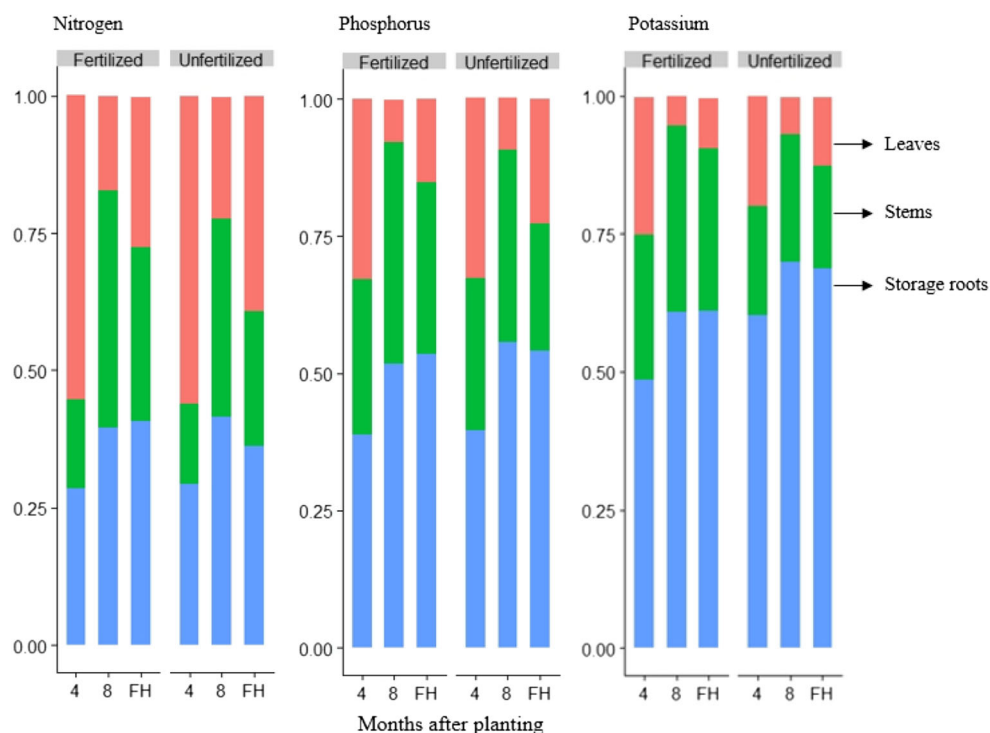
***Significant at $P < 0.001$

+Standard errors (SE) in parentheses and relates only to comparisons between significant terms

−One year available data for the period, yet uptake rates differed by treatments at 4 MAP

ns not significant

Fig. 3 Average N, P, and K concentrations (g/kg) per treatment across locations and years in leaves, stems, and storage roots at different cassava growth stages. The lines represent treatments: — Control, --- N150P40K180, - - - NfPfKf



P, and K concentration in unfertilized compared with the fertilized treatments (Fig. 4). The N, P, and K concentration in the leaves of the unfertilized treatment at 4 MAP (43, 2.8, and 8.2 g/kg) decreased to 39, 2.0, and 7.1 g/kg during the dry season (8 MAP) and increased later to almost the initial value when drought stress was relieved. For the fertilized treatment, N, P, and K concentration of leaves (46, 3.1, 12.5 g/kg) decreased at 8 MAP to 39.4, 2.0, and 8.18 g/kg. Nitrogen and P increased to the initial value at final harvest, while leaf K concentration was slightly reduced to 12.1 g/kg from the initial values. There was a steady decrease in P, K concentration in stems and roots. Also, N concentration in roots decreased,

but increased in stems at 8 MAP before declining towards FH (Fig. 4). There were no signs of dilution in the leaves, with concentration increasing with leaf biomass (Fig. S1, panel B). The opposite pattern was found for stems, with the greatest concentration of N at 8 MAP. The concentrations of P in leaves showed a strong seasonal pattern, while P in stems and storage roots strongly declined during development. The concentrations of K in leaves varied over the growth period, while K in stems and storage roots declined more strongly for fertilized treatments than for unfertilized treatments (Fig. 4).

At 4 MAP, N, P, and K concentrations in stems of the unfertilized treatments were 8.9, 2.1, and 5.3 g/kg compared

Table 3 Observed vs. literature values of minimum and maximum concentration of nutrients in cassava from 4 MAP to maturity across treatments, locations, and years

Nutrient	Measured values		Literature values		Sources
	Minimum	Maximum g/kg	Minimum	Maximum	
Leaves					
N	39.0	55.0	33.0	60.0	Howeler and Cadavid (1983); Howeler (2012); Santos et al. (2014)
P	1.8	4.4	2.4	3.8	
K	6.0	21.0	11.0	22.0	
Stems					
N	6.0	12	7.8	17.0	
P	0.6	2.6	1.8	2.4	
K	2.3	12.5	8.0	15.0	
Storage roots					
N	3.2	16.0	2.7	11.0	Howeler and Cadavid (1983)
P	0.6	2.2	0.9	6.0	
K	2.7	13.0	3.4	11.0	

to 9.7, 2.1, and 9.1 g/kg for the fertilized treatments. At about 8 MAP, stem N concentration increased to 10.5 and 11.7 g/kg in unfertilized and fertilized treatments, respectively, while P decreased to 1.16 g/kg in all treatments and K to 3.51 and 6.07 g/kg in unfertilized and fertilized treatments. At FH, there were decreases of 23, 59, and 48% of stem N, P, and K concentrations when compared to 4 MAP. Also, the storage root N, P, and K concentrations in unfertilized treatment (7.6, 1.0, and 7.4 g/kg) and 10, 1.5, and 9.3 g/kg in the fertilized treatment decreased in concentration at FH (Fig. 4). The observed maximum and minimum concentrations of N, P, and K are compared with values from the literature in Table 3.

Concentrations of nutrients in the cassava leaves varied with the growth stage, but within a narrow range throughout the season, as previously observed by Howeler (2012). The leaf N concentrations we observed were within the sufficiency range of 45 to 60 g/kg suggested for cassava (Santos et al. 2014). Contrary to the finding of Howeler (2012), stem N concentration increased at 8 MAP (dry season) (Fig. 4), while P and K concentration decreased in stems and roots (Fig. 4). This could be due to remobilization of N from senescing leaves and storage in the stems. At this stage, stem mass increased, thereby diluting the P and K concentration in the stem tissue. In addition, He and Dijkstra (2014) observed that plant P concentration decreased more than N during dry periods. This was because available soil N concentrations increased while those of P decreased. Potassium concentration varied least in the storage roots; consistent with reports from Howeler (2012). Also, Mallarino and Higashi (2009) observed in cereal crops that K concentrations vary less in grain than in vegetative tissues across a range of conditions. Understanding these trends in nutrient concentrations during cassava growth stages are

important to determine times of sampling and interpretation of plant analysis results to identify nutrient deficiencies.

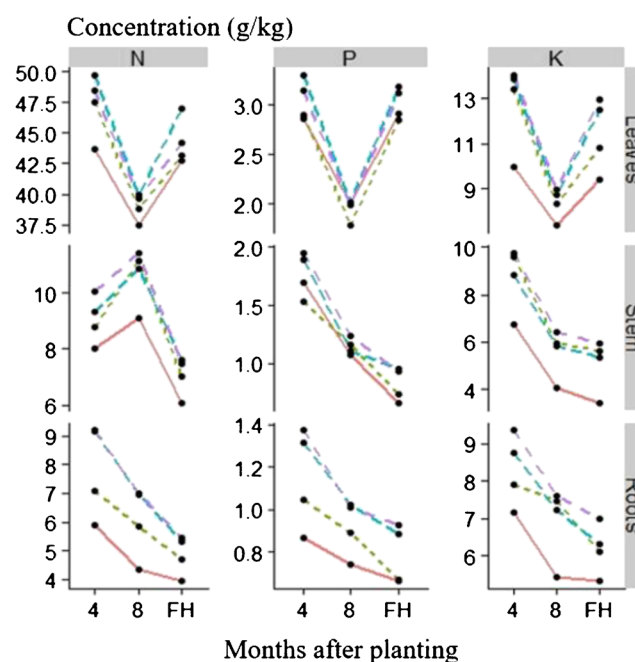
3.4 Nutrient dilution at different nutrient application rates

The plant concentrations of N, P, and K varied between 5 and 33, 0.6 and 2.0, and 3.0 and 11.4 g/kg, respectively. The nutrient dilution pattern for the different treatments (Control, N150P40K180, NfPfK180, and NfPfKf) with varied rates of applied N (0, 150, and 300 kg/ha), P (0, 40, and 100 kg/ha), and K (0, 180, and 300 kg/ha) are shown in Table 4 and Fig. 5. The concentrations of N, P, and K in the total biomass declined as DM increased during the growth period. The fertilized treatments had a larger *a* parameter value than the unfertilized (Table 4). The dilution coefficient parameter *b* for N and P was higher in the fertilized than unfertilized treatment, but parameter *b* for K varied among the treatments (Table 4).

3.4.1 Nutrient dilution curve for maximum growth rate

The NfPfKf treatment was considered to be non-nutrient limiting, and the associated dilution curve for this treatment was used to determine the nutrient concentration of cassava required for maximum growth (Fig. 5). The nutrient dilution pattern for total and shoot biomass was similar (Fig. 5). The equations indicate that $N_c = 82$, $P_c = 7.4$ and $K_c = 43$ g/kg DM, when total biomass equals 1 t ha^{-1} for cassava in tropical conditions of West Africa. About 73, 57, and 71% of the variation for total biomass were explained by the N, P, and K concentration from 4 MAP to FH. There was a declining trend of nutrient concentration with increasing DM and crop age (Fig. 5). The *a* parameter in the

Fig. 4 Proportions of total uptake of N, P, and K in leaves (red), stems (green), and storage roots (blue) at different growth stages, from approximately 4 months after planting to final harvest (FH) across location and years



dilution equation was derived for N, when set at 55 and 106 g/kg, P at 4.5 and 9.5 g/kg, and K at 25 and 45 g/kg for the C_{\min} and C_{\max} curves.

Our results suggest that nutrient dilution was stronger in cassava than in other crops (Greenwood et al. 1990; Justes et al. 1994; Ciampitti et al. 2013). The nutrient dilution may have been affected by the rapid storage root growth and translocation of assimilates to the roots, especially, under non-nutrient limiting conditions and water availability, as was the case in potato (Gomez et al. 2018). The NfPfKf treatment allowed a significant increase in growth rate and the data points were considered corresponding to sufficiency level (Fig. 5). As expected, the plant nutrient concentration for maximum growth ($N_c = 82\text{DM}^{-0.61}$, $P_c = 7.4\text{DM}^{-0.54}$, and $K_c = 43\text{DM}^{-0.54}$) decreased with increasing biomass resulting mainly from greater accumulation of assimilates in the storage roots and stems. The decrease in nutrient concentration of plant material is driven by changes in plant physiological processes as the plant ages. This is as a result of decrease in leaf area ratio (leaf area per unit of plant mass), as plants invest a greater proportion of biomass in structural (development of stems and storage roots) relatively to metabolic (e.g. leaf) tissues (He et al. 2017). The P and K requirements for optimal plant growth are 3–10 and 20–50 g/kg plant material (Hawkesford et al. 2012). Generally, the nutrient dilution of cassava is somewhat similar to potato and fodder beet (Chakwizira et al. 2016; Gómez et al. 2018), with higher dilution coefficients (b) than cereals (Ciampitti et al. 2013; He et al. 2017). Cassava and potato accumulate mainly starch in roots or tubers, thus plant N, P, and K concentrations would decline more rapidly with increasing crop mass as storage organ filling occurs. On the contrary, grain and legume crops accumulate large amounts of proteins in the grains, with smaller assimilate conversion efficiency hence less decline in plant N, P, and K concentration as the plants develop (Lemaire 2012). Also, differences in environmental conditions could contribute to the larger a and b coefficients in cassava due to high temperature and radiation in the tropics. As more radiation is captured, energy is made available for the plants to produce more assimilates and increase biomass. He et al. (2017) reported differences in dilution coefficients of rice (*Oryza sativa* L.) cultivated in southern and eastern China, which was attributed to differences in temperature and solar radiation, as lower temperature and radiation resulted in slower dilution. In our study, the amount of dry matter explained about 65% of

variation in nutrient concentrations for N, P, and K. This indicates that other factors may have contributed to the nutrient dilution e.g., crop age, sampling/harvest time spacing, nutrient availability, and self-shading of leaves.

3.5 Nutrition indices and relative biomass yield of N, P, and K

With the established C_{\max} and C_{\min} dilution curves (Fig. 5), the nitrogen nutrition index (NNI), phosphorus nutrition index (PNI), and potassium nutrition index (KNI) were obtained. The largest nutrition indices were obtained from the full treatment (NfPfKf) at 4 MAP and FH (Fig. 6). Except in the NfPfKf treatment, NI were generally small among treatments at 8 MAP (during the dry season). There was a linear relationship between relative biomass yield and NI across the locations. In Edo, about 69, 54, and 65% of the variation for the relative biomass for all treatments were explained by NNI, PNI, and KNI (Fig. 6). In Cross River, 72, 69, and 66% of the variation were explained (Fig. 6), while in Benue, 72, 69, and 66% of the variation were obtained (Fig. 6). The NNI and PNI values for Edo fell on the 1:1 line, whereas KNI was shifted to the left. This indicates that K was lower than in Cross River at equivalent biomass amounts. For Cross River, NNI and PNI were lower than for Edo, suggesting that K supply was most limiting in Edo, while in Cross River, K supply was sufficiently and N and P were less abundantly available. At Benue, the NNI, PNI, and KNI were on the left side of the 1:1 line, indicating strong dilution of the three nutrients. Especially in 2016, the final harvest in Benue had relatively low nutrient uptake when compared to Edo and Cross River, resulting in low nutrient concentrations and low NNI, PNI, and KNI values. The largest uptake rates after the dry period for Benue however were similar to the other sites (Table 2). The low NI value may have been due to a temporary lack of available nutrients resulting from a dry topsoil, coupled with low plant nutrient reserves, while high uptake rates after the rains resumed were sufficient to sustain maximum growth rates leading to strong nutrient dilution. This indicates that under very dry conditions, plant nutrient concentrations poorly reflect nutrient availability. A combination of NNI, PNI, and KNI explain 84% of the observed variation in relative yields (Table S5 and Fig. S4). However, harvest

Table 4 Estimated dilution coefficients of N, P, and K in the plant for different treatments

Treatment	N	R^2	P	R^2	K	R^2	Range DM t ha ⁻¹
Control	32 (DM) ^{-0.55}	0.53	3.1 (DM) ^{-0.48}	0.45	19 (DM) ^{-0.6}	0.57	5–57
N150P40K180	107 (DM) ^{-0.82}	0.84	9 (DM) ^{-0.73}	0.77	47 (DM) ^{-0.67}	0.74	5–57
NfPfK180	90 (DM) ^{-0.67}	0.67	8 (DM) ^{-0.6}	0.72	40 (DM) ^{-0.58}	0.80	5–57
NfPfKf	82 (DM) ^{-0.61}	0.73	7.4 (DM) ^{-0.54}	0.57	43 (DM) ^{-0.54}	0.71	5–57

time was a significant factor ($p < 0.001$, Table S6) due to slightly higher NI values for the second harvest, indicating that relationships between nutrition indices and yield vary in a season.

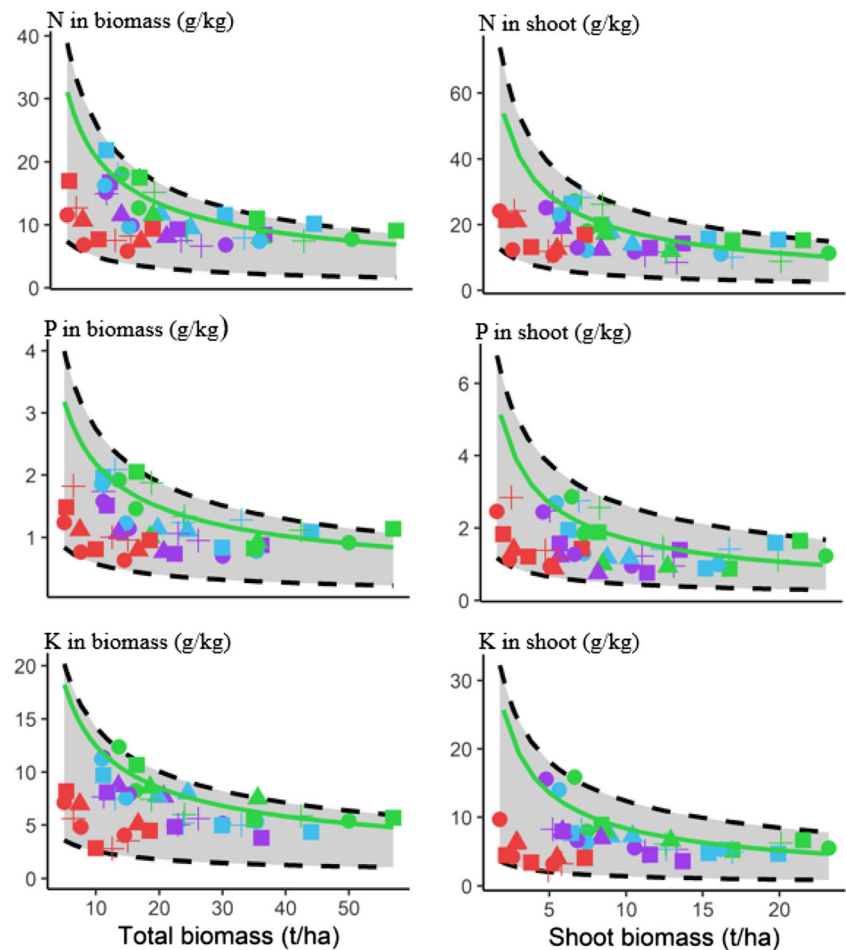
Nutrition indices indicate nutrient deficiency, sufficiency, luxury consumption, or excesses (He et al. 2017; Gómez et al. 2018). In our study, NI of the non-nutrient limiting treatments at 4 MAP and FH in Edo and Cross River were assumed to be in the sufficiency or luxury consumption zones. The obtained NNI ranged between 0.1 and 1.08 (4 MAP–FH), while most studies reported NNI between 0.25 and 1.5 for potato (Gómez et al. 2018) and 0.45 and 1.53 for rice (He et al. 2017). However, these authors obtained NNI by dividing the N concentration in the DM by the critical N concentration. For PNI, (Zamuner et al. 2016) recorded values > 1 when potato was supplied with 100 kg/ha P, in the Pampas region of Argentina. Though there is yet no known reported values of KNI either on cassava or other crops, the standard used to quantify the status of NNI and PNI were used to evaluate that of KNI values obtained from this study. The lowest nutrition indices of N, P, and K were obtained from the unfertilized treatments and during the dry season (Fig. 6). The NI can be used to assess the effect of nutrient on crop yield, as greater yields

in this study were associated with high nutrient amounts in the crop (Fig. 6). We observed positive linear relationships between relative biomass yield and NI estimated at different growth stages which is consistent with findings of Gómez et al. (2018) and He et al. (2017) for potato and rice, respectively. Relative biomass increased with increasing nutrition indices, and linear combinations of NNI, PNI, and KNI explained 84% of the variation in relative yields when accounting for site effects.

4 Conclusion

Our study provides essential insight in the dynamics of nutrient uptake and uptake rates of cassava under West African conditions for the first time. Results indicated that one-third of the total biomass expected at 12–14 MAP is achieved at 4 MAP under non-water limiting conditions. This can be used as a proxy for estimating final harvest biomass at 4 MAP. More than half of the total nutrient uptake was also required at that period, providing insights into optimizing timing of nutrient applications and management for maximum yield response. Also, our results enable an understanding of the

Fig. 5 N, P, and K dilution curves for plant nutrient concentrations as function of total plant and shoot biomass per treatment, location, and year. Each observation represents an average of three replications for each treatment. The black broken lines are the upper and lower “envelope curves”— C_{max} and C_{min} ; and the green line represents the N, P, and K dilution curves $NfPfKf$. The colors reflect treatments with red, purple, blue, and green for control, N150P40K180, NfPfK180, and NfPfKf respectively. The circles and triangles represent data from Cross River in 2016 and 2017 and the squares and crosses data from Edo in 2016 and 2017 respectively. Estimated dilution coefficients of N, P, and K in the shoot for NfPfKf treatments were as follows: $N_c = 86DM^{-0.68}$; $R^2 = 0.64$, $P_c = 8.2DM^{-0.68}$; $R^2 = 0.44$ and $K_c = 42DM^{-0.69}$; $R^2 = 0.55$, while that of the total biomass is $N_c = 82DM^{-0.61}$; $R^2 = 0.73$, $P_c = 7.4DM^{-0.54}$; $R^2 = 0.57$ and $K_c = 43DM^{-0.54}$; $R^2 = 0.71$



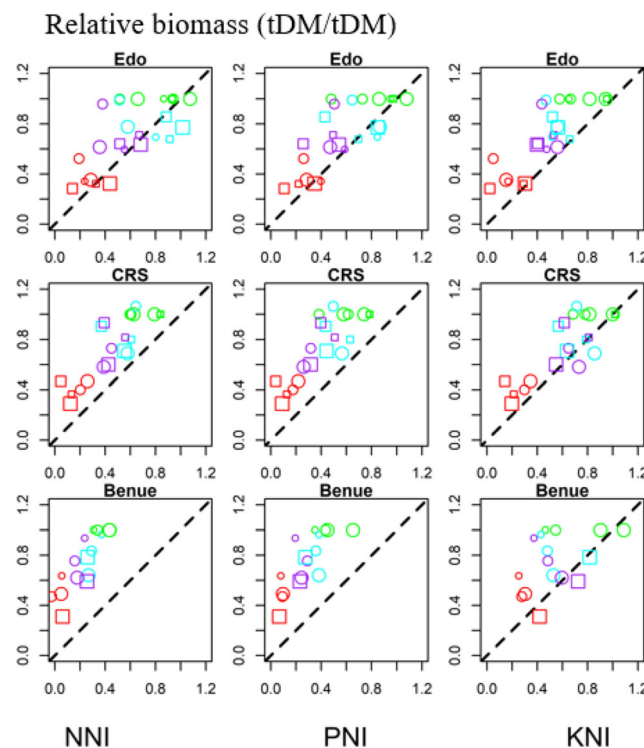


Fig. 6 Relationships between the relative accumulated biomass in tons dry matter (DM) and the N, P, and K nutrition indices (NNI, PNI, and KNI) for cassava at 4 and 8 months after planting and at final harvest with different N, P, and K application rates in three locations—Edo, Cross River (CRS), and Benue. Relative biomass is defined here as the ratio of biomass in each plot and the mean of the biomass in the three NfPfKf plots per location for each harvest. Different symbols indicate values recorded in plots for the year with squares for 2016 and circles for 2017

dynamics of nutrient concentrations among cassava plant parts during growth. This is important in terms of time of sampling and interpretation of plant analysis results. Nutrient dilution curves for N, P, and K at different application rates were quantified for the first time in cassava. We observed stronger nutrient dilution coefficients than those reported for most crops. Under conditions without water deficiency, the defined nutrition indices were linearly related to relative crop growth rates. Nutrition index values varied during the season but in combination they explained 84% of the variability in relative yield. These insights are key to further develop water- and nutrient-limited crop growth models that help to further optimize nutrition and to help us understand how water and nutrient limitations interact with crop growth rates and fertilizer response under a range of environments. Determining nutritional status of cassava at different growth stages from N, P, and K dilution curves allows identification of specific deficiencies and will in future enable adjustments in supply of these elements to increase yields.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s13593-020-00649-w>.

and colors for treatments (red for control, purple for N150P40K180, cyan for NfPfK180, and green for NfPfKf). The small and intermediate symbol sizes were used for the 4 and 8 MAP sampling while the largest symbol was used for final harvest. The black dashed line is the 1:1 line. There were overlap or missing points due to either; relative biomass for Cross River at 4 and 8 MAP in 2016 did not differ much for treatments or no available data for Benue 2016 and Cross River 2017 at 4 MAP

Acknowledgments The first author is grateful to the Netherlands Fellowship Program (NUFFIC) for a PhD scholarship. The research was carried out in the framework of the African Cassava Agronomy Initiative (ACAI), led by the International Institute of Tropical Agriculture (IITA) and funded by the Bill & Melinda Gates Foundation. We are grateful to Chinaza Ifenkwe for his assistance in the field and Rob van den Beuken for technical assistance.

Compliance with ethical standards

Funding This study was supported by the Netherlands Fellowship Programme (NUFFIC) (3183620098).

Conflict of interest The authors declare that they have no conflict of interest.

Author contribution Joy Geraldine Adiele: designing the experiments, data collection, analysis, writing, reviewing, and editing; Antonius GT Schut: designing the experiments, analysis, writing, reviewing, and editing; Kodjovi S Ezui, Pieter Pypers, and Ken E Giller: designing the experiments, reviewing, and editing.

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