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Modelling varietal differences in response to phosphorus in West African sorghum

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ABSTRACT

In West Africa's highly weathered soils, plant-available soil-P levels determine sorghum performance and yield to a far greater extent than projected variability in climate. Despite local landrace varieties having excellent adaptation to the environment and a relatively stable yield, sorghum grain yield remains quite low, averaging less than 1 t ha^{-1} . Low P availability in West African soils has significant effects on crop development and growth with potential grain yield losses of more than 50%. Use of mechanistic models, which integrate physiological processes, could assist with understanding the differences in P-uptake among varieties and guide effective P management. Yet only few crop models include a soil-plant P model for simulating crop yield response to P management. A generic soil-plant P module was developed for crop models in the Cropping System Model (CSM) of the Decision Support System for Agrotechnology Transfer (DSSAT) but the module was adapted and tested only on two crops, groundnut and maize. The aim of the study was to adapt the soil-plant P module for sorghum and perform initial testing on highly weathered soils in West Africa. Data used in adapting and testing the soil-plant P model for sorghum consisted of in-season P concentrations and dry weights of stems, leaves and grain from four sorghum varieties covering a range of maturities and photoperiod sensitivities and grown in high-P and P-deficient soils at ICRISAT-Mali. Results showed that the coupled CERES-Sorghum – P module reasonably reproduced the vegetative and grain yield reductions experienced in the field experiments with an average RMSE of 1561 and 909 kg ha^{-1} under high P conditions and 1168 and 466 kg ha^{-1} under low P conditions, respectively. The simulations are in most cases within the observation error. We also confirmed that contrasting variety types differ in their P-uptake dynamics relative to above-ground growth change over time, and hence respond differently to available P.

1. Introduction

Sorghum (*Sorghum bicolor*) was domesticated in Africa and remains an important staple crop for West African smallholder farmers. Domestication and long-term selection under variable and low-input environments has resulted in sorghums' diversity for adaptation to a wide range of several edaphic and climatic stresses, including limited phosphorus (P) availability, variable sowing dates and corresponding length of growing periods, drought, and water-logging, as well as biotic

stresses such as parasites and diseases attacking foliage, stems and/or grain. Despite landrace varieties' diverse adaptive traits contributing to relatively stable yields, grain productivity remains limited by low soil fertility, with yield averaging less than 1 t ha^{-1} (vom Brocke et al., 2010). Multi-year and multi-location testing with and without P-fertilization has shown that low plant available soil-P results in major yield losses, averaging 54% (Leiser et al., 2012).

Sorghum in West Africa is generally grown with limited or no fertilization on soils already deficient in available P. For example, the

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Table 1
Soil physical and chemical properties at four soil depths at the experimental site.

Soil layer cm	Particle size distribution (%)		Bulk density g cm ⁻³	pH (soil water)	Soil organic carbon%	Total soil N%	Bray 1 P (mg kg ⁻¹)		CEC Cmol(+) kg ⁻¹
	Clay	Silt					+ P	- P	
0–20	7.8	33.1	1.42	5.2	0.2	0.03	20.4	4.4	1.9
20–70	7.8	33.1	1.42	5.2	0.2	0.03	20.3	4.3	1.9
70–120	23.6	39.9	1.43	5.3	0.18	0.03	18	4.0	2.9
> 120	29.7	42.7	1.37	5.1	0.12	0.03	18	3.5	2.9

median plant-extractable P level of 5.5 mg[P] kg⁻¹ soil Bray 1-P in Malian sorghum fields (Leiser et al., 2012) is below the 7 mg[P] kg⁻¹ soil Bray 1-P considered to be the critical P-sufficiency threshold for West African sorghum production systems (Doumbia et al., 1993). West African production systems are characterized by a rapid agricultural intensification, coupled with a general tendency to reduce or eliminate fallow periods due to increasing human population pressure (Falconnier et al., 2016). Additionally, access to mineral fertilizers and credit to purchase fertilizers is highly variable, which creates both challenges and opportunities for farmers seeking to increase sorghum productivity.

Sorghum exhibits significant genetic variability for adaptation to low-P conditions, allowing breeders to select for improved productivity under low-input conditions (Leiser et al., 2012). Certain germplasm groups, particularly photoperiod sensitive and later-maturing landrace varieties, were identified as superior source materials for low-P adaptation breeding (Leiser et al., 2015, 2014). However, the physiological basis supporting this diversity in adaptation has not been documented. For example, it was not clear from the studies by Leiser et al. whether late maturity and/or photoperiod sensitivity in sorghum varieties are associated with low P adaptation. Such knowledge on physiological mechanisms explaining P uptake and use by grain sorghum is critical to designing efficient P management systems. Because crop models already integrate physiological relationships between crops and their environment, using the available data on sorghum response to P, to parameterize a crop model provides a framework for studying and understanding P uptake differences among varieties.

The Decision Support System for Agrotechnology Transfer (DSSAT)'s Cropping System Model (CSM)-CERES-sorghum model has been evaluated and tested widely for its ability to simulate crop development, growth and yield (White et al., 2015). However, the CERES-sorghum model currently does not account for P limitation effects, limiting the applicability of the model in P deficient environments. DSSAT includes a generic soil-plant P model designed in a way that allows it to be linked to any crop model within DSSAT, provided data are available for parameterization. Currently, DSSAT's P model has been linked to CROPGRO-groundnut (Naab et al., 2015) and CERES-Maize and parameterized for soybean and maize (Dzotsi et al., 2010).

The aim of this paper is to present current efforts to link and parameterize the generic DSSAT-P model for CSM-CERES-Sorghum. The objectives of the study are to (1) improve the current version of CSM-CERES-Sorghum to simulate sorghum growth and development responses to different P-soil conditions, and (2) use the improved model to better understand varietal differences in P-uptake dynamics.

2. Materials and methods

2.1. Field experiments

Four sorghum varieties were chosen based on their selection history, phenology (maturity and photoperiod sensitivity) and grain yield productivity to represent contrasting sorghum types cultivated in West Africa. These included the early maturing photoperiod insensitive CSM 63E, the intermediate maturity and photoperiod sensitive varieties CSM 335 and Fadda, and the later maturing and most highly photoperiod-sensitive IS 15401. The varieties CSM 63E, CSM 335 and IS 15401 are

open-pollinated Guinea-race landrace varieties, whereas Fadda is a single-cross hybrid with Guinea-race derived parents and grain yield productivity exceeding that of farmers' local varieties (Rattunde et al., 2016). Although all four varieties are currently cultivated by farmers in the zone of experimentation, CSM 335 can be considered as a local check as it originated in the experimentation zone.

Field trials were conducted during two growing seasons (2014 and 2015) at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) station in Samanko, Mali (12.52N; 8.07W). This location is part of the West African Savannah sorghum zone which has unimodal rainfall, averaging 950 mm annually and falling mainly between June and October, and an average temperature of 28 °C. Temperature, solar radiation and rainfall were measured on a daily basis by an automatic weather station installed at a distance of 500 m from the experimental site.

The trials were rain-fed and conducted in adjacent fields managed for contrasting plant-available P levels with annual inorganic P fertilization in the high-P (HP) and no P fertilization since 2006 in the low-P (LP) fields. Soil samples collected to 1 m depth before sowing were analyzed for Bray 1-P at the ICRISAT-Niger laboratory. The P content was 4.43 mg [P] kg⁻¹ soil Bray 1-P in the low P site, and 20.4 mg [P] kg⁻¹ soil in the high P site (Table 1). The HP field was fertilized with 100 kg ha⁻¹ diammonium phosphate (DAP) as basal fertilizer and 50 kgha⁻¹ urea as top dressing, i.e. 41 kg[N] ha⁻¹ and 20 kg[P] ha⁻¹. The LP field received only split top dressings of nitrogen (N) in the form of urea, with the same N rate and timing applied to the HP field.

Each trial consisted of sixteen plots of 42 m² (seven 8-m rows with 0.75 m distance between rows and 0.20 m between hills; with one plant per hill), representing a completely randomized block design, with four replications, within each P field conditions. The outer two rows were excluded from sampling to prevent border effect on the measurements. The leaf area index was measured at maximum canopy cover (appearance of flag leaf), and above-ground biomass (leaves + stems) was sampled on 5 consecutive plants at 15-day intervals beginning one month after sowing until 10 days after anthesis. Final harvest at maturity was conducted on an area of 4 m² in 2014 and 3 m² in 2015 per plot to determine final biomass and grain yield. Total fresh weights were measured on a plot basis with subsamples oven-dried at 70 °C for 72 h. P concentration of dried total biomass (leaves + stems) were analyzed at the Laboratoire Sol-Eau-Plante of INERA Farako-Ba, Burkina Faso.

2.2. Model

The CSM-CERES-Sorghum crop model (Alagarswamy et al., 1989; White et al., 2015) simulates crop growth based on radiation use efficiency, adjusted for CO₂ air concentration. Leaf area is simulated based on an initial potential leaf size and the cumulative leaf number derived from the phyllochron parameter characterizing the cultivar simulated. A key parameter that influences leaf expansion is a leaf size-related scalar, G1, which affects leaf growth as follows:

$$PLA = A \times e^{\{-10.34 \times e^{-(0.13 + 0.003G1) \times LVN}\}} \quad (1)$$

with PLA the leaf area of the primary shoot in m² per plant, A the maximum leaf area, set to 0.6 m².plant⁻¹, and LVN the cumulative leaf

number.

The model simulates five phenological phases using thermal time and photoperiod: from emergence to end of juvenile phase (P1), end of juvenile phase to panicle initiation (P2), from flag leaf elongation extension to anthesis (P3), from anthesis to beginning of grain filling (P4) and finally from beginning of grain filling to physiological maturity (P5). The CSM-CERES-Sorghum accommodates the photoperiod sensitivities of West African sorghums that enables them to flower at fairly fixed dates prior to the end of the rainy season independent of widely differing planting dates (Sanon et al., 2014; Traoré et al., 2007). Key model parameters related to this process are P2O, defining the longest day length at which progress to flowering occurs at a maximum rate, and P2R, the delay of panicle initiation when daily photoperiod exceeds P2O. Partitioning of assimilate follows rules which vary with development stages. Leaf biomass during the vegetative phase depends mostly on leaf expansion through specific leaf area. Stem biomass allocation is proportional to leaf biomass and related to tillering. Panicle and grain dry matter accumulation begins with the reproductive phase (P5) and depends on rate of biomass production during this phase and the biomass level at the beginning of this phase and a parameter (G2) that scales the proportion of assimilates allocated to the panicle.

2.3. Coupling of soil and plant P modules with CSM-CERES-Sorghum

In DSSAT v4.5, the CSM-CERES-Sorghum model includes algorithms for water and nitrogen stress dynamics (White et al., 2015) but previously did not include P stress response, which limited the applicability of the model in P deficient environments. The modular format of the DSSAT-CSM model (Jones et al., 2003) facilitated coupling of the generic soil and plant P modules to crop models in DSSAT, specifically CERES-Maize (Dzotsi et al., 2010) and CROPGRO-Peanut (Naab et al., 2015). The generic P model comprises three modules, the soil P organic module, the soil P inorganic module, and the plant P module, based on Daroub et al. (2003). The version of the P model currently in DSSAT v4.5 contains a number of improvements (Dzotsi et al., 2010), including i) modifications to organic P dynamics to make organic P transformations consistent with the CENTURY soil organic matter model, ii) a decision tree for initialization of P pools based on readily-available soil data and extractable P, iii) changes to the calculation of soil solution P to account for the effect of soil water, soil texture and soil organic matter, and iv) re-parameterization of the optimum and minimum shoot P concentration. More detail on the P model in DSSAT v4.5 can be found in Dzotsi et al. (2010).

While movement of organic P follows soil organic matter flows (as simulated by the CENTURY model), inorganic P is affected by P immobilization or mineralization from soil organic matter, P additions from fertilizers, and plant P uptake. P movements among the inorganic pools, labile, active and stable, are governed by rate constants, which depend upon the degree of soil weathering as well as other soil properties. The inorganic pools are further partitioned into “root zone” or “no root zone” pools (representing P in the soil that is inaccessible by roots) with root P uptake occurring in the “root zone” labile inorganic pool. This root zone is an actual soil volume defined according to root length density to be predicted in the different soil layers and a radius adjacent to roots length (ROOTRAD), in which P is taken up. This modeling philosophy forces P uptake to occur within a defined radius adjacent to roots (ROOTRAD), which is consistent with the particularly slow movement, characteristic of P in soils.

The plant P module uses P concentration in the shoot tissues to determine the level of P stress experienced by the crop. Shoot P concentration is defined as the ratio of shoot P mass to shoot dry mass. P mass increases as a result of P uptake and dry matter increases as a result of growth. The model calculates optimum (critical) and minimum P concentrations during the season, to characterize the crop P status at optimum P uptake and maximum P stress, respectively. Beginning at optimum P concentration at emergence, the actual shoot P

concentration decreases when uptake is insufficient to meet the growth demand, resulting in crop P stress that reduces growth and leaf expansion. Uptake of P is the minimum of P supply (from the “root zone” labile inorganic P pool) and P demand, calculated as the P mass needed to bring existing and new shoot dry matter to optimum concentration.

The P model uses a P stress factor to modify photosynthesis, dry matter accumulation and partitioning using two main parameters: the vegetative partitioning sensitivity ratio (SRATPART), and the photosynthesis sensitivity ratio (SRATPHOTO). SRATPHOTO affects the daily plant growth rate and leaf senescence, while the SRATPART affects leaf expansion and growth of stems. These two parameters are thresholds below which photosynthesis is reduced (SRATPHOTO) or vegetative partitioning is affected (SRATPART), in response to P deficit. As the values of SRATPART or SRATPHOTO decrease, earlier and more severe stresses impact plant processes (Eqs. (2) & (3)).

$$PStressFactorPhotosynthesis = \text{MIN} \left(1, \frac{PStressRatio}{SRATPHOTO} \right) \quad (2)$$

$$StressFactorPartitioning = \text{MIN} \left(1, \frac{PStressRatio}{SRATPART} \right) \quad (3)$$

where

$$PStressRatio = \text{MIN} \left(1, \frac{(PConc_{Shoot} - PConc_{ShootMin})}{(PConc_{ShootOpt} - PConc_{ShootMin})} \right) \quad (4)$$

with $PConc_{Shoot}$ is the actual P concentration, $PConc_{ShootOpt}$ and $PConc_{ShootMin}$, optimum P concentration the optimum and minimum limits of shoot P concentrations, respectively.

To parameterize the P model for CSM-CERES-Sorghum model, experimental data were used to define the optimum and minimum limits of shoot P concentrations, which were initially considered as independent of the sorghum varieties studied. To test for varietal differences in P stress expression an analysis of variance (ANOVA) was performed for maximum leaf area index, grain yield and above-ground biomass under contrasting soil-P conditions using the statistical model:

$$\mu_{ijk} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \gamma_{jk} + \varepsilon_{ijk} \quad (5)$$

where μ is the grand mean, α_i is the main effect for varieties, β_j is the main effect for the P level, and $\alpha\beta_{ij}$ the interaction factor; γ_{jk} is the replication factor within each P level; and ε_{ijk} is the error.

When a significant interaction ($p < 0.05$) between the two factors (varieties and P level) was found for leaf area index, final biomass and grain yield, we adjusted the P stress factors (SRATPART, SRATPHOTO) to mimic the observed varietal differences.

The soil P module was initialized using data in Table 1.

2.4. Model calibration and evaluation

We calibrated the P model for four contrasting West African sorghum varieties using 2014 experimental data by manually adjusting the parameters influencing crop P stress to fit the observed reduction in crop growth attributable to P. The calibration followed a two-step approach. First variety parameters (mostly related to phenology) were set based on parameters from Akinseye et al. (2017). This calibration was based on phenology and final yield data, as well as P concentration in vegetative biomass in high P conditions in 2014. Next, we adjusted the P parameters, SRATPART, SRATPHOTO and ROOTRAD, to reproduce the P stress conditions observed in the LP treatments in the 2014 data.

For model evaluation we used the 2015 dataset. The observed vegetative biomass (leaves + stems) dynamics and P concentration in vegetative biomass from HP and LP treatments as well as phenology and final yield data collected in 2015 were compared with simulated values.

The relative mean absolute error (rMAE) and the root mean square error (RMSE), calculated based on the observation and simulation pairs

were used to evaluate the ability of the model to simulate the in-season vegetative biomass and vegetative P concentration and phenological development, and final vegetative and grain yields.

The rMAE and RMSE were calculated using the following equations:

$$rMAE = \frac{1}{n} \sum_{i=1}^n \left(\frac{|Si - Oi|}{Si} \right) \quad (6)$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^r (Si - Oi)^2}{r}} \quad (7)$$

with Si is the simulated value and Oi the observed value, $i = 1, \dots, n$, with n the in-season observations (varying from 5 to 8 according to the varietal cycle length), and r the number of repetition.

We used computed values of rMAE and RMSE based on the 2014 data to assess the accuracy of the model calibration, prior to conducting the evaluation using the 2015 data. The lower the rMAE and RMSE values, the better the agreement between simulations and observations.

To understand the phosphorus efficiency strategy of the different varieties, we calculated the daily phosphorus acquisition efficiency (PAE) as follow:

$$PAE = \frac{PUPD}{PAVLD} \quad (8)$$

with $PUPD$ the P plant uptake from the soil in $\text{kg}[P] \text{ ha}^{-1}$ per day and $PAVLD$ the soil P available to plant, based on simulated root volume and simulated soluble P in that volume in $\text{kg} [P] \text{ ha}^{-1}$

The computation of PAE is only possible using a crop model as soil available P content is not commonly measured in the field. The PAE value over the growing season should help us to pinpoint whether different growth patterns could impact early or late P uptake, while the phosphorus use efficiency will show when the plant will take advantage of the cumulative P taken up during the growing season.

3. Results

3.1. Model calibration with 2014 data

Among the main calibrated parameters for the four sorghum varieties, those for phenology differed most (Table 2). The most photoperiod (PP) sensitive variety (IS 15401) had the longest cumulative degree days from end of juvenile stage until flowering and the highest

P2R value, Fadda and CSM335 were moderately PP sensitive, and CSM63 was the least PP sensitive. Further, scalers (G1 and G2) were adjusted to represent the potential growth of each variety, with Fadda having a higher grain yield potential and thus a higher value for G2, and IS15401 a higher biomass potential and therefore a lower value for G1.

Table 3 presents the results of simulations and the comparisons to observed data for the calibration and validation data. The RMSEs for phenology were 1–3 days for flowering and maturity dates, respectively, in 2014 under high P conditions. The 2014 final simulated yields (vegetative biomass and grain yield) agreed reasonably with observed values for all varieties except for Fadda grain yield (in high P conditions) which was highly overestimated (explanation in the discussion section). RMSEs varied from 135 to 2680 kg ha^{-1} for final vegetative biomass and from 253 to 2259 kg ha^{-1} for final grain yield (Table 3a). Once the growth and development parameters were calibrated for the high P conditions, parameters representing the P dynamics were adjusted using the in-season vegetative biomass and P concentration data from the 2014 experiment, and final yields were evaluated again for the low P conditions.

Plant phosphorus concentration parameters (critical and minimal concentrations) were determined based on the observed shoot P concentrations averaged across the four varieties in the 2014 data (Fig. 1). We kept the same P concentrations for all varieties, as done in the maize and peanut models.

With respect to the parameters influencing plant P stress (SRATPHOTO, SRATPART and ROOTRAD), we considered them to be the same for the four varieties (Table 2b) because the ANOVA did not show any significant interaction ($p < 0.05$) between the varieties and the P treatments for maximum leaf area index, grain yield and final biomass (Table 4).

SRATPART and SRATPHOTO were calibrated by manually adjusting their values to get the smallest deviation between observed and simulated P concentrations and vegetative biomass in the 2014 data (Fig. 2). The standard value of ROOTRAD for maize (0.002 m) was used for sorghum as well because data were not available to calibrate this parameter. The calibration resulted in reasonable agreement between simulations and observations for all varieties under high- and low-P conditions, except for Fadda for which the model showed a tendency to overestimate the P stress affecting vegetative biomass (rMAE = 0.51, Table 3a and Fig. 2a). Although the vegetative biomass for IS15401 was

Table 2

Key crop model parameters derived for the four contrasting West African sorghum varieties (a) and parameters specific to the phosphorus module (b) coupled to the DSSAT-CERES-Sorghum model.

DSSAT ID	Definitions	units	Parameter values			
			CSM335	CSM63E	Fadda	IS15401
(a) cultivar coefficient						
P1	Thermal time from seedling emergence to the end of the juvenile phase during which the plant is not responsive to changes in photoperiod (PP)	$^{\circ}\text{C}\text{-day}$	400	300	300	500
P2	Thermal time from the end of the juvenile stage to panicle initiation under short days	$^{\circ}\text{C}\text{-day}$	252	102	252	300
P2O	Critical photoperiod or the longest day length at which progress to flowering still occurs at a maximum rate, with PP values larger than the optimal P2O reducing the rate of development	hours	12.8	12.8	12.8	12.8
P2R	Delay in progress to panicle initiation per hour PP increase in photoperiod above P2O	$^{\circ}\text{C}\text{-day}$	1000	100	1000	1800
PANTH	Thermal time from the end of panicle initiation to anthesis	$^{\circ}\text{C}\text{-day}$	617.5	647.5	617.5	640.5
P3	Thermal time from complete flag leaf extension to anthesis	$^{\circ}\text{C}\text{-day}$	252.5	142.5	152.5	300.5
P4	Thermal time from anthesis to beginning grain filling	$^{\circ}\text{C}\text{-day}$	81.5	61.5	81.5	81.5
P5	Thermal time from beginning of grain filling to physiological maturity	$^{\circ}\text{C}\text{-day}$	400	450	350	350
PHINT	Phylochron interval; the interval in thermal time between successive leaf tip appearances	$^{\circ}\text{C}\text{-day}$	60	55	49	55
G1	Scaler for relative leaf size	unitless	10	16	10	0.5
G2	Scaler for partitioning of assimilates to the panicle	unitless	3	3	6	2
(b) species coefficient						
SRATPHOTO	Photosynthesis sensitivity ratio to P stress		0.8			
SRATPART	Partitioning sensitivity ratio to P stress		0.2			
FracPMobil	Maximum fraction of P which can be mobilized from leaf and stem per day		0.1			
ROOTRAD	Radius of cylinder around roots from which soil P can be extracted	m	0.002			

Table 3

Relative mean absolute error for in-season growth (rMAE) for vegetative biomass and vegetative phosphorus concentration, and root mean square errors (RMSE) for key phenology dates and final biomass and grain yield, evaluated in low P and high P field conditions in (a) 2014 and (b) 2015. 'na' indicates that data were not available.

		High P conditions				Low P conditions			
		CSM335	CSM63E	FADDA	IS15401	CSM335	CSM63E	FADDA	IS15401
a) Experiment and simulation from 2014									
rMAE	Vegetative aboveground biomass	0.18	0.3	0.29	0.27	0.12	0.28	0.51	0.33
	Vegetative P concentration	0.15	0.22	0.3	0.3	0.19	0.07	0.2	0.46
RMSE	Flowering date (days)	1	1	na	na	2	1	5	4
	Maturity date (days)	3	2	3	3	8	13	8	13
	Final Vegetative aboveground biomass (kg ha ⁻¹)	1447	135	1631	2680	417	948	1753	957
	Grain yield (kg ha ⁻¹)	258	253	2259	515	275	479	665	429
b) Experiment and simulation from 2015									
rMAE	Vegetative aboveground biomass	0.34	0.37	0.34	0.34	0.39	0.49	0.44	0.48
	Vegetative P concentration	0.21	0.19	0.15	0.17	0.3	0.39	0.44	0.52
RMSE	Flowering date (days)	0	1	na	na	1	12	11	14
	Maturity date (days)	2	1	5	4	7	35	7	35
	Final Vegetative aboveground biomass (kg ha ⁻¹)	1317	897	1600	2779	1162	542	1296	2265
	Grain yield (kg ha ⁻¹)	1073	453	892	1573	468	488	571	353

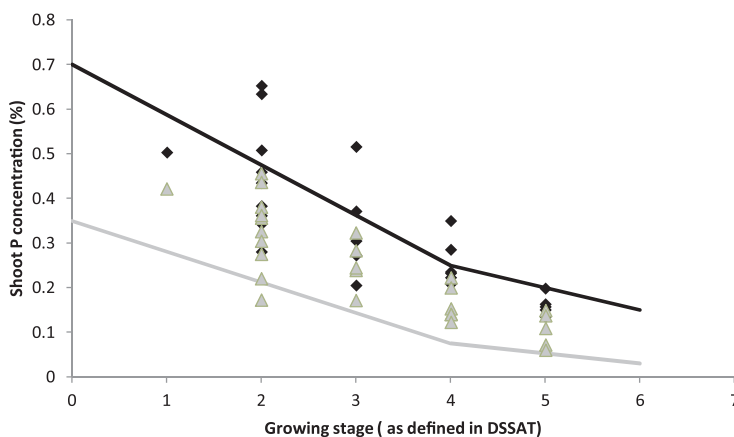
reasonably simulated in low P conditions, the corresponding P concentrations were overestimated (rMAE = 0.46), especially towards the end of the growing season (Fig. 2b). The rMAE values in 2014 low P conditions varied for vegetative biomass from 0.12 for CSM335 to 0.51 for Fadda, and for shoot P concentration from 0.07 for CSM63E to 0.46 for IS15401 (Table 3a).

Under low P conditions in the experiment, flowering and maturity dates were delayed. This delay in phenology due to P was not simulated by the model, resulting in RMSEs as high as 13 days in 2014 (Table 3a). The 2014 RMSEs for final vegetative biomass under low P conditions ranged from 417 to 1753 kg ha⁻¹ and for grain yield from 275 to 665 kg ha⁻¹ (Table 3). The model estimates were within the observation error for the final vegetation biomass (Fig. 3a). Likewise for grain yield for the high P conditions, the model estimates were within the observation error for CSM63E and CSM 335, but not for Fadda and IS15401 which exhibited a lower yield in the experiment. Under low P conditions, the model showed a tendency to slightly underestimate grain yield by 26% on average (Fig. 3b).

3.2. Model evaluation with 2015 data

The model accurately predicted the phenology in high P conditions with a maximum of 5 days deviation for maturity date. However, consistent with the 2014 experiment, the model predicted maturity occurrence much earlier than observed in low P conditions, up to a month (Table 3b).

The simulations were in good agreement with the vegetative

**Table 4**

Mean squares and the significance level of each treatment for leaf area index (LAI), aboveground biomass (AGB) and grain yield of the 4 varieties evaluated in low P and high P field conditions in 2014 and 2015.

Source of variation	df	Mean Squares and P Value		
		LAI	AGB	Grain Yield
Year	1	4.261***	596246 ***	5
Variety	3	1.649**	238171704***	5065137***
P treatment	1	0.033	711868620**	8480929***
YEAR*Variety	3	0.588	125934761*	338945
Year*P treatment	1	0.406	106465447*	11608380***
Variety*P treatment	3	0.089	83949281*	802251⁺
Year*Variety*P treatment	3	0.505	61438968 ⁺	1129343*

+, **, ***, = F-statistics of respective mean squares significant at p-level < 0.1, 0.05, 0.01, 0.001, respectively.

biomass data, with RMSE varying from 542 to 2779 kg ha⁻¹ (Table 3b). These simulations were within the observation error (Fig. 3a), except for IS15401 in high P conditions, for which the model overestimated final vegetative biomass. For grain yield the RMSE ranged from 353 up to 1573 kg ha⁻¹. Grain yield reduction due to P stress was reasonably simulated for Fadda and CSM63E (Fig. 3b). For CSM335 and IS15401, the model underestimated grain yield in the high P treatment and failed to simulate the magnitude of the response to P.

The rMAEs were reasonable for P concentration (mostly under 30% in high P conditions), but higher for vegetative biomass. The simulated

Fig. 1. Optimum and minimum P concentrations in vegetative tissue as a function of growing stages for sorghum. Lines represent the optimum (black) and minimum (grey) shoot P concentration used in the P module for the sorghum model, and the observed sorghum shoot P concentration in the +P field (black dots) and -P field (grey dots) for each of the varieties in 2014. Stages 0–2 represent the vegetative phase, with the end of stage 2 being the panicle initiation, stages 3 and 4 represent the reproductive stage with 4 being the flowering stage (from flag leaf to the beginning of grain filling) and stages 5–6 being the grain filling period, with 7 the harvesting time.

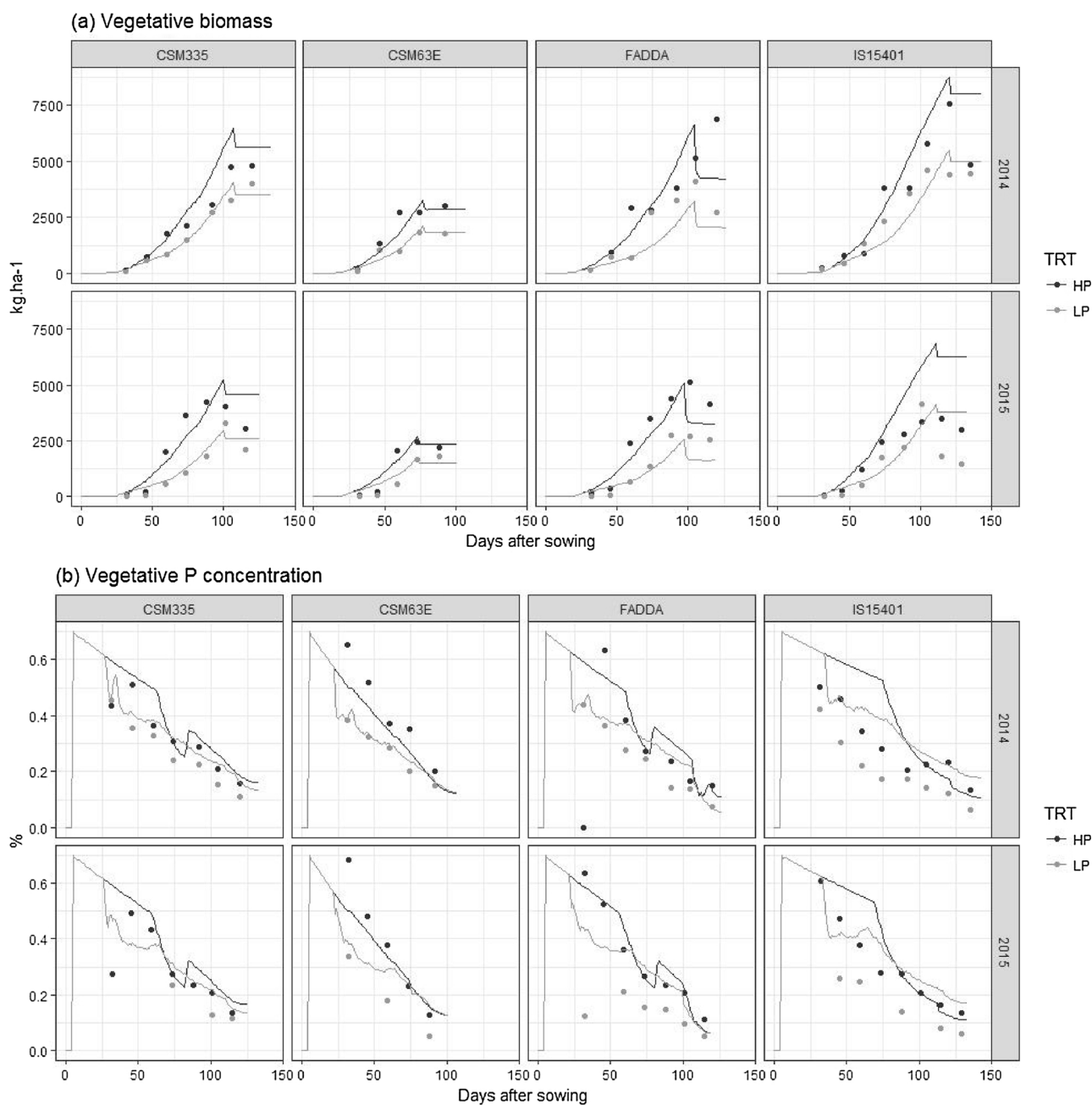


Fig. 2. Comparison of simulated (lines) vs. observed (points) for (a) vegetative biomass (VWAD: stems + leaves dry matter in kg ha⁻¹) and (b) phosphorus concentration in vegetative biomass for four varieties in 2014 and 2015 under high P (HP, black) and low P (LP, gray) conditions.

in-season biomasses in 2015 were in concordance with in-season observations, consistent with 2014 results. An outlier was IS15401 under high-P conditions, for which 2015 vegetative biomass was overestimated by the model, with a rMAE of 0.48 (Table 3b). The model simulated vegetative P concentrations were generally lower than observed while showing a tendency of overestimation of end-season P concentrations.

Overall, the model could reproduce vegetative biomass and grain yield reduction due to P stress and these simulated variables were within the observation error (Fig. 3). However, in some cases, the observed data showed a surprisingly negative response to P treatments (i.e. the final vegetative or grain yield was higher in low P conditions than in high P conditions). This negative response was observed especially for Fadda grain yield in 2014 and for IS15401 vegetative biomass in 2015 (Fig. 3). As expected the model could not reproduce this behavior, and for these particular cases, the simulations were not within

the observation error. This will be discussed in details in the quality of field data, and model improvements sections.

3.3. Modeling plant P dynamics for two contrasting varieties

The simulated P acquisition efficiency (PAE) for the two most contrasting varieties, i.e. CSM63E (early maturing and PP insensitive) and IS15401 (later maturing and highly PP sensitive) showed different dynamics under high P conditions (Fig. 4a). CSM63E had a higher P acquisition efficiency at the beginning of the growing season while IS15401 appeared to be more efficient later in the vegetative phase. Although both varieties were exposed to the same root zone available P initially (Fig. 4b), CSM63E extracted more P at the beginning of the growing season while IS15401 had a higher uptake rate and PAE later during the growing season (Fig. 4c).

These differences due to crop growth patterns differences help to

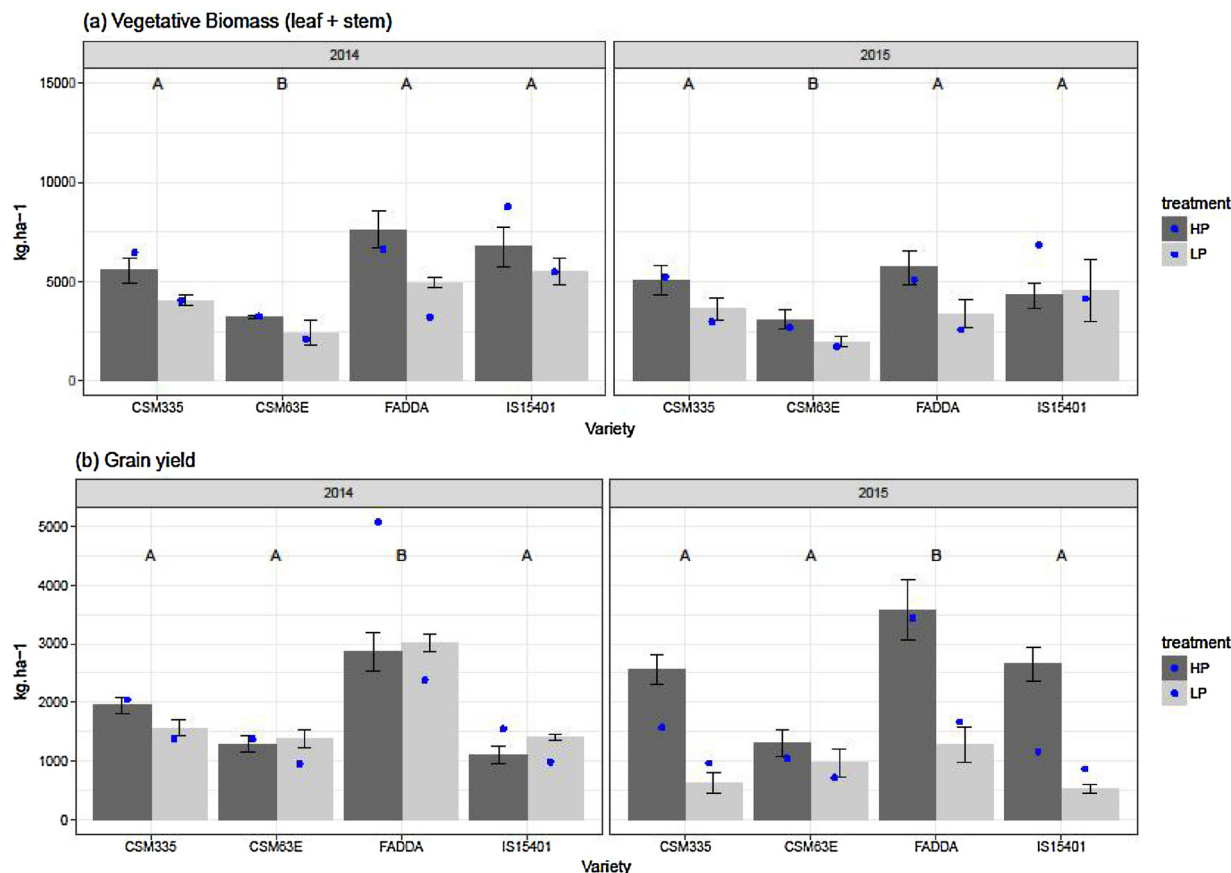


Fig. 3. Comparison of observed (bars) and simulated (blue points) (a) final vegetative biomass and (b) grain yield of the four varieties grown under high (HP) and low (LP) soil phosphorus conditions in 2014 and 2015. Letters represent the significant differences among varieties with confidence interval ($P < 0.05$). The error bar represents the standard error of the observations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

explain why the model could accurately simulate varietal differences despite using the same P parameters in the model for all varieties. The ANOVA did not reveal any significant differences in variety \times P level interactions, suggesting that the same crop P parameters should be used

for all varieties. However, the model was able to simulate the observed varietal differences for low P biomass and grain yield reductions (Fig. 3). CSM63E was the variety with the least observed relative grain yield reduction due to low-P (12% reduction) while the local variety,

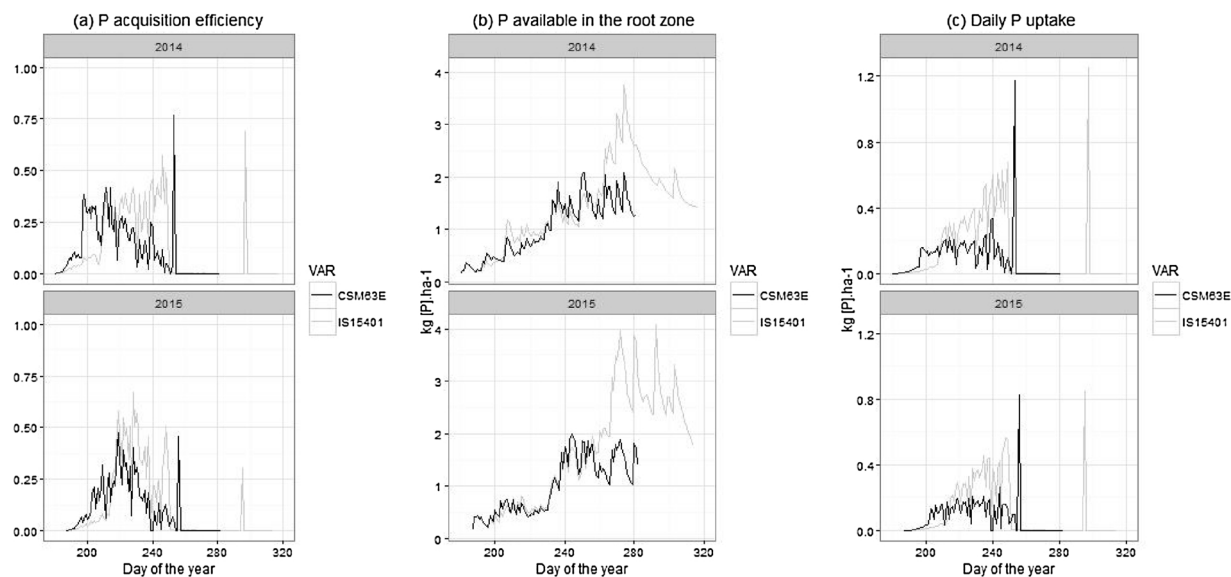


Fig. 4. Simulated daily (a) phosphorus acquisition efficiency, (b) phosphorus available to the plant, and (c) phosphorus uptake by two contrasting sorghum varieties, CSM63E (black line) and IS15401 (grey line) in high phosphorus conditions in 2014 and 2015 experiments. Even if P is available till day 280 and 320, PAE and daily Puptake stop at days 245 as there is no P uptake during the grain filling period.

CSM335 showed a greater grain yield reduction of 55% (Fig. 3b). For vegetative biomass, IS15401 was the most tolerant to low P conditions with only 8% reduction, while Fadda had the strongest reduction (36%) (Fig. 3a).

4. Discussion

Adaptation of the CSM-CERES-Sorghum to simulate P-limited growth demonstrated that a crop model can be used to simulate sorghum growth response to P deficiency and to confirm and understand P uptake patterns according to variety. The improved CSM-CERES-Sorghum model was used in this study to confirm previous findings by Leiser et al. (2015) that contrasting sorghum variety types differ in their P-uptake dynamics relative to above-ground growth change over time, and hence respond differently to soil P availability. Although, no variety-specific crop P parameters were used, the model simulated the observed biomass and grain yield reduction due to low soil available P for all varieties with reasonable accuracy (Fig. 3).

4.1. Quality of field trials data

Measured data from our experiments showed no significant variety by P level interaction for grain yield, therefore species crop P stress parameters were employed for modeling yield irrespective of the variety. Additionally, we identified the need to set SRATPART to a lower value than the initial default value to represent the lack of significant effect of P treatment on the leaf area index (Table 4). By doing so, we lowered the effect of P stress on the leaf area dynamics. Employing the P module, the model was able to simulate the vegetative- and grain-yield reductions in low P relative to high P conditions, attaining the same average level of grain-yield reduction as reported in Leiser et al. (2014): reductions from 38 to 57% under low-P (4.4 mg [P] kg⁻¹ soil Bray 1-P) soil versus under P-fertilized condition. The rather high RMSE for grain yield for Fadda in 2014 might be due to an unusually high observed grain yield, especially under low P conditions. However, vegetative biomass could be considered as a better measure than grain yield to assess P stress, as vegetative biomass is less modified by exterior factors causing changes in dry matter partitioning and loss (i.e. birds, midge, etc.). This probably explains why, for Fadda in 2014, P stress was observed on vegetative biomass but not on grain yield, which is more likely to be affected by biotic factors (i.e. midge) in the experiments (Fig. 3).

4.2. Model improvements

The poor simulation results for grain yield for IS15401 and CSM335 under high P conditions in 2015 are probably due to simulated P stress that was not observed during the experiment. The simulated P stress was primarily modeled by a reduction of plant P demand from panicle initiation to anthesis. In the original CSM-CERES-Sorghum model (White et al., 2015) the stem growth rate is dependent upon development stages. In late maturing, photoperiod sensitive varieties, this modeling philosophy means that the stem extension stage is extended over a longer period of time, which can create an artificial slow stem growth rate, hence a low P uptake. This issue was discussed in Lopez et al. (2017) who adapted CSM-CERES-Sorghum for sweet sorghum, by calculating the stem growth rate as a linear function of thermal time. This adjustment enables the partitioning of more dry matter to the stem. Further, the above-ground growth rate of photoperiod sensitive sorghum (in all aspects, stem elongation, leaf appearance, even senescence) slows after the plants reach a certain number of leaf primordia (about 25), resulting in a bi-linear growth rate (Clerget et al., 2008). However, the root biomass rate of growth of photoperiod sensitive sorghums (as observed by rooting depth) was found to stay constant (Leiser et al., 2015). It was thus hypothesized that this bi-linear above-ground growth rate and constant root growth could provide adaptive

benefits for photoperiod sensitive sorghums under soil fertility deficiencies (Leiser et al., 2015) rather than increase P stress as the model seems to simulate. Also, as P concentrations in plant organs are dependent on growth stages, at grain filling stage, there is a high P demand due to grain growth. The high P uptake at the end of the simulation (Fig. 4c) is a consequence of this transition of development stages. In-season data of separate leaves and stems biomass would be critical to improve the dynamics of biomass partitioning within the model.

The delayed development in low P conditions, observed in our experiments was also documented in Leiser et al. (2012). In particular, the delay in flowering due to P deficiency was more pronounced in PP insensitive varieties than in PP sensitive varieties (Leiser et al., 2015). This was also confirmed in the present study with the PP insensitive CSM63E (largest observed delay in flowering under low P) and most sensitive IS15401 having highest RMSE for phenology under low-P conditions (Table 3), and all varieties having higher RMSE for phenology under low-P than under high-P conditions. This suggests that improvement of the linked CSM-CERES-Sorghum – P-model is needed to account for flowering/maturity delays under P deficiency. This model improvement should also take into account the effect of variety-specific photoperiod sensitivity on the development delay under P deficiency.

4.3. Specificities of the P-aware sorghum model

Past modeling efforts pertinent to our study include work by Dzotsi et al. (2010) and Naab et al. (2015) on linking CSM-CERES-Maize and CSM-CROPGRO-Peanut to DSSAT's P model. Our study showed that acceptable simulation of plant P concentration could be obtained without variety-specific critical P concentration curves. We used a higher P stress effect on the photosynthesis process compared to the CSM-CERES maize model (Dzotsi et al., 2010) but lowered the stress effect on partitioning processes as no significant effect of the P treatment was experienced on leaf area index in our experiment. This is a major difference between sorghum and maize, indicating that maize is likely more sensitive to P deficiency than sorghum. Also, we observed a delay in phenology in the experiments for which the DSSAT generic plant P model did not account, because past studies of the P model only considered P stress effects on photosynthesis and vegetative partitioning. Further, compared to previous studies, access to in-season data in our experiments allowed us to more accurately model the in-season plant P concentration and gain insights into characteristics of sorghum P uptake over time. The ability to model varietal differences in growth patterns is critical to understanding variety-specific P uptake potential reported in Leiser et al. (2014). Although IS15401 could take up P more efficiently later during the season (Fig. 4), CSM63E through a higher uptake efficiency and biomass growth rate earlier during the season, appeared to be less affected by P deficiency. These growth – P-uptake pattern interactions are consistent with findings by Leiser et al. (2014) who demonstrated that while photoperiod sensitive varieties tend to have a higher P uptake efficiency, photoperiod insensitive varieties tend to have higher P-use efficiency.

4.4. Concluding remarks

A linked CSM-CERES-Sorghum – P model allows the opportunity to explore the consequences of a host of possible scenarios related to season lengths, varietal vegetative growth periods, photoperiod sensitivity, wide range of soil P conditions, interactions between P- and water-availability, climate change in specified target regions. Such a model can be instrumental in testing chances of success of alternative adaptation strategies for specific geographic regions, through the definition of target population environment with a focus on phosphorus stress. This is particularly useful given the limited number and capacity of experiment stations in West Africa, which constrains the ability of

researchers to sample the diverse low-P soil and climatic conditions of the region.

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