Observed and modeled response of water yam (Dioscorea alata L.) to nitrogen supply: Consequences for nitrogen fertilizer management in the humid tropics

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ABSTRACT

Yam (*Dioscorea* spp.) is an important source of food for millions of people throughout the tropics. Yam yields are constrained by several factors such as low soil fertility and a poor response of the crop to nutrient supply. Here we present an experimental and modeling study performed to test the hypothesis that N leaching in the humid tropics is a key factor that explains the poor response of water yam (*Dioscorea alata* L.) to N fertilization. A field experiment was carried out to assess the impact of three levels of N supply (50, 125 and 200 kg N ha^{-1}) on crop growth and soil N availability. The N fertilizer was split into two equal doses (i.e., 50%/50% split ratio), one applied just before emergence and the other a month after tuber initiation, which corresponds to the current management used by farmers. The CropSyst-Yam model was adapted to include a new soil-crop N component describing the effects of limiting N conditions on yam growth, and then to test different N fertilizer managements. The experimental results indicated that all variables linked to the soil-crop system were affected by the increase in N supply (soil N availability, crop biomass, leaf area and N uptake), and the model well described these impacts. Nitrogen leaching throughout the field experiment represented about one third of the total N supplied by each treatment. Observed and predicted data revealed that N leaching reduced yam growth under the N50 and N125 treatments by reducing soil N availability near the tuber initiation stage. This effect was not observed under the N200 treatment. Model results showed that N leaching and its negative impact near tuber initiation in N50 and N125 could be diminished by advancing the second N application by two or three weeks, and by using a split ratio of 70%/30%. Model results also indicated that this fertilizer strategy would even be suitable during very rainy growing seasons.

1. Introduction

Yam is a multispecies tuber crop grown throughout the humid subtropics and tropics. Despite increasing demand, particularly in West Africa, Central America, the Caribbean, Pacific Islands and Southeast Asia, yam yields remain low (Onyeka et al., 2006; Asiedu and Sartie, 2010). Because declining soil fertility is a major problem in tropical regions, higher yields could be achieved using mineral fertilizers (Hgaza et al., 2012). However, many authors have indicated a limited effect of fertilizer on yam tuber yield (Cornet, 2005; Hgaza et al., 2019). Hgaza et al. (2012) highlighted the very shallow rooting systems of yams and proposed a need to investigate the relationship between yield and limitations on nutrient uptake. In many tropical regions, N is the main limiting nutrient for the photosynthetic process, plant hormone and proteomic changes and the growth-development of plants in order to complete their life cycle (Anas et al. 2020). In humid tropics high annual rainfall considerably exceeds potential evapotranspiration (Sansoulet et al., 2007; Jankowski et al., 2018), and then N leaching combined with the shallow rooting system might explain the poor response of yam to N fertilization.

Below-ground soil-plant interactions are difficult to assess in field experiments (Toal et al., 2000). However, a mechanistic understanding of such interactions is clearly needed to increase current yam yields by improving the management of N supply in the humid tropics (O'Sullivan, 2010). The development of comprehensive models, aimed mainly at increasing our understanding of the interactions between crops and their main growth factors, has enabled the investigation of these interactions (Marcos et al., 2009). In a detailed review of the models developed for tuber crops, Raymundo et al. (2014) reported that although more than thirty had been proposed for potato, only three yam models had been described in the literature. They pointed out that the detailed field experiments and agronomic research necessary to test and improve crop models were rare regarding yam crops. The CropSyst-Yam model has thus proved to be a powerful tool to identify the underlying mechanisms affecting yam yields and to assess the climatic factors involved in the high year-to-year variability observed in yam yields (Marcos et al. 2009, 2011).

As the original version of CropSyst-Yam only performs under non-limiting N conditions, in the present study we modified the model to include a more detailed simulation of N balance in the soil-yam system, in order to evaluate yam performance under N limited conditions. More specifically, the goal of the study was to test the hypothesis that losses of available N by leaching in the humid tropics is a key factor to explain the poor response of water yam (*Dioscorea alata* L.) to N supply. The model was calibrated using experimental

77 data obtained from a field experiment and then used to investigate the factors involved in the
78 optimization of N supply management.

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2. Materials and Methods

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2.1. Site and field experiment

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85 The field experiment was carried out during the 2007-2008 growing season. The
86 experimental site was located in Guadeloupe (French Antilles) in the Caribbean, at the
87 Duclos Experimental Station (16°12'N, 61°39'W, 112 m asl) of the Institut National de
88 Recherche en Agriculture, Alimentation et Environnement (INRAE). At this site, the mean
89 daily temperature is 24.5°C and the mean annual rainfall is 2400 mm, with a slightly dryer
90 season from December to May (i.e., about 40% of annual rainfall) (Fig. 1). The soil is a
91 Ferralsol (FAO Taxonomy) which is slightly acid (pH 5.3) and has a 70% clay content
92 dominated by halloysite and aluminum and iron hydrous oxides (Sierra et al., 2003). The 0-
93 0.4 m layer of the soil is relatively homogenous and its chemical characteristics are: organic
94 C 21.1 g kg^{-1}, organic N 2.0 g kg^{-1}, exchangeable Ca 7.1 cmol kg^{-1}, exchangeable Mg 1.6
95 cmol kg^{-1}, exchangeable K 1.1 cmol kg^{-1}, and exchangeable Na 0.1 cmol kg^{-1}.

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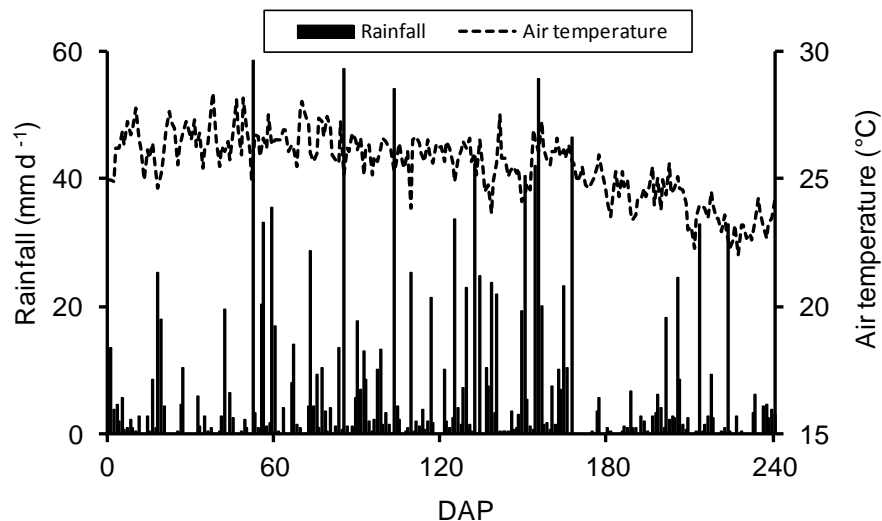
Fig. 1. Rainfall and air temperature during the field experiment expressed in days after
planting (DAP). DAP 0 (yam planting) corresponds to 24 May 2007, and DAP 240 (harvest)
corresponds to 19 January 2008. Air temperature decreased from 26.5°C at planting to
23.0°C at harvest. Total rainfall during the field trial was 1,444 mm.

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113 The field trial applied a randomized complete block design with two replications and
114 three treatments corresponding to the different N fertilizer rates: 50 kg N ha^{-1} (treatment

N50), 125 kg N ha^{-1} (N125) and 200 kg N ha^{-1} (N200). The fertilizer rates were selected to represent the broad range of rates applied by farmers in Guadeloupe. A control treatment without N application was not included in our study because the natural N availability of ferralsols is very low (Sierra et al., 2003), and water yam cultivation is frequently not viable on these soils without an external input of N (Chamber of Agriculture of Martinique, 2014). Each experimental unit comprised seven 10 m-long ridges, with a planting density of 22,000 plant ha^{-1} (1.5 m between the ridges, 0.3 m between plants within the ridges). Yam sets of about 50 g fresh matter were planted on the ridges on 24 May 2007; the crop was not staked. The water yam variety used during the experiment was Belep, which is resistant to anthracnose (Marcos et al., 2009) and is currently cultivated by farmers in the Caribbean. Phosphorus (80 kg P ha^{-1} as triple superphosphate) and potassium (120 kg K ha^{-1} as potassium sulfate) were applied to the ridges six days before planting. Nitrogen fertilizer (urea) was applied to the ridges and split into two applications, each representing 50% of the total N rate of each treatment: at 33 days after planting (i.e., DAP 33) and at DAP 113 (about one month after tuber initiation, TI). Fertilizer management was based on the current practices applied by farmers in French Antilles (Chamber of Agriculture of Martinique, 2014). To ensure uniform nutrient distribution, all fertilizers were applied by hand. Weeds were controlled manually every 10-15 days. Irrigation was not applied. A manual harvest was carried out on 19 January 2008 (DAP 240). Rainfall, solar radiation, air humidity and minimum and maximum air temperatures were recorded daily by a standard weather station located within the experimental plot.

2.2. Soil sampling and data collection for the CropSyst-Yam model

Plant biomass was determined six times during the growing season, at DAP 42 (i.e., three days after emergence, EM), DAP 82 (i.e., about four days after TI), DAP 109, DAP 152, DAP 182 and DAP 240 (i.e., at harvest). EM was determined as the date when 50% of plants had emerged (Marcos et al., 2009). Plants were sampled at random within one of the five innermost ridges over an area of 1.5 m^2, corresponding to 1 m on the ridge and three plants for each experimental unit. Leaves, stems and tubers were collected separately, and then the three samples of each plant organ were combined for measurements (i.e., two replicates of each plant organ by treatment and sampling date). Leaf area index (LAI) at each sampling date was measured using an area meter (LI-3100-B, LI-COR Biosciences, USA). After this, the plant organs were dried at 70°C for three days to determine the dry matter content, and then ground (<0.2 mm) for N analysis (Elemental analyzer; TermoQuest Italia SPA, Italy). Sampling of the 0-0.4 m soil layer of the ridges was carried out eight times during the experiment, at DAP 0, DAP 29, DAP 56, DAP 96, DAP 123, DAP 168, DAP 196 and DAP 240. The soil was sampled using a 0.06 m-diameter auger. From each experimental unit, soil

samples were collected in duplicate and then combined for the analysis of NO_3-N and NH_4-N. Soil mineral N was measured colorimetrically with an autoanalyzer (Technicon Industrial Systems, USA) after extraction with 0.5 M KCl. The soil water content was determined after oven drying the fresh samples at 105°C for 24 h.

2.3. The CropSyst-Yam model

In this section we present the main traits of the model, further details on its functioning and on the crop N component are provided in Appendix A.

Marcos et al. (2009, 2011) developed CropSyst-Yam based on the CropSyst-Simpotato model (Alva et al., 2004). Under CropSyst-Yam, the duration of the EM-TI and TI-harvest (HA) phases of water yam are calculated as a function of photoperiod and temperature (Marcos et al., 2009). Yam growth is partially described by the CropSyst-Simpotato approach to simulate C partitioning (Marcos et al., 2011). During the EM-TI phase, roots, leaves and stems are the dominant sinks for C, while tubers priority increases from TI and becomes the major sink of C after the inflection point of the sigmoid curve of growth. Changes in LAI are controlled by C assimilation, the canopy's relative mean leaf age and the competition with tubers for C and N mainly after TI. Leaf senescence begins when old leaves reach their maximum duration, which corresponds approximately to the inflection point of the curve of tuber growth. The model describes the variation in Radiation Use Efficiency (RUE) after TI as a function of the canopy's relative mean leaf age, a season-dependent maximum RUE value and the development stage (Marcos et al., 2011). The model was calibrated and tested using datasets from 15 field experiments carried out in Guadeloupe under non-limiting conditions for water and nutrients and over a wide range of planting dates and photoperiods (Marcos et al., 2009, 2011).

During the present study, we modified the original CropSyst-Yam model in order to include a more detailed simulation of N balance in the soil-yam system, and then to be able to evaluate yam performance under N limiting conditions. The soil in the ridge (i.e., 0.4 m depth) was divided into eight 0.05 m-layers, and soil processes were computed for each soil layer. The soil N component of the original model was modified to describe separately mineralization and nitrification, and then soil available N is characterized by NO_3 and NH_4 contents. Nitrification is controlled by soil acidity, which can partially inhibit this process, as proposed by Sierra et al. (2003). We also included a retention factor for NO_3 to simulate the effect of the anion exchange capacity (AEC) of acid ferralsols on the reduction of NO3 leaching (Sierra et al., 2003; Sansoulet et al., 2007). Although plant N uptake is proportional to the content in each mineral N form (with no preference for either form), leaching only affects NO_3. It is important to note that N volatilization and denitrification were not considered

during this study because some properties of our soil, such as acidity and fast water drainage, do not favor these processes (Sierra et al., 2001, 2003).

Concerning plant N, we included new, detailed N partitioning and redistribution schemes between plant organs so that the model would be appropriate with more flexible N dynamics while retaining the simplicity of a field scale crop model. Nitrogen limited growth was thus computed based on the balance between available N (soil N uptake plus remobilized N and seed-tuber N) and the N plant demand calculated using these additional N partitioning and redistribution schemes. If daily available N is not sufficient to meet plant N demand at critical N concentrations, growth is reduced accordingly. After available N and N plant demand are compared, actual soil N uptake is calculated and used to update soil mineral N status. Prior to leaf senescence, the leaf N/steam N ratio is not affected by N availability and varies as a function of crop development. In other words, stem N is not a buffering compartment between leaf N and tuber N (see Appendix A). After leaf senescence, a limitation of N availability induces a sharply decrease in this ratio as a consequence of a strong remobilization of leaf N to tubers.

2.4. Model calibration and simulations

Model parameter values were those reported by Marcos et al. (2009, 2011), except for maximum daily N uptake and the soil N concentration at which N uptake limitation begins, which were set for this study. The maximum N uptake was set at 1.5 kg N ha^{-1} d^{-1}, which corresponds to the value observed by Hgaza et al. (2012) for water yam under non-limiting N conditions. We assumed that N uptake limitation starts at 1 mg N kg^{-1}, which corresponds to the mean value reported by Greenwood and Draycott (1995) for potato. We assessed the performance of the model by comparing observed and predicted data of soil mineral N, dry and N biomass, LAI, the N content of aboveground biomass and yield. Comparisons between observed and predicted data were made using regression analysis and Root Mean Square Error (RMSE) values (Marcos et al., 2009).

After model calibration, several simulations were carried out to assess the impact of changes to the management of N fertilizer on N leaching and yam growth (e.g., timing, rate and split of the N supply). Simulations of the timing of N applications were performed using the same fertilizer rates and split ratios applied in the field experiment, and consisted in advancing the second N application by two weeks (i.e., at DAP 99), without changing the first application. Simulations to test the fertilizer rate and split ratio were carried out considering the same timing of N fertilization applied in the field experiment. We tested nine fertilizer rates (ranging from 0 to 200 kg N ha^{-1}) and five split ratios (from 50%/50% to 100%/0%). We also performed some simulations for the 2005-2006 growing season, which was characterized by the highest level of rainfall in French Antilles in the past twenty years. The

228 aim was to assess the effect of the changes to N fertilizer practices in an extremely wet
229 growing season on N leaching and yam growth. For these simulations we used the same
230 rates and split ratios described above, and considered the same planting date and timing of
231 N fertilization applied in the field experiment.

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3. Results

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236 To simplify this section, some of the results are presented in Appendix A from Fig. A4
237 to Fig. A14, which involve predicted data as well as some of the observed data obtained
238 during the field experiment. Differences between treatments were considered to be
239 statistically significant at $P < 0.05$.

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3.1. Yam growth and yield

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243 Emergence (EM) was observed at DAP 39 and TI at DAP 78 under the three
244 treatments. The observed yam growth increased significantly from N50 to N200 (Figs 2a-c).
245 Differences between treatments for total dry biomass were significant from DAP 109; these
246 were mainly associated with aboveground biomass and secondarily with tuber biomass. For
247 example, the differences between N125 and N200 for tuber biomass were only significant at
248 harvest (Figs 2b,c). Observed yam fresh yield increased significantly with the fertilizer rate;
249 e.g., 15, 21 and 24 Mg ha^{-1}, respectively for N50, N125 and N200. Differences between
250 treatments for LAI were significant from DAP 152 (Figs 2d-f). The maximum LAI (LAI$_{max}$) was
251 2.7 m^2 m^{-2} for N50, 3.3 m^2 m^{-2} for N125, and 3.4 m^2 m^{-2} for N200. Only differences between
252 N50 and N125-N200 were significant for LAI$_{max}$. The CropSyst-Yam model described yam
253 growth and LAI reasonably well (Fig. 2). The R^2 values obtained from the comparison
254 between observed and predicted data averaged 0.95 for aboveground biomass, 0.98 for
255 tuber biomass, and 0.96 for LAI. RMSE values were relatively low and averaged 0.1 Mg ha^{-1}
256 for aboveground biomass, 0.2 Mg ha^{-1} for tuber biomass, and 0.1 m^2 m^{-2} for LAI.

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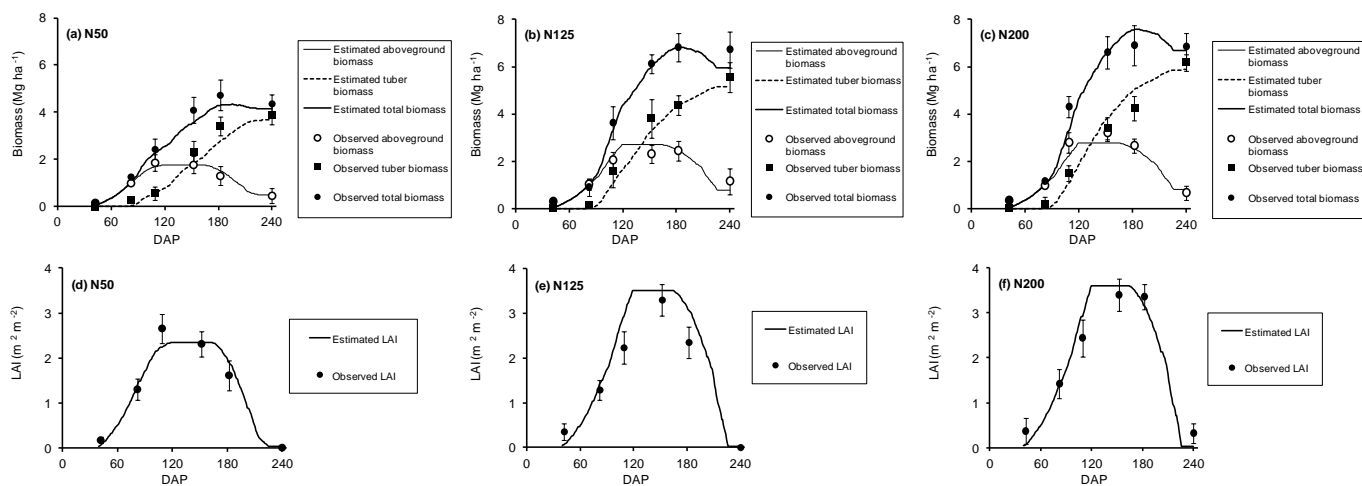
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Fig. 2. Observed and predicted (a-c) plant biomass and (d-f) leaf area index (LAI) for the three treatments applied during this study (N50, N125 and N200). Vertical bars indicate standard deviations.

3.2. Leaf N content and crop N biomass

For N125 and N200, the observed N content in leaves was close to the critical level estimated by the model throughout the field experiment (Fig. 3a) (see Appendix A for the calculation of the critical dilution curve). For N50, leaf N content was lower than the critical level for almost the entire growth cycle. Leaf N content was used to calculate the N stress factor (NSF) (see Appendix A). The observed NSF averaged 49% for N50, 4% for N125 and 1% for N200. The predicted NSF averaged 54% for N50, 2% for N125 and was nil for N200. The tuber N content was 0.02 g N g^{-1} at TI and around 0.01 kg N kg^{-1} thereafter (Fig. A4), and there were no significant differences between the treatments.
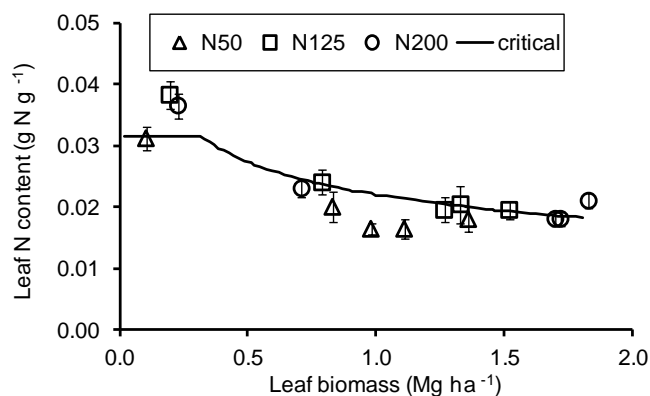

Fig. 3. Observed N content in leaves for the three treatments compared with the critical N value estimated by the model. Vertical bars indicate standard deviations.

303   The maximum N biomass values were observed at DAP 182: 54 kg N ha^{-1} for N50, 80

304 kg N ha^{-1} for N125 and 91 kg N ha^{-1} for N200, which were significantly different (Fig. A5). The

305 model produced a satisfactory description of changes in N biomass (Fig. A5). The R^2 values

306 obtained from the comparison between observed and predicted data averaged 0.90 for

307 aboveground N biomass, 0.98 for tuber N biomass and 0.97 for total N biomass. The RMSE

308 values were relatively low and averaged 2.1 kg N ha^{-1} for aboveground N biomass, 1.5 kg N

309 ha^{-1} for tuber N biomass and 2.2 kg N ha^{-1} for total N biomass.

310   Total N biomass increased linearly with the increase in LAI from emergence to LAI$_{max}$

311 in the three treatments (Fig. A6). The slope of linear regression, expressed in kg ha^{-1} per unit

312 of LAI, was 18 for N50, 24 for N125 and 26 for N200; only differences between N50 and

313 N125-N200 were significant. There were no significant differences between treatments for

314 the leaf N/stem N ratio during the field experiment (Fig. A7).

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317 *3.3. Soil mineral N and water content*

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319   Observed total soil mineral N (i.e., NO_3 + NH_4) increased following a fertilizer

320 application and decreased thereafter, and was quite low just before the second N application

321 on DAP 113, except for N200; e.g., <15 kg N ha^{-1} for N50 and N125, and 35 kg N ha^{-1} for

322 N200 (Fig. 4). Ammonium accounted for 50%-70% of observed soil mineral N between DAP

323 0 and DAP 123, after which it represented less than 50% of mineral N (Fig. A8). The model

324 described reasonably well the time course of soil mineral N (Fig. 4); e.g., the R^2 values

325 between observed and predicted data averaged 0.86 and RMSE averaged 3.4 kg N ha^{-1}.

326 Observed and predicted data indicated that the fall in soil mineral N levels after both N

327 applications was greater than the amount of N taken by the crop. For example, the predicted

328 data indicated that for N200 during the DAP 50-DAP 112 period, the decrease in soil mineral

329 N (85 kg N ha^{-1}) was 60% greater than crop N uptake (53 kg N ha^{-1}). Similar results were
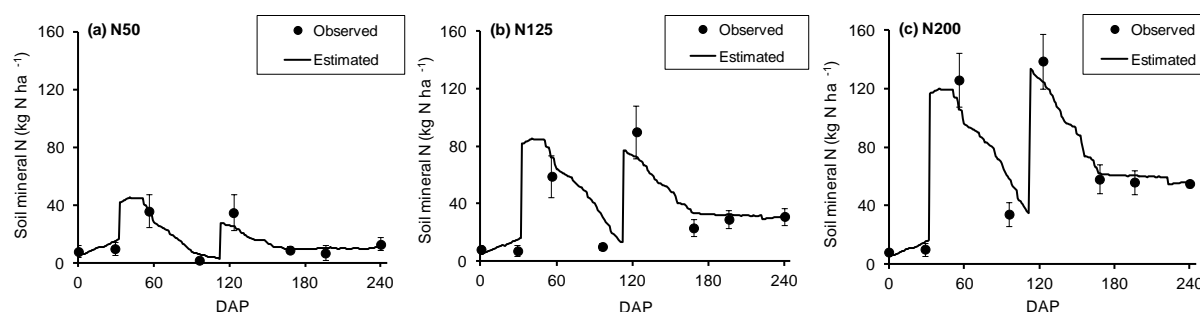
330 observed with N50 and N125.

Fig.4. Observed and predicted soil mineral N content (nitrate + ammonium) within the yam ridge (0-0.4 m) under the three treatments. Vertical bars indicate standard deviations.

Model results indicated that differences between the reduction in soil mineral N and crop N uptake were associated with N leaching, which was relatively high in our study (Fig. 5). The predicted cumulated N leaching for the entire field experiment was 19 kg N ha^{-1} for N50, 40 kg N ha^{-1} for N125 and 77 kg N ha^{-1} for N200. In average N leaching was equivalent to 36% of the total applied N. Moreover, the observed and predicted data indicated that differences between treatments relative to dry matter and N biomass accumulation occurred when the content in soil mineral N was lower than about 25 kg N ha^{-1}. That was the case mainly between DAP 71 and DAP 112 for N50 (Fig. 4a), and from DAP 97 to DAP 112 for N125 (Fig. 4b). Under N200, the soil mineral N content was always >35 kg N ha^{-1}, except just before the first N fertilizer application (Fig. 4c).
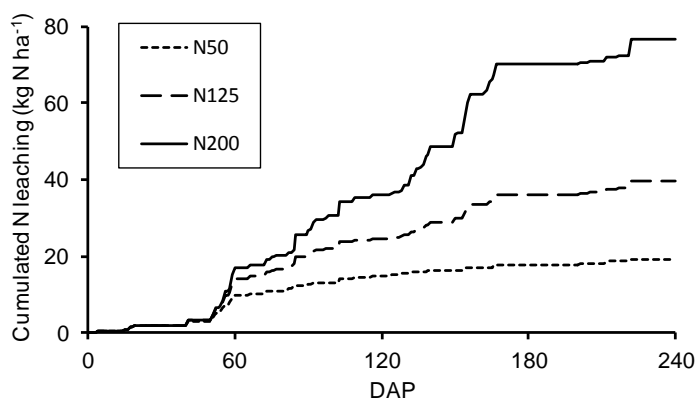
Fig. 5. Cumulated N leaching under the three treatments as predicted by the model.

The observed and predicted data indicated that soil moisture expressed as water filled porosity (WFP) averaged 95% between DAP 0 and DAP 170, and 71% after DAP 170 (i.e., start of the dry season) (Fig. A9). Model outputs indicated that there was no water stress throughout the entire field experiment.

3.4. Model simulations of N fertilizer management

Advancing the second application by two weeks enabled an increase in yam yields of 4% under N50 and 7% under N125 by reducing the impact of leaching on N availability during the first stages of tuber bulking (Fig. A10). Changing the timing of the second N application had no effect on yam yield under N200. In fact, N availability under N200 was always sufficiently high to ensure tuber growth regardless of the timing of N application.

Model simulations indicated that the minimum N fertilizer rate required to achieve maximum yield (e.g., 22.6 Mg fresh matter ha^{-1}) was reached at 150 kg N ha^{-1} for a split ratio of 70%/30% (Fig. 6a). Differences between split ratios were negligible with fertilizer rates ≥175 kg N ha^{-1}. Nitrogen leaching increased in line with the fertilizer rate; e.g. from 12 kg N ha^{-1} for N0 to 97 kg N ha^{-1} on average for N200 (Fig. 6b). Leaching also increased with the

379 rise in the split ratio; e.g. for N200, from 77 kg N ha^{-1} for a 50%/50% ratio to 123 kg N ha^{-1} for
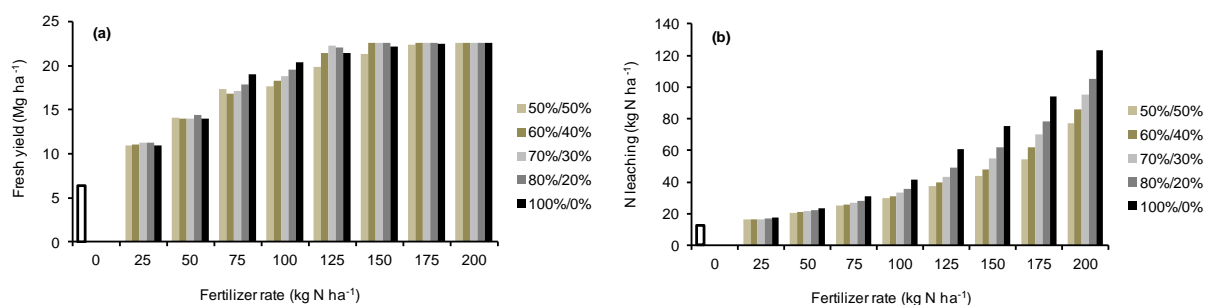380 100%/0% (Fig. 6b).

Fig. 6. Predicted (a) yam yields and (b) N leaching as a function of the N fertilizer rate and the split ratio between the first and second N applications. The first application was set at DAP 33 and the second at DAP 113, as during the field experiment. Data correspond to the 2007-2008 growing season.

3.5. Model simulations of the 2005-2006 growing season

Rainfall during the 2005-2006 season reached 2129 mm (47% higher than during the 2007-2008 season) and water drainage was 883 mm (35% higher than during the 2007-2008 season). The trend of the simulated results was similar to that presented in Fig. 6 for the 2007-2008 season, but yam yields fell on average by 25% and N leaching increased by 26% (Fig. A11). The fall in crop yields was associated with lower soil N availability at TI when compared to the 2007-2008 season (Fig. A12), which was due to a higher N leaching in 2005-2006. The minimum fertilizer rate necessary to attain maximum crop yield (i.e., 19.9 Mg fresh matter ha^{-1}) was achieved with 175 kg N ha^{-1} at the split ratio of 70%/30% (Fig. A11).

4. Discussion

Because the field experiment analyzed in this study was conducted in the absence of soil water, pest and P and K constraints, soil N availability was the principal factor controlling differences between the treatments. The CropSyst-Yam model offered a helpful tool to assess the factors controlling N supply and their interactions during the vegetative and tuberization phases.

4.1. Factors affecting N uptake throughout the yam growth cycle

During the present study, the observed yam growth and yield were significantly affected by the increase in N supply. In a detailed review of 218 field studies about the response of several yam species (e.g., *D. alata*, *D. rotundata*, *D. cayenensis*) to N fertilization, Cornet et al. (2005) reported that only 25% of them presented a significant response. The percentage was the lowest for *D. alata* (e.g., 15%). Some authors suggested that the poor response of yam to N supply might be linked to the shallow-rooting and low root density of yam species (Hgaza et al., 2012, 2019). Hgaza et al. (2019) observed that root length density in the yam mound averaged 0.3 cm cm^{-3}. However, this value seem to be too small in relation to the root density data reported for other crops; e.g., from 11 cm cm^{-3} to 16 cm cm^{-3} for potato (Ahmadi et al., 2014; Nyawade et al., 2018). Although we did not measure root density in our study, model results indicated that yam root density in the three N treatments were of the same order of magnitude but 2-3 times lower than those reported for potato (e.g., 5.4 cm cm^{-3} at tuber maturation, Fig. A13). Nevertheless, as highlighted by Milroy et al. (2019) for potato, we consider that while the rooting characteristics of yam species may explain the variable response to N supply, it does not appear to be an absolute limitation because yields as high as 50 Mg fresh matter ha^{-1} are frequently reported in many tropical regions; e.g., Diby et al. (2011) in Ivory Coast, and Marcos et al. (2011) in Guadeloupe. The observed and simulated data on soil mineral N obtained during the present study suggested that the leaching of available N was a major factor to explain the differences between N treatments. This is in line with the results reported by several authors concerning the impact of N leaching on the poor response of yam to N supply in humid tropics (e.g., O'Sullivan, 2010; Hgaza et al., 2012). Indeed, the negative effect of N leaching on crop growth might be exacerbated in a crop such as yam which has a shallow root system; e.g., up to 0.4 m according to Melteras et al. (2008) and O'Sullivan (2008).

Under our modeling approach the limitation of crop N uptake occurred when the mineral N content was <1 mg N kg^{-1} in at least one soil layer, being the value observed by Grenwood and Draycott (1995) for potato. For N50, this threshold was attained between DAP 83 (start of tuber growth) and DAP 113 (second N application) and from DAP 120 to the end of the growth cycle. The limitation of N uptake during these periods was linked to N leaching and also to the rapid increase in biomass production and N demand by the crop after TI (Marcos et al., 2011). Although the second N application removed the N limitation observed under N50 near TI, this N supply was not sufficient to compensate for leaching and crop N demand after DAP 120. For N125, the threshold for N limitation was attained between DAP 100 and the second N fertilization at DAP 113. No limitation on N uptake was observed for this treatment after DAP 113. In other words, just two weeks of N limitation during the start of tuber growth caused an important reduction in LAI and biomass production compared to the N200 treatment, which did not display any N limitation during the growth cycle. This short-term effect of low N availability under N125 induced a 10% reduction in yam yields compared

to N200, thus revealing the importance of the TI stage to determining the response of yam to N fertilization in humid tropical regions characterized by high N leaching.

4.2. Changes in leaf N content, radiation interception and radiation use efficiency

In our study, leaf N content was sensitive to reflect the low soil N availability observed in the N50 treatment. This was in line with the results obtained by Cornet (2005) concerning a field experiment on the same yam variety as that used here (i.e., Belep). To our knowledge, the study by Cornet (2005) and ours are the only studies to have determined the critical N dilution curve for yam. By contrast, numerous studies have shown that the dilution curve concept is a useful tool to assess crop N status in potato (e.g., Giletto et al., 2020; Nyiraneza et al., 2021) and other main crops (e.g., Ciampitti et al., 2021, for maize, wheat and tall fescue). Nevertheless, the differences in yam growth observed between N125 and N200 were not reflected by the leaf N dilution curve. From our theoretical approach, this result reflected the higher priority given by the model to maintaining leaf N status at the expense of an increase in leaf area under slight N stress, as observed under N125. From a physiological point of view, this would imply a trade-off between leaf N content and LAI. Quantifying the relevance of such an effect requires further experimental and analytical work on the response of yam to N restriction.

The linear relationship observed between crop N biomass and LAI up to LAI_{max} (Fig. A6) is similar to that reported by Lemaire et al. (2007) for the vegetative phase of several main crops; e.g., wheat, maize, sunflower, rice and sorghum. Differences in the slope of that relationship only were significant between N50 and N125-N200, which is in agreement with the results of the dilution curve of leaf N content. This indicates that the relative N allocation in leaves was similar in N125 and N200 in spite of the N limitation observed in the former; this supports the hypothesis of a trade-off between leaf expansion and leaf N content in water yam. It is interesting to note that the similar leaf N/stem N ratio observed for the three treatments confirms that stem was not a buffering compartment between leaf N and tuber N. That is, N limitation for tuber growth in N50 and N125 was not offset by a higher N remobilization from steam.

Under our modeling approach, RUE is affected by leaf N status via its effect on the mean leaf age of the canopy (Marcos et al., 2011). However, model results indicated that this effect was much lower that the impact of LAI on the absorbed Photosynthetically Active Radiation (PAR) (Fig. A14). In this way differences in yam growth between treatments were mainly controlled by the level of absorbed PAR. For tuber and root crops, several authors also found that N supply promoted crop growth by increasing absorbed PAR rather than RUE; e.g., Diby et al. (2011) for water yam, Zhou et al. (2016, 2017) for potato, and Chakwizira et al. (2018) for fodder beet.

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4.3. Impact of N fertilizer management

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495　　　Model simulations concerning N fertilizer management focused on overcoming the negative effects of N leaching around the start of tuber growth, as observed N50 and N125. In this respect, advancing the second N application by two weeks was useful in reducing the effect of N leaching on yam growth and induced an increase in yields in N50 and N125. However, advancing this application requires a determination of the time of TI, which might be difficult under field conditions because it varies as a function of planting date (Marcos et al., 2009); e.g., the earlier the planting date, the longer the duration of the EM-TI phase. It thus appears that advancing the second N application by two weeks (for later dates) or three weeks (for earlier dates) might be an acceptable practice to reduce the risk of N limitation at TI.

505　　　The splitting of N fertilization is an appropriate approach to improve the balance between N need and supply while reducing the risk of N leaching (Goffart et al., 2008), and it is a practice that is currently applied in the humid tropics (Hgaza et al., 2019; Raphael et al., 2020). Several authors have reported that the positive effects of splitting the N application on yields and N leaching in potato were particularly noticeable in a context of rainy growing seasons inducing high N leaching (Goffart et al., 2008; Rens et al., 2018). This is in line with our model results which indicated that for fertilizer rates >125 kg N ha^{-1}, a single N application near EM (e.g., split ratio 100%/0% in Fig. 6) was less effective in terms of yield and N leaching than the other split ratios. Moreover, under that fertilizer rate, a split ratio of 70%/30% was more effective than the 50%/50% ratio in ensuring sufficient N availability at TI and increasing yam yields. This was also found during the 2005-2006 season which experienced higher rainfall and N leaching.

517　　　We performed additional calculations to test an N fertilization strategy that combined a split ratio of 70%/30% with advancing the second N application by two weeks. We found that yam yield achieved under N125 was close to that obtained for the initial simulations for N200 with a 50%/50% split ratio. This result was associated with higher N availability at TI in the tested combination (Fig. A10). It appears that the fertilizer rate could be reduced while maintaining yields and reducing N leaching, by combining a change in the current split ratio and in the time of the second N application. Moreover, the reduction of the fertilizer rate would diminish the risk of diffuse pollution of water resources, which is a major concern in French Antilles.

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5. Conclusions

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During this study we tested a hypothesis regarding the key role played by N leaching in the humid tropics in terms of controlling the response of yam to N supply. One major result obtained from the field experiment was that N leaching near the start of tuber growth strongly impacted the subsequent crop phases and yield. Although model results indicated that a change in the current N fertilizer practices (timing and split ratio) would allow reduce soil N limitation at tuber initiation, N leaching was always very high and accounted for about one third of the fertilizer rate under all the experimental and simulated conditions analyzed during this study. Indeed, other practices need to be implemented, together with the change of the N fertilizer strategy, in order to assure yam yields while reducing the risk of diffuse pollution of water resources. Among these practices, the use of organic fertilizers and soil mulching could be easily adopted by smallholder farmers involved in yam production.

Leaf N status correctly reflected severe soil N constraints (i.e., in N50), but it failed to match the negative effect on yam yields of N limitation occurring during short-term periods (i.e., two weeks in N125). The results suggested a trade-off between leaf N and LAI if no severe N shortage was present, which might correspond to a trait of a crop like yam which originally grew under rain forest conditions. Further research is now needed to assess this effect which may contribute to developing new crop-based N indicators to correct N deficiencies during the growing season.

Credit authorship contribution statement

Denis Cornet: Conceptualization, Investigation, Validation, Formal analysis, Writing original draft; Javier Marcos: Conceptualization, Investigation, Software, Validation, Formal analysis; Régis Tournebize: Conceptualization, Resources, Investigation, Data Curation, Writing original draft; Jorge Sierra: Conceptualization, Software, Formal analysis, Writing original draft, Supervision.

Declaration of Competing Interest

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

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Appendix A. Supporting information

579 Supplementary data associated with this article can be found in the online version at

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