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

3
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21 **ABSTRACT**

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23
24 Yam (*Dioscorea* spp.) is an important source of food for millions of people throughout the
25 tropics. Yam yields are constrained by several factors such as low soil fertility and a poor
26 response of the crop to nutrient supply. Here we present an experimental and modeling
27 study performed to test the hypothesis that N leaching in the humid tropics is a key factor
28 that explains the poor response of water yam (*Dioscorea alata* L.) to N fertilization. A field
29 experiment was carried out to assess the impact of three levels of N supply (50, 125 and 200
30 kg N ha⁻¹) on crop growth and soil N availability. The N fertilizer was split into two equal
31 doses (i.e., 50%/50% split ratio), one applied just before emergence and the other a month
32 after tuber initiation, which corresponds to the current management used by farmers. The
33 CropSyst-Yam model was adapted to include a new soil-crop N component describing the
34 effects of limiting N conditions on yam growth, and then to test different N fertilizer
35 managements. The experimental results indicated that all variables linked to the soil-crop
36 system were affected by the increase in N supply (soil N availability, crop biomass, leaf area
37 and N uptake), and the model well described these impacts. Nitrogen leaching throughout
38 the field experiment represented about one third of the total N supplied by each treatment.
39 Observed and predicted data revealed that N leaching reduced yam growth under the N50
40 and N125 treatments by reducing soil N availability near the tuber initiation stage. This effect
41 was not observed under the N200 treatment. Model results showed that N leaching and its
42 negative impact near tuber initiation in N50 and N125 could be diminished by advancing the
43 second N application by two or three weeks, and by using a split ratio of 70%/30%. Model
44 results also indicated that this fertilizer strategy would even be suitable during very rainy
45 growing seasons.

39 *Keywords:* Crop model, Nitrate leaching, Split N fertilization, Tropical soil, Tuber initiation

42 **1. Introduction**

44 Yam is a multispecies tuber crop grown throughout the humid subtropics and tropics.
45 Despite increasing demand, particularly in West Africa, Central America, the Caribbean,
46 Pacific Islands and Southeast Asia, yam yields remain low (Onyeka et al., 2006; Asiedu and
47 Sartie, 2010). Because declining soil fertility is a major problem in tropical regions, higher
48 yields could be achieved using mineral fertilizers (Hgaza et al., 2012). However, many
49 authors have indicated a limited effect of fertilizer on yam tuber yield (Cornet, 2005; Hgaza et
50 al., 2019). Hgaza et al. (2012) highlighted the very shallow rooting systems of yams and
51 proposed a need to investigate the relationship between yield and limitations on nutrient
52 uptake. In many tropical regions, N is the main limiting nutrient for the photosynthetic
53 process, plant hormone and proteomic changes and the growth-development of plants in
54 order to complete their life cycle (Anas et al. 2020). In humid tropics high annual rainfall
55 considerably exceeds potential evapotranspiration (Sansoulet et al., 2007; Jankowski et al.,
56 2018), and then N leaching combined with the shallow rooting system might explain the poor
57 response of yam to N fertilization.

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

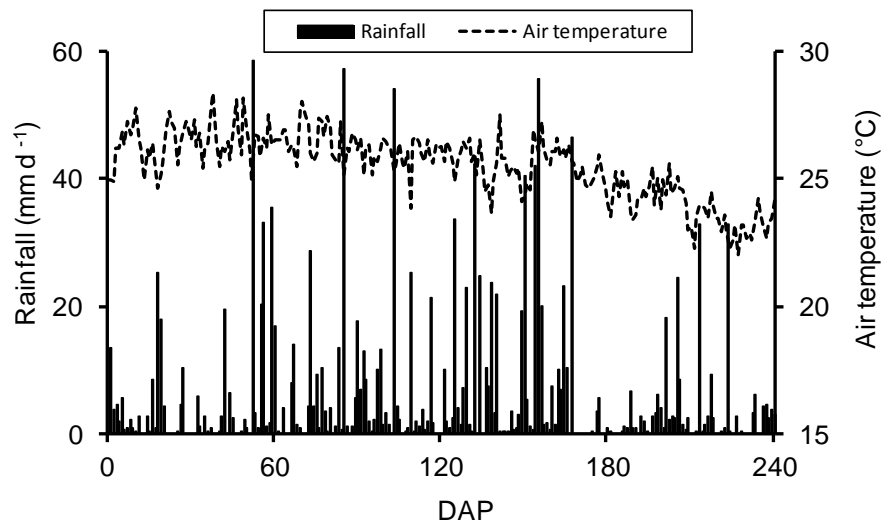
71 As the original version of CropSyst-Yam only performs under non-limiting N
72 conditions, in the present study we modified the model to include a more detailed simulation
73 of N balance in the soil-yam system, in order to evaluate yam performance under N limited
74 conditions. More specifically, the goal of the study was to test the hypothesis that losses of
75 available N by leaching in the humid tropics is a key factor to explain the poor response of
76 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.

81 2. Materials and Methods

83 2.1. Site and field experiment

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.



108 **Fig. 1.** Rainfall and air temperature during the field experiment expressed in days after
 109 planting (DAP). DAP 0 (yam planting) corresponds to 24 May 2007, and DAP 240 (harvest)
 110 corresponds to 19 January 2008. Air temperature decreased from 26.5°C at planting to
 111 23.0°C at harvest. Total rainfall during the field trial was 1,444 mm.

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

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

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

136
137
138
139 Plant biomass was determined six times during the growing season, at DAP 42 (i.e.,
140 three days after emergence, EM), DAP 82 (i.e., about four days after TI), DAP 109, DAP 152,
141 DAP 182 and DAP 240 (i.e., at harvest). EM was determined as the date when 50% of plants
142 had emerged (Marcos et al., 2009). Plants were sampled at random within one of the five
143 innermost ridges over an area of 1.5 m², corresponding to 1 m on the ridge and three plants
144 for each experimental unit. Leaves, stems and tubers were collected separately, and then the
145 three samples of each plant organ were combined for measurements (i.e., two replicates of
146 each plant organ by treatment and sampling date). Leaf area index (LAI) at each sampling
147 date was measured using an area meter (LI-3100-B, LI-COR Biosciences, USA). After this,
148 the plant organs were dried at 70°C for three days to determine the dry matter content, and
149 then ground (<0.2 mm) for N analysis (Elemental analyzer; TermoQuest Italia SPA, Italy).

150 Sampling of the 0-0.4 m soil layer of the ridges was carried out eight times during the
151 experiment, at DAP 0, DAP 29, DAP 56, DAP 96, DAP 123, DAP 168, DAP 196 and DAP
152 240. The soil was sampled using a 0.06 m-diameter auger. From each experimental unit, soil

153 samples were collected in duplicate and then combined for the analysis of $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$.
154 Soil mineral N was measured colorimetrically with an autoanalyzer (Technicon Industrial
155 Systems, USA) after extraction with 0.5 M KCl. The soil water content was determined after
156 oven drying the fresh samples at 105°C for 24 h.

157 158 *2.3. The CropSyst-Yam model*

159
160 In this section we present the main traits of the model, further details on its
161 functioning and on the crop N component are provided in Appendix A.

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

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

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

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

205 206 *2.4. Model calibration and simulations*

207
208 Model parameter values were those reported by Marcos et al. (2009, 2011), except
209 for maximum daily N uptake and the soil N concentration at which N uptake limitation begins,
210 which were set for this study. The maximum N uptake was set at $1.5 \text{ kg N ha}^{-1} \text{ d}^{-1}$, which
211 corresponds to the value observed by Hgaza et al. (2012) for water yam under non-limiting N
212 conditions. We assumed that N uptake limitation starts at 1 mg N kg^{-1} , which corresponds to
213 the mean value reported by Greenwood and Draycott (1995) for potato. We assessed the
214 performance of the model by comparing observed and predicted data of soil mineral N, dry
215 and N biomass, LAI, the N content of aboveground biomass and yield. Comparisons
216 between observed and predicted data were made using regression analysis and Root Mean
217 Square Error (RMSE) values (Marcos et al., 2009).

218 After model calibration, several simulations were carried out to assess the impact of
219 changes to the management of N fertilizer on N leaching and yam growth (e.g., timing, rate
220 and split of the N supply). Simulations of the timing of N applications were performed using
221 the same fertilizer rates and split ratios applied in the field experiment, and consisted in
222 advancing the second N application by two weeks (i.e., at DAP 99), without changing the first
223 application. Simulations to test the fertilizer rate and split ratio were carried out considering
224 the same timing of N fertilization applied in the field experiment. We tested nine fertilizer
225 rates (ranging from 0 to 200 kg N ha^{-1}) and five split ratios (from 50%/50% to 100%/0%). We
226 also performed some simulations for the 2005-2006 growing season, which was
227 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.

3. Results

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

3.1. Yam growth and yield

Emergence (EM) was observed at DAP 39 and TI at DAP 78 under the three
treatments. The observed yam growth increased significantly from N50 to N200 (Figs 2a-c).
Differences between treatments for total dry biomass were significant from DAP 109; these
were mainly associated with aboveground biomass and secondarily with tuber biomass. For
example, the differences between N125 and N200 for tuber biomass were only significant at
harvest (Figs 2b,c). Observed yam fresh yield increased significantly with the fertilizer rate;
e.g., 15, 21 and 24 Mg ha⁻¹, respectively for N50, N125 and N200. Differences between
treatments for LAI were significant from DAP 152 (Figs 2d-f). The maximum LAI (LAI_{max}) was
2.7 m² m⁻² for N50, 3.3 m² m⁻² for N125, and 3.4 m² m⁻² for N200. Only differences between
N50 and N125-N200 were significant for LAI_{max}. The CropSyst-Yam model described yam
growth and LAI reasonably well (Fig. 2). The R^2 values obtained from the comparison
between observed and predicted data averaged 0.95 for aboveground biomass, 0.98 for
tuber biomass, and 0.96 for LAI. RMSE values were relatively low and averaged 0.1 Mg ha⁻¹
for aboveground biomass, 0.2 Mg ha⁻¹ for tuber biomass, and 0.1 m² m⁻² for LAI.

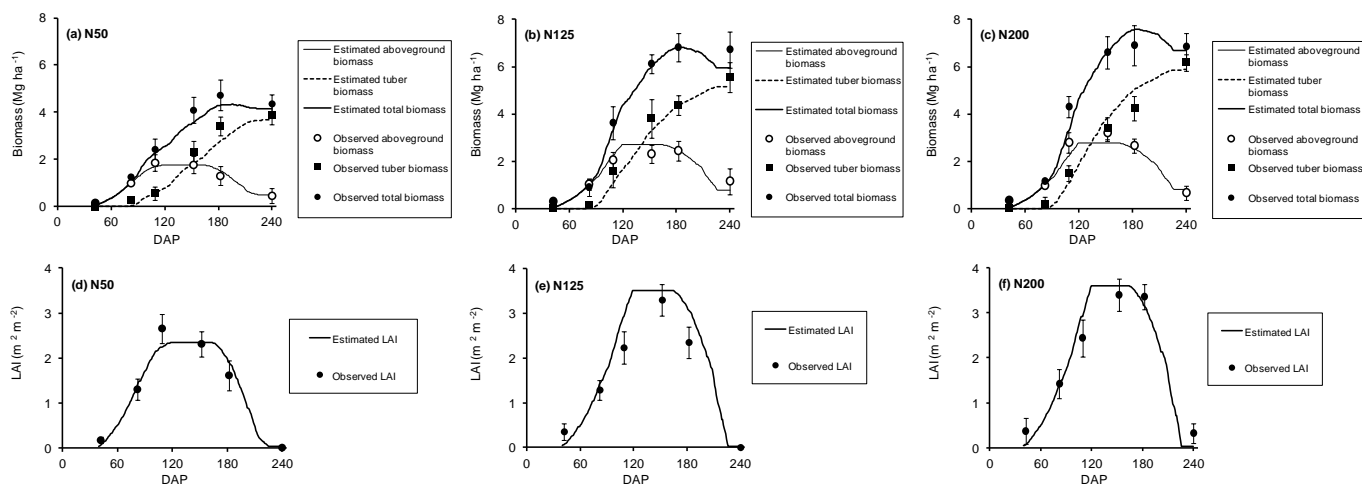


Fig. 2. Observed and predicted (a-c) plant biomass and (d-f) leaf area index (LAI) for the three treatments applied during this study (N50, N125 and N200). Vertical bars indicate standard deviations.

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.

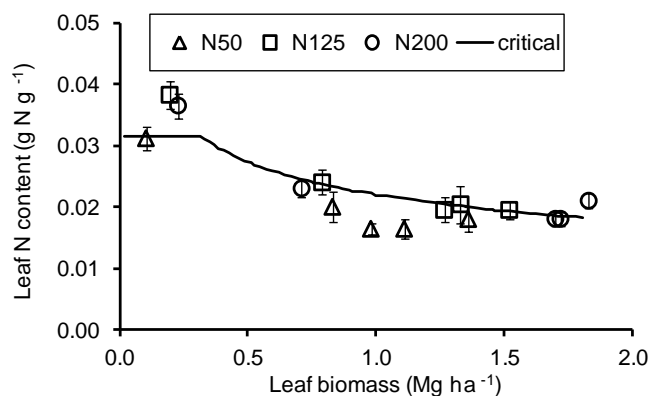


Fig. 3. Observed N content in leaves for the three treatments compared with the critical N value estimated by the model. Vertical bars indicate standard deviations.

The maximum N biomass values were observed at DAP 182: 54 kg N ha⁻¹ for N50, 80 kg N ha⁻¹ for N125 and 91 kg N ha⁻¹ for N200, which were significantly different (Fig. A5). The model produced a satisfactory description of changes in N biomass (Fig. A5). The R^2 values obtained from the comparison between observed and predicted data averaged 0.90 for aboveground N biomass, 0.98 for tuber N biomass and 0.97 for total N biomass. The RMSE values were relatively low and averaged 2.1 kg N ha⁻¹ for aboveground N biomass, 1.5 kg N ha⁻¹ for tuber N biomass and 2.2 kg N ha⁻¹ for total N biomass.

Total N biomass increased linearly with the increase in LAI from emergence to LAI_{max} in the three treatments (Fig. A6). The slope of linear regression, expressed in kg ha⁻¹ per unit of LAI, was 18 for N50, 24 for N125 and 26 for N200; only differences between N50 and N125-N200 were significant. There were no significant differences between treatments for the leaf N/stem N ratio during the field experiment (Fig. A7).

3.3. Soil mineral N and water content

Observed total soil mineral N (i.e., NO₃ + NH₄) increased following a fertilizer application and decreased thereafter, and was quite low just before the second N application on DAP 113, except for N200; e.g., <15 kg N ha⁻¹ for N50 and N125, and 35 kg N ha⁻¹ for N200 (Fig. 4). Ammonium accounted for 50%-70% of observed soil mineral N between DAP 0 and DAP 123, after which it represented less than 50% of mineral N (Fig. A8). The model described reasonably well the time course of soil mineral N (Fig. 4); e.g., the R^2 values between observed and predicted data averaged 0.86 and RMSE averaged 3.4 kg N ha⁻¹. Observed and predicted data indicated that the fall in soil mineral N levels after both N applications was greater than the amount of N taken by the crop. For example, the predicted data indicated that for N200 during the DAP 50-DAP 112 period, the decrease in soil mineral N (85 kg N ha⁻¹) was 60% greater than crop N uptake (53 kg N ha⁻¹). Similar results were observed with N50 and N125.

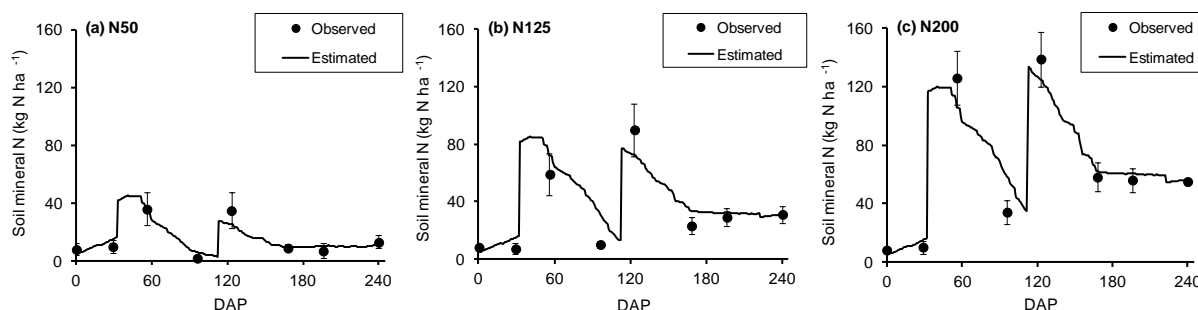
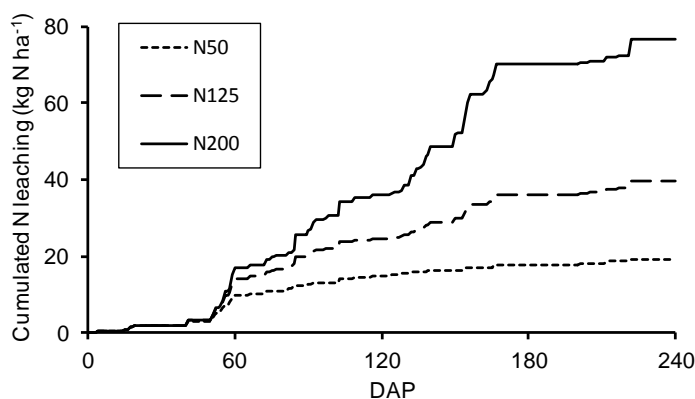


Fig.4. Observed and predicted soil mineral N content (nitrate + ammonium) within the yam ridge (0-0.4 m) under the three treatments. Vertical bars indicate standard deviations.

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



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360 **Fig. 5.** Cumulated N leaching under the three treatments as predicted by the model.

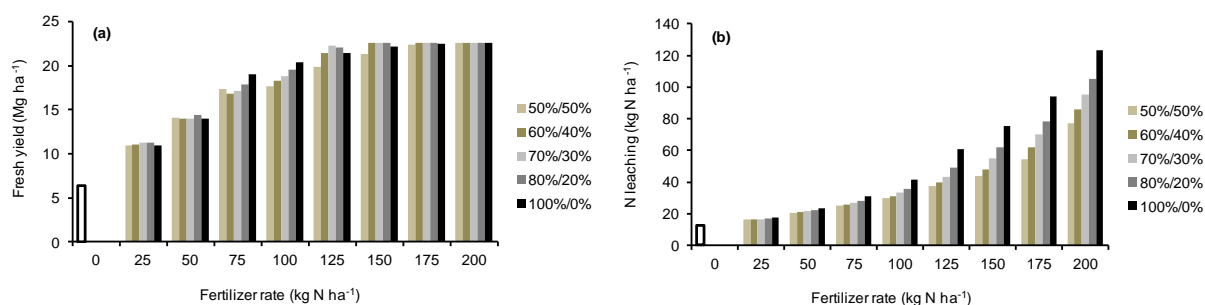
361
362 The observed and predicted data indicated that soil moisture expressed as water
 363 filled porosity (WFP) averaged 95% between DAP 0 and DAP 170, and 71% after DAP 170
 364 (i.e., start of the dry season) (Fig. A9). Model outputs indicated that there was no water
 365 stress throughout the entire field experiment.

366 367 3.4. Model simulations of N fertilizer management

368
369 Advancing the second application by two weeks enabled an increase in yam yields of
 370 4% under N50 and 7% under N125 by reducing the impact of leaching on N availability
 371 during the first stages of tuber bulking (Fig. A10). Changing the timing of the second N
 372 application had no effect on yam yield under N200. In fact, N availability under N200 was
 373 always sufficiently high to ensure tuber growth regardless of the timing of N application.

374 Model simulations indicated that the minimum N fertilizer rate required to achieve
 375 maximum yield (e.g., 22.6 Mg fresh matter ha⁻¹) was reached at 150 kg N ha⁻¹ for a split ratio
 376 of 70%/30% (Fig. 6a). Differences between split ratios were negligible with fertilizer rates
 377 ≥175 kg N ha⁻¹. Nitrogen leaching increased in line with the fertilizer rate; e.g. from 12 kg N
 378 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).



389 **Fig. 6.** Predicted (a) yam yields and (b) N leaching as a function of the N fertilizer rate and
 390 the split ratio between the first and second N applications. The first application was set at
 391 DAP 33 and the second at DAP 113, as during the field experiment. Data correspond to the
 392 2007-2008 growing season.

394 3.5. Model simulations of the 2005-2006 growing season

396 Rainfall during the 2005-2006 season reached 2129 mm (47% higher than during the
 397 2007-2008 season) and water drainage was 883 mm (35% higher than during the 2007-2008
 398 season). The trend of the simulated results was similar to that presented in Fig. 6 for the
 399 2007-2008 season, but yam yields fell on average by 25% and N leaching increased by 26%
 400 (Fig. A11). The fall in crop yields was associated with lower soil N availability at TI when
 401 compared to the 2007-2008 season (Fig. A12), which was due to a higher N leaching in
 402 2005-2006. The minimum fertilizer rate necessary to attain maximum crop yield (i.e., 19.9 Mg
 403 fresh matter ha⁻¹) was achieved with 175 kg N ha⁻¹ at the split ratio of 70%/30% (Fig. A11).

404 4. Discussion

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

411 4.1. Factors affecting N uptake throughout the yam growth cycle

416 During the present study, the observed yam growth and yield were significantly
1 417 affected by the increase in N supply. In a detailed review of 218 field studies about the
2 418 response of several yam species (e.g., *D. alata*, *D. rotundata*, *D. cayenensis*) to N
3 419 fertilization, Cornet et al. (2005) reported that only 25% of them presented a significant
4 420 response. The percentage was the lowest for *D. alata* (e.g., 15%). Some authors suggested
5 421 that the poor response of yam to N supply might be linked to the shallow-rooting and low root
6 422 density of yam species (Hgaza et al., 2012, 2019). Hgaza et al. (2019) observed that root
7 423 length density in the yam mound averaged 0.3 cm cm⁻³. However, this value seem to be too
8 424 small in relation to the root density data reported for other crops; e.g., from 11 cm cm⁻³ to 16
9 425 cm cm⁻³ for potato (Ahmadi et al., 2014; Nyawade et al., 2018). Although we did not measure
10 426 root density in our study, model results indicated that yam root density in the three N
11 427 treatments were of the same order of magnitude but 2-3 times lower than those reported for
12 428 potato (e.g., 5.4 cm cm⁻³ at tuber maturation, Fig. A13). Nevertheless, as highlighted by
13 429 Milroy et al. (2019) for potato, we consider that while the rooting characteristics of yam
14 430 species may explain the variable response to N supply, it does not appear to be an absolute
15 431 limitation because yields as high as 50 Mg fresh matter ha⁻¹ are frequently reported in many
16 432 tropical regions; e.g., Diby et al. (2011) in Ivory Coast, and Marcos et al. (2011) in
17 433 Guadeloupe. The observed and simulated data on soil mineral N obtained during the present
18 434 study suggested that the leaching of available N was a major factor to explain the differences
19 435 between N treatments. This is in line with the results reported by several authors concerning
20 436 the impact of N leaching on the poor response of yam to N supply in humid tropics (e.g.,
21 437 O'Sullivan, 2010; Hgaza et al., 2012). Indeed, the negative effect of N leaching on crop
22 438 growth might be exacerbated in a crop such as yam which has a shallow root system; e.g.,
23 439 up to 0.4 m according to Melteras et al. (2008) and O'Sullivan (2008).

38 440 Under our modeling approach the limitation of crop N uptake occurred when the
39 441 mineral N content was <1 mg N kg⁻¹ in at least one soil layer, being the value observed by
40 442 Greenwood and Draycott (1995) for potato. For N50, this threshold was attained between DAP
41 443 83 (start of tuber growth) and DAP 113 (second N application) and from DAP 120 to the end
42 444 of the growth cycle. The limitation of N uptake during these periods was linked to N leaching
43 445 and also to the rapid increase in biomass production and N demand by the crop after TI
44 446 (Marcos et al., 2011). Although the second N application removed the N limitation observed
45 447 under N50 near TI, this N supply was not sufficient to compensate for leaching and crop N
46 448 demand after DAP 120. For N125, the threshold for N limitation was attained between DAP
47 449 100 and the second N fertilization at DAP 113. No limitation on N uptake was observed for
48 450 this treatment after DAP 113. In other words, just two weeks of N limitation during the start of
49 451 tuber growth caused an important reduction in LAI and biomass production compared to the
50 452 N200 treatment, which did not display any N limitation during the growth cycle. This short-
51 453 term effect of low N availability under N125 induced a 10% reduction in yam yields compared
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454 to N200, thus revealing the importance of the T1 stage to determining the response of yam to
455 N fertilization in humid tropical regions characterized by high N leaching.

457 *4.2. Changes in leaf N content, radiation interception and radiation use efficiency*

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

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

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

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4.3. Impact of N fertilizer management

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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.

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.

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.

5. Conclusions

530 During this study we tested a hypothesis regarding the key role played by N leaching
1 531 in the humid tropics in terms of controlling the response of yam to N supply. One major result
2 532 obtained from the field experiment was that N leaching near the start of tuber growth strongly
3 533 impacted the subsequent crop phases and yield. Although model results indicated that a
4 534 change in the current N fertilizer practices (timing and split ratio) would allow reduce soil N
5 535 limitation at tuber initiation, N leaching was always very high and accounted for about one
6 536 third of the fertilizer rate under all the experimental and simulated conditions analyzed during
7 537 this study. Indeed, other practices need to be implemented, together with the change of the
8 538 N fertilizer strategy, in order to assure yam yields while reducing the risk of diffuse pollution
9 539 of water resources. Among these practices, the use of organic fertilizers and soil mulching
10 540 could be easily adopted by smallholder farmers involved in yam production.

11 541 Leaf N status correctly reflected severe soil N constraints (i.e., in N50), but it failed to
12 542 match the negative effect on yam yields of N limitation occurring during short-term periods
13 543 (i.e., two weeks in N125). The results suggested a trade-off between leaf N and LAI if no
14 544 severe N shortage was present, which might correspond to a trait of a crop like yam which
15 545 originally grew under rain forest conditions. Further research is now needed to assess this
16 546 effect which may contribute to developing new crop-based N indicators to correct N
17 547 deficiencies during the growing season.

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20 550 **Credit authorship contribution statement**

21 551

22 552 Denis Cornet: Conceptualization, Investigation, Validation, Formal analysis, Writing
23 553 original draft; Javier Marcos: Conceptualization, Investigation, Software, Validation, Formal
24 554 analysis; Régis Tournebize: Conceptualization, Resources, Investigation, Data Curation,
25 555 Writing original draft; Jorge Sierra: Conceptualization, Software, Formal analysis, Writing
26 556 original draft, Supervision.

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29 559 **Declaration of Competing Interest**

30 560

31 561 The authors declare that they have no known competing financial interests or
32 562 personal relationships that could have appeared to influence the work reported in this paper.

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16 577 **Appendix A. Supporting information**

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 18 579 Supplementary data associated with this article can be found in the online version at
 19 580
 20 581

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