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Root biomass plasticity in response to nitrogen fertilization and soil fertility in sugarcane cropping systems

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ABSTRACT

Soil fertility is crucial for plant growth as it influences root development, nutrient uptake, and overall plant health. Optimizing fertilization practices is essential for productivity and sustainability in sugarcane (*Saccharum officinarum*) cropping systems, especially on Reunion Island, where soil types and climatic conditions vary. The aim of this study was to assess the influence of mineral nitrogen fertilization and soil fertility on sugarcane root development, with particular focus on root biomass production and distribution. The study was conducted across ten sites on Reunion Island, each site representative of one of five soil types in two distinct climatic zones. Using a mechanical auger, root biomass and distribution were measured in fertilized and unfertilized plots down to a depth of 50 cm and at three distances from the row of sugarcane at harvest. Root biomass varied markedly depending on the site: it ranged from 4 to 12 Mg ha^{-1}, corresponding to root-to-shoot ratios varying from 0.10 to 0.43. Root biomass increased by 15 % and root nitrogen concentration decreased by 9 % in unfertilized plots, while root nitrogen mass was not affected. Root biomass was influenced by chemical soil fertility and decreased with declining P availability. Chemical and physical soil properties also influenced the proportion of roots in the superficial soil layers. These findings underscore the plasticity of root biomass allocation in response to soil fertility and fertilization. Given the significant role of roots in soil carbon sequestration, understanding their dynamics is crucial for refining fertilization strategies and enhancing the sustainability of sugarcane cropping systems.

1. Introduction

Soil fertility affects both aboveground biomass and root development. Fertile soils provide essential nutrients including nitrogen (N), phosphorus, and potassium, which are vital for various physiological processes in plants (Ericsson, 1995; Lopez-Bucio et al., 2003). In cropping systems, soil fertility directly influences root growth patterns, as roots tend to proliferate in nutrient-rich zones (Hodge, 2009, 2004; Stanford, 2015). The relationship between soil fertility and root development is critical because roots respond actively to the availability of nutrients in the soil by modifying their growth and architecture to optimize nutrient uptake (Hermans et al., 2006; Linkohr et al., 2002; Liu, 2021; Rao et al., 2016).

Nitrogen is an essential nutrient for plant growth and large amounts of N are consequently supplied as fertilizer (Torsten Ingestad, 1977). However, excessive N fertilization disrupts the natural nitrogen cycle, thereby damaging the soil, water, and air quality (Erisman et al., 2011). Recent global reports highlight the fact that high annual N inputs in agricultural systems cannot be sustained without causing significant environmental alterations, mainly through nitrous oxide emissions and

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leaching (ITPS, 2015).

The physical, chemical, and biological components of soil fertility and fertilization practices interact to create an environment that can either promote or inhibit root growth depending on the cropping system concerned (Anderson, 1988; Chen et al., 2019; Oikeh et al., 1999; Reynolds and D'Antonio, 1996). Evidence for the effect of N fertilization on root growth remains contradictory. A recent review of 50 studies across 14 species found that, in most cases, N fertilization increased root biomass (Lopez et al., 2023). Roots are crucial in soil organic carbon enrichment, even more than aboveground plant parts or litter (Boone, 1994; Deng et al., 2021; Menichetti et al., 2015; Sokol et al., 2019). Soil organic carbon is known to have a significant impact on reducing the greenhouse gas CO_2, thereby helping to mitigate climate change (Christopher et al., 2009). Encouraging root production through agricultural practices is thus a key lever for sequestering more carbon (Dignac et al., 2017); this requires proper management of fertilization to encourage strong root development while minimizing loss of N from agricultural soils.

Sugarcane (*Saccharum officinarum*) is the source of a significant proportion of sugar and ethanol production and is also a source of raw material for the production of electric energy in tropical and subtropical regions (Leal et al., 2013). On Reunion Island, sugarcane accounts for 54 % of the agricultural area, making it the island's most widespread crop (Agreste, 2022). The N requirements of sugarcane for a yield of 100 Mg ha^{-1} have been estimated at an average of 220 kg N ha^{-1}, but this varies with the type of soil and the supply of nutrients (Fillols and Chabalier, 2007). With increasing global demand for sugarcane (Goldemberg et al., 2014; Leal et al., 2013), in Reunion Island there is mounting pressure to increase sugarcane production despite a continuous decrease in land available for agriculture (-12 % since 2010, Agreste, 2022). In this context, optimizing fertilization practices is crucial, not by increasing N inputs but by using existing resources more efficiently to boost production sustainably.

Roots have been relatively understudied in sugarcane cropping systems. A few studies have assessed how sugarcane root development is influenced by soil physical fertility (Otto et al., 2011; Trouse and Humbert, 1961) or mineral fertilization (Otto et al., 2009; Versini et al., 2020). The island's diverse climates, soil types, and varying levels of fertility present unique challenges and opportunities for sugarcane cultivation. Previous studies have shown how N fertilization can significantly affect root growth. On the one hand, Versini et al. (2020) showed that the absence of fertilization led to an overall increase in the proportion of roots in the topsoil layers in Reunion Island. On the other hand, in Brazil, Otto et al. (2009) showed that no fertilization had no effect on root biomass but that the absence of fertilization led to a more homogeneous distribution of roots in the soil profile. Understanding these dynamics is particularly important in sugarcane systems, where optimizing root growth could increase both productivity and sustainability.

As reported for other cropping systems, changes in root biomass and distribution can have a significant impact on soil biological, chemical, and physical fertility (Dos Santos Nascimento et al., 2021; Larkin et al., 2021; Ojeda et al., 2018). Additionally, knowledge of the amount of N in the root compartment could help calculate N use efficiency (Poultney, 2021) and determine doses of fertilizer recommended by existing decision-support tools depending on the type of soil (Versini et al., 2018). Given the importance of nutrient uptake and overall plant health, it is essential to understand how soil fertility influences root development in sugarcane which, in turn, will help refine fertilization practices to boost yields and enhance the sustainability of sugarcane production on Reunion Island.

The aim of the present study was thus to assess the influence of nitrogen mineral fertilization and soil fertility on the development of sugarcane roots through root biomass production and distribution across ten different field sites. The sites were selected to represent five different soil types in the two distinct climatic zones of Reunion Island. We hypothesized that N fertilization 1) decreases root total biomass production without altering the amount of accumulated N and 2) influences the distribution of root biomass in the root profile by promoting root biomass production close to the row and in the topsoil. We also hypothesized that root development is influenced in the same way as mineral fertilization by physical and chemical soil fertility.

2. Materials and methods

2.1. Study area

The study was conducted on the volcanic island of Reunion Island, located in the Indian Ocean, coordinates 21°06'52'' S and 55°31'57'' E. Reunion Island has a tropical climate with significant contrasts due to its oceanic location. The island has two distinct climatic zones: the windward (eastern) coast, which is very wet, and the leeward (western) coast, which is drier. The island's rugged terrain creates various microclimate zones, resulting in high rainfall variability, ranging from 700 mm to 1000 mm y^{-1} in areas where sugarcane is cultivated (Dumont et al., 2022). Sugarcane is grown from sea level up to 1000 m a.s.l. (Dumont et al., 2022) and is irrigated at low altitudes in the western part of the island.

2.2. Experimental network and management

The experimental network comprised ten sugarcane field sites located in different soil and climate conditions throughout the island (Table 1). A ratoon crop was used in each site, i.e. the sugarcane crops were in regrowth and not in the planting year: six fields were located on-farm (CTICS technical institute and growers), and four fields were located on-station (TERO projects; Février et al., 2018). Each site included three blocks with two fertilization conditions: fertilised, in which 100 % of the plant nitrogen requirements were met (hereafter F), or not fertilized (hereafter NF). Each elementary plot was 7.5 m wide and 11 m long, with inter-row spacing of 1.5 m. Nitrogen requirements were estimated using the SERDAF decision support tool (Table 1), based on a soil analysis carried out at each site before planting. The results of the analysis are used to formulate fertilization plans according to the type of soil, soil N supply, and expected yield (Versini et al., 2018). The sites were chosen so to have two representatives of the main soil types in the two contrasted climatic zones (the windward coast and the leeward coast). Fertilized plots (F) received a split application of urea granules, the first application was made one month after the previous harvest and the second application four months after the harvest.

In areas with limited precipitation, sprinkler irrigation was applied to ensure non-limiting water conditions, i.e. at sites 1, 3, 4, and 5 (Table 1). Depending on the location, different sugarcane varieties were planted following the recommendations of the technical centers in Reunion (eRcane and CTICS), to ensure the varieties were well suited to each area. Harvesting was carried out on different dates (Table 1). The rest of the crop management was similar at all the sites. The sugarcane straw was left in place after the previous harvest, and chemical herbicides were used for weed control at all the sites.

Table 1
Description of the ten sites: meteorological conditions, annual rainfall, mean daily temperature (T_{MEAN}), mean global radiation (Rg), and soil types (N = Nitisol, C = Cambisol, AC = Andic Cambisol, ANP = Non-Perhydrated Andosol, AP = Perhydrated Andosol), ratooning year (defined as rx where x is the number of years since planting), the harvest date and the dose of mineral N fertilizer applied.

Site number	Name of the site	Rainfall (mm y^{-1})	T_{MEAN} (°C)	Rg (MJ m^{-2} d^{-1})	Variety	Soil type	Ratoon	Harvest date	N dose (kgN ha^{-1})
1	La Mare	1898	25.4	20	R582	N	r4	17/7/2019	198
2	Ste-Suzanne	2154	24.4	18	R579	N	r5	08/10/2019	124
3	Le Gol	1241	24.3	17	R586	C	r1	14/1/2020	173
4	St-Louis	2263	23.9	18	R584	C	r1	28/8/2019	189
5	Piton St-Leu	1570	22.0	16	R579	AC	r3	12/11/2019	138
6	Bras-Panon	2628	24.0	18	R579	AC	r5	03/12/2019	201
7	Menciol	3103	23.2	17	R579	ANP	r3	23/7/2019	157
8	St-Benoit	2409	24.1	17	R585	ANP	r2	03/10/2019	97
9	Ste-Rose	2811	22.4	16	R584	AP	r4	12/8/2019	140
10	St-Philippe	3103	24.2	15	R585	AP	r1	13/1/2020	145

2.3. Soil analysis and climate

At each site, soil bulk density was measured in three soil cores (5 cm diameter x 5 cm height) sampled at two depths (0–5 cm and 5–10 cm soil layers) and dried to constant weight. To estimate coarse elements, soil stoniness was measured by excavating three soil monoliths (30 cm edge cubes). In each plot, five samples collected from the 0–30 cm soil layer were pooled for physico-chemical analyses at the CIRAD Soil Laboratory in Saint-Denis, Reunion Island (Table S1). Soil pH was quantified using two methods: water and KCl extractions. Soil organic carbon (SOC) and total nitrogen (Ntot, g kg^{-1}) were quantified using the Dumas combustion method with an elemental analyzer (Elementar VarioMax Cube). Due to the absence of carbonates, SOC is expressed as total carbon content (g kg^{-1}). Soil phosphorus content was determined using the modified Dabin Olsen method and is expressed in mg kg^{-1}. Cation exchange capacity (mol kg^{-1}) and exchangeable cations: potassium, calcium, magnesium, and sodium (K^+, Ca^{2+}, Mg^{2+}, Na^{2+}, in cmol kg^{-1}) were quantified using a cobalt hexamine trichloride solution. Field capacity (pF 2.5) was measured using the matric potential method.

Climatic variables were obtained from the network of weather stations established across Reunion Island and available in the CIRAD METEOR web application (https://smartis.re/METEOR). The selected data included solar radiation (MJ m^{-2} d^{-1}), rainfall (mm y^{-1}), and average temperature (°C).

2.4. Root biomass sampling

Soil cores were sampled at the sugarcane harvest (around 12 months after the previous harvest, Table 1). In each plot, three soil cores were sampled in the central inter-rows of each plot at three distances from the row of sugarcane, 12.5, 37.5, and 62.5 cm (Fig. S1). As the interrow between sugarcane was 1.5 m in width, we considered the root system would be symmetrical for a distance of 0–75 cm on each side of the row. The three distances were therefore selected to represent this area. The three samples were taken from the same randomly selected sugarcane stool using a Cobra TT thermal drill with a 50 cm long gouge with a 9 cm internal diameter. The cores were then divided according to three soil layers: 0–10, 10–30, and 30–50 cm. A total of 54 samples were taken at each site (2 fertilization conditions x 3 repetitions x 3 distances from the row x 3 soil layers). Each sample was placed in a transparent bag and stored in a cold room at 4 °C before being processed within two months after harvest.

The soil samples were washed successively several times to recover as many roots as possible. To this end, the samples were immersed in buckets, and roots were collected using 50 μm sieves. They were then separated from the organic material. The roots were dried at 60 °C for three days then weighed. The root biomass density (RBD, g dm^{-3}) was estimated in each soil layer based on the volume of the soil core. All the root samples collected in each plot were then pooled for nitrogen analysis. To this end, the roots were crushed to 1 mm in a bowl mill. The concentration of nitrogen (R [N], kgN Mg^{-1}) in the samples was determined using the DUMAS method (O_2 combustion of the sample). The total root dry biomass (RDM, Mg ha^{-1}) and total nitrogen mass of the roots (R N mass, kgN ha^{-1}) were calculated for the entire 50 cm soil core.

2.5. Shoot sampling

Fresh aboveground biomass, (hereafter termed shoot biomass), was measured at harvest (12 months) using a tractor equipped with a weighing scale. The stem + leaf biomass in the three central rows were weighed along the entire length of the plot, excluding the two border rows. The sugarcane's shoot dry biomass (SDM, Mg ha^{-1}) was calculated from the dry matter content measured after drying two 500 g sub-samples at 105 °C for 48 hours. For analysis of nitrogen content, another 1 kg sub-sample was dried at 60 °C for 72 hours. Shoot nitrogen concentration (S [N], kgN Mg^{-1}) in the samples was determined using the DUMAS method (O_2 combustion of the sample) and the total nitrogen mass of shoots (S N mass, kgN ha^{-1}) was calculated. In the following, all aerial (SDM) and root biomass (RDM) values are expressed in dry mass. Using the dry shoot and root biomasses and the nitrogen content of both shoot and root parts, we calculated the root-to-shoot dry biomass ratio (RS DM) and the root-to-shoot nitrogen mass ratio (RS N mass).

2.6. Statistical analysis

Statistical analyses were performed with Rstudio software: R version 4.3.1 (R Core Team, 2023). The influence of nitrogen fertilization on SDM, shoot N concentration, shoot N mass, total root biomass, root N concentration, total root N mass, root-to-shoot DM ratio, and root-to-shoot N mass ratio was tested using a linear model combined with analysis of variance (ANOVA) with the fertilization treatment, the site and their interaction as fixed effects. The influence of fertilization on root biomass density and the proportion of root dry mass in the different soil layers and distance from the row were tested using a mixed linear analysis of variance with the fertilization treatment, soil depth, distance from the row, site, and their interaction as fixed effects, and the plot as a random effect (nlme package; Pinheiro and Douglas, 2000). Before the

analysis of variance, the total root biomass, root density, and root proportion variables were transformed using a box Cox transformation (MASS package; Venables and Ripley, 2002) to ensure residue normality. Non-significant interactions were removed from the models based on AIC and BIC criteria. Pairwise comparisons were performed with a Tukey p adjustment method using the emmeans function (emmeans package; Lenth, 2024).

2.7. Random forest approach

A random forest approach was used to assess the non-linear influence of soil characteristics and climate on shoot biomass, root biomass, root-to-shoot ratio, and the proportion of roots in the top 10 cm of the soil. As soil characteristics and meteorological variables were highly correlated (Fig. S2), a principal component analysis (PCA) with a rotation method (varimax) was performed using the R principal function of the psych package to create principal components using an unsupervised approach (Revelle, 2024). Note that the variables were scaled before the PCA. Thirteen soil and two meteorological variables were summarized into four principal components. These four components were then used as explanatory variables in the random forest models (ranger package; N. Wright and Ziegler, 2017) fitted with 1000 trees and mtry = 2 (parameter selection based on rRMSE criteria). To assess model quality, a relative root mean square error (rRMSE, %) was calculated between predicted and observed values in the training dataset. The importance of a variable for model prediction was calculated using the Gini index (Tangirala, 2020). Partial correlation plots over the principal component ranges were performed using an expand grid method on these variables. Smoothing conditional means based on loess regressions were plotted to facilitate visualization (geom_smooth function).

3. Results

3.1. Effect of nitrogen fertilizer on shoot and root biomass, N concentration, Nmass

All above- and belowground variables, except for root N mass, were influenced by the interaction between the site and the fertilization treatment (shoot N concentration and N mass) or by the fertilization treatment alone (Table 2). The shoot and root compartments showed opposite responses to fertilization. On average across sites, sugarcane SDM was 17 % lower in no fertilization (NF) conditions compared to in fertilization (F) conditions (31 Mg ha^{-1} compared to 37 Mg ha^{-1}, p = 0.0001, Fig. 1a). Conversely, RDM increased by 15 % in NF conditions compared to in F conditions (p = 0.0132, Fig. 1d). On average in NF conditions, RDM was 9 Mg ha^{-1} with a minimum of 3 Mg ha^{-1} and a maximum of 22 Mg ha^{-1} depending on the site. In F conditions, the average RDM was 7 Mg ha^{-1} with a minimum of 3 Mg ha^{-1} and a maximum of 17 Mg ha^{-1} (Fig. 1d). As a consequence, there was a 32 % increase in the root-to-shoot dry mass ratio (p = 0.0001) in NF conditions (0.31 on average with a minimum of 0.07 and a maximum of 0.60) compared to in F conditions (0.21 on average with a minimum of 0.08 and a maximum of 0.45, Fig. 1g).

Both shoot and root N concentrations responded similarly to fertilization treatment (Fig. 1b, e). The overall trend in shoot N concentration was a 13 % decrease in NF conditions (2.8 kgN Mg^{-1}) compared to in F conditions (3.2 kgN Mg^{-1}), but the decrease was only significant in sites 3 (39 %), 5 (25 %), 6 (25 %) and 7 (22 % decrease). Similarly, root N concentrations were 9 % lower in NF (6.6 kgN Mg^{-1}) than in F conditions (7.2 kgN Mg^{-1}) across all sites (p = 0.0139). The site also influenced root concentration (p < 0.0001), in particular site 8 which had a significantly lower R[N] than the other sites.

While root N mass was not influenced by fertilization (p = 0.58), shoot N mass was significantly lower in NF than F conditions in six out of ten sites (Fig. 1c, f). The overall trend was a 22 % decrease in shoot N mass in NF compared to in F conditions. Consequently, the root-to-shoot N mass ratio increased by 36 % in NF compared to in F conditions (p = 0.0003, Fig. 1h). The average root-to-shoot N mass ratio in NF conditions was 0.84 with a minimum of 0.15 and a maximum of 1.38 (Fig. 1h). In fertilized conditions, the average was 0.55, with a minimum of 0.24 and a maximum of 1.00. Nonetheless, the sites influenced root N mass (p < 0.0001) with values ranging from 99 to 28 kgN ha^{-1} depending on the site (Fig. 1f).

3.2. Effects of nitrogen fertilizer on root distribution

Root biomass density (RBD) and the proportion of root dry mass were significantly influenced by the interaction between fertilization x site x distance (p = 0.0033 and p = 0.0011), fertilization x site x depth for RBD only (p = 0.0359), and the interaction between distance x depth (p = 0.0276 and 0.0234, Table 3). RBD decreased with increasing distance from the sugarcane row and increasing soil depth, with the highest RBD (3.84 g dm^{-3} on average) observed in the top 10 cm of the soil and close to the sugarcane row (12.5 cm, Fig. 2). At this distance (12.5 cm) the proportion of root dry mass was higher in the NF condition than in the F condition (p = 0.0007). However, the difference was slight (Fig. 3a). Conversely, a higher proportion of root dry mass was observed at a greater distance from the sugarcane row (distances of 37.5 and 62.5 cm) in the F condition compared to in the NF condition. Nevertheless, in the pairwise comparison, the effect of fertilization on the proportion of root dry mass at the shortest distance from the row was significant in only four out of the 10 sites, sites 2, 5, 7, and 9 (Fig. 3b).

Table 2
Effect of the fertilization condition, the experimental site and their interactions on sugarcane shoot (SDM) and root dry mass (RDM), shoot (S [N]) and root N concentration (R [N]), shoot (S N mass) and root N mass (R N mass), and root-to-shoot dry mass ratio (RS DM) and N mass (RS N mass). Variance (F) analyses were performed using a linear model (ANOVA). The degree of freedom (df) and *P*-value are indicated. All non-significant interactions were removed from the analysis.

	Fertilization			Site			Fertilization:Site		
	F	df	*P*	F	df	P	F	df	*P*
SDM	18.63	1, 50	0.0001	10.45	9, 50	< 0.0001			
S [N]	18.12	1, 41	< 0.0001	14.357	9, 41	< 0.0001	4.82	9, 41	0.0002
S N mass	17.21	1, 41	0.0002	9.54	9, 41	< 0.0001	2.45	9, 41	0.0247
RDM	6.61	1, 50	0.0132	13.82	9, 50	< 0.0001			
R [N]	6.50	1, 50	0.0139	27.86	9, 50	< 0.0001			
R N mass	0.31	1, 50	0.5824	8.76	9, 50	< 0.0001			
RS DM	18.43	1, 50	0.0001	7.29	9, 50	< 0.0001			
RS N mass	15.19	1, 50	0.0003	5.51	9, 50	< 0.0001			

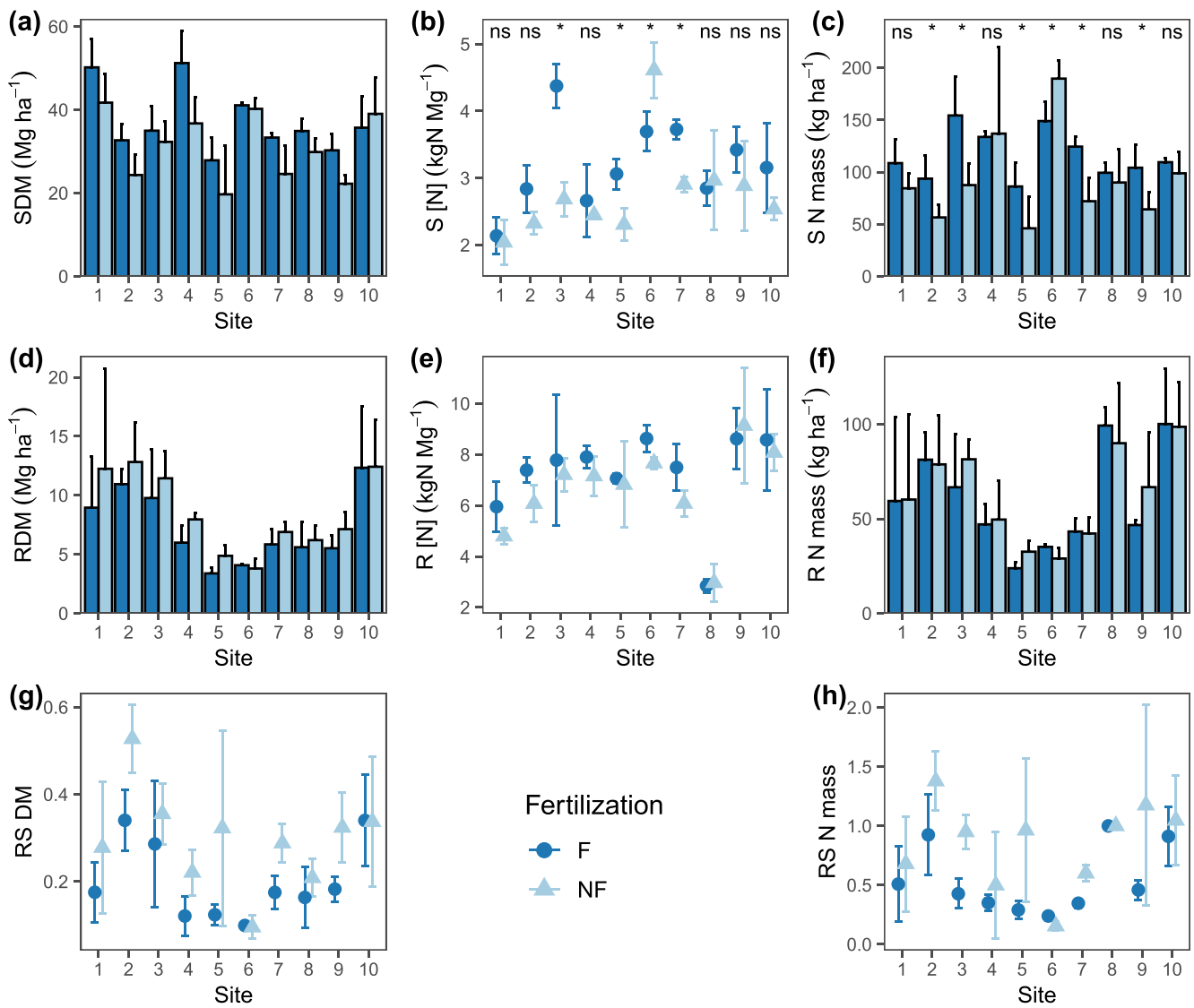

Fig. 1. Shoot dry mass (SDM, a), shoot N concentration (S [N], b), shoot N mass (S N mass, c), root dry mass down to a depth of 50 cm (RDM, d), root N concentration (R [N], e), root N mass (R N mass, f), root-to-shoot dry mass ratio (RS DM, g), and root-to-shoot N mass ratio (RS N mass, h) of sugarcane depending on nitrogen fertilization conditions (F nitrogen fertilization, NF no nitrogen fertilization). Bars indicate standard deviation (n = 3). In (b) and (c), the fertilization effect at each site is indicated by * when $p < 0.05$, and by 'ns' when non-significant.

Table 3
Effect of fertilization condition, experimental site, distance from the sugarcane row, depth of the soil layer, and their interactions on sugarcane root biomass density (RBD, g dm^{-3}) and the proportion of root dry mass (DM) (%). F values, degree of freedom (df), and *P*-values are presented. The non-significant third-order interactions were removed from the analysis.

	RBD			Root DM proportion		
	F	df	*P*	F	df	*P*
Fertilization	1.29	1, 42	0.2622	5.50	1, 42	0.0238
Site	11.76	9, 42	< 0.0001	0.54	9, 42	0.8406
Distance	95.98	2, 412	< 0.0001	118.82	2, 412	< 0.0001
Depth	136.42	2, 412	< 0.0001	57.67	2, 412	< 0.0001
Fertilization:Site	0.34	9, 42	0.9557	1.03	9, 42	0.4358
Fertilization:Distance	4.00	2, 412	0.0190	4.92	2, 412	0.0077
Fertilization:Depth	3.21	2, 412	0.0416	2.57	2, 412	0.0778
Site:Distance	2.47	18, 412	0.0008	3.35	18, 412	< 0.0001
Site:Depth	5.17	18, 412	< 0.0001	5.10	18, 412	< 0.0001
Distance:Depth	2.76	4, 412	0.0276	2.86	4, 412	0.0234
Fertilization:Site:Depth	1.70	18, 412	0.0359	1.62	18, 412	0.0529
Fertilization:Site:Distance	2.20	18, 412	0.0033	2.41	18, 412	0.0011

There was no significant difference concerning changes in the proportion of root dry mass with soil depth between the F and NF conditions. On average, across all sites, 31 %, 31 %, and 38 % of root dry mass were found in the 0–10 cm, 10–30 cm, and 30–50 cm soil layers, respectively (Fig. 4), and the interactions between depth and fertilization ($p = 0.0778$) and between depth, site and fertilization ($p = 0.0529$) were not significant (Table 3).

3.3. Impact of soil fertility and climate

The principal component analysis summarised the soil and climate variables into four principal components (PC_{Chem}, PC_{Phys}, PC_{Clim}, and PC_{Phos}). The first component (PC_{Chem}, 38 % of data variance), which was mainly explained by acid-base properties (pH_K, pH_W, CEC) and mineral concentrations (K^+, Ca^{2+}, Mg^{2+} and Na^{2+}), was related to nutrient availability and reflects chemical soil fertility (Fig. 5). The second component (PC_{Phys}, 33 % of data variance) was mainly explained by the physical soil characteristics relative to the level of pedogenetic development of these volcanic soils such as stoniness (Stn), field capacity (FC), bulk density (BD), C and N content (Fig. 5). The third component (PC_{Clim}, 14 % of data variance) was mainly explained by the climate variables: global radiation (Rg) and temperature (Tm, Fig. 5). Finally, the fourth component (PC_{Phos}, 9 % of data variance) represented phosphorus (P) availability (Fig. 5).

The random forest models for shoot biomass (SDM), root biomass (RDM), root-to-shoot ratio of dry mass (RS DM), and the proportion of root in the 0–10 cm soil layer (%R10cm) exhibited R^2 of 0.42, 0.4, 0.31, and 0.38, respectively, and rRMSE of 7.27, 3.16, 0.11, and 2.47 %. Variations in SDM and RDM were mainly explained by the PC_{Clim} component (Gini index), while the RS DM was mainly explained by PC_{Chem} and %R10cm by PC_{Phys} and PC_{Chem} (Fig. 6).

Shoot and root biomass showed relatively similar trends regarding soil and climatic components (Fig. 6). Both SDM and RDM showed a rapid increase with an increase in the climatic PC_{Clim} component, from 30 to 38 Mg ha^{-1} for SDM, and 6.4–9.8 Mg ha^{-1} for RDM (Fig. 6b,d). Nonetheless, the faster increases in SDM than in RDM induced a non-linear response in the root-to-shoot ratio. SDM and RDM also increased with increased soil acidity and with the mineral component PC_{Chem}, but the increase was mainly associated with a threshold in PC_{Chem}. PC_{Chem} had little impact on the root-to-shoot dry mass ratio except at low values (Fig. 6f). The phosphorus PC_{Phos} component had less impact (Gini index) on SDM and RDM. However, both variables

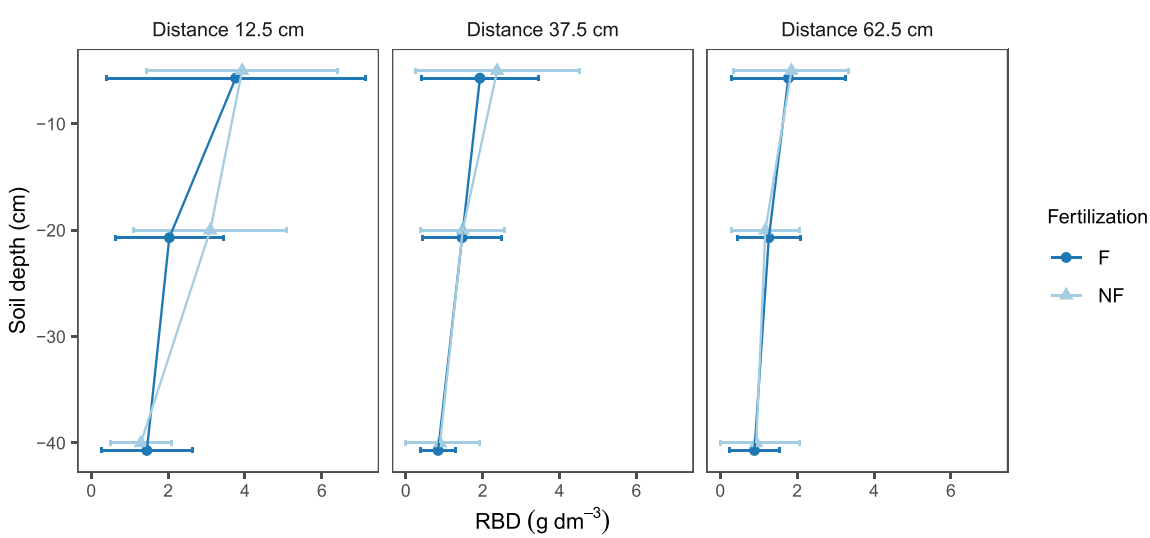

Fig. 2. Average sugarcane root biomass density (RBD) across sites, depending on nitrogen fertilization (F nitrogen fertilization, NF no nitrogen fertilization), soil depth, and distance from the sugarcane row (12.5 cm, 37.5 cm, and 62.5 cm). Bars indicate the standard deviation (n = 30).

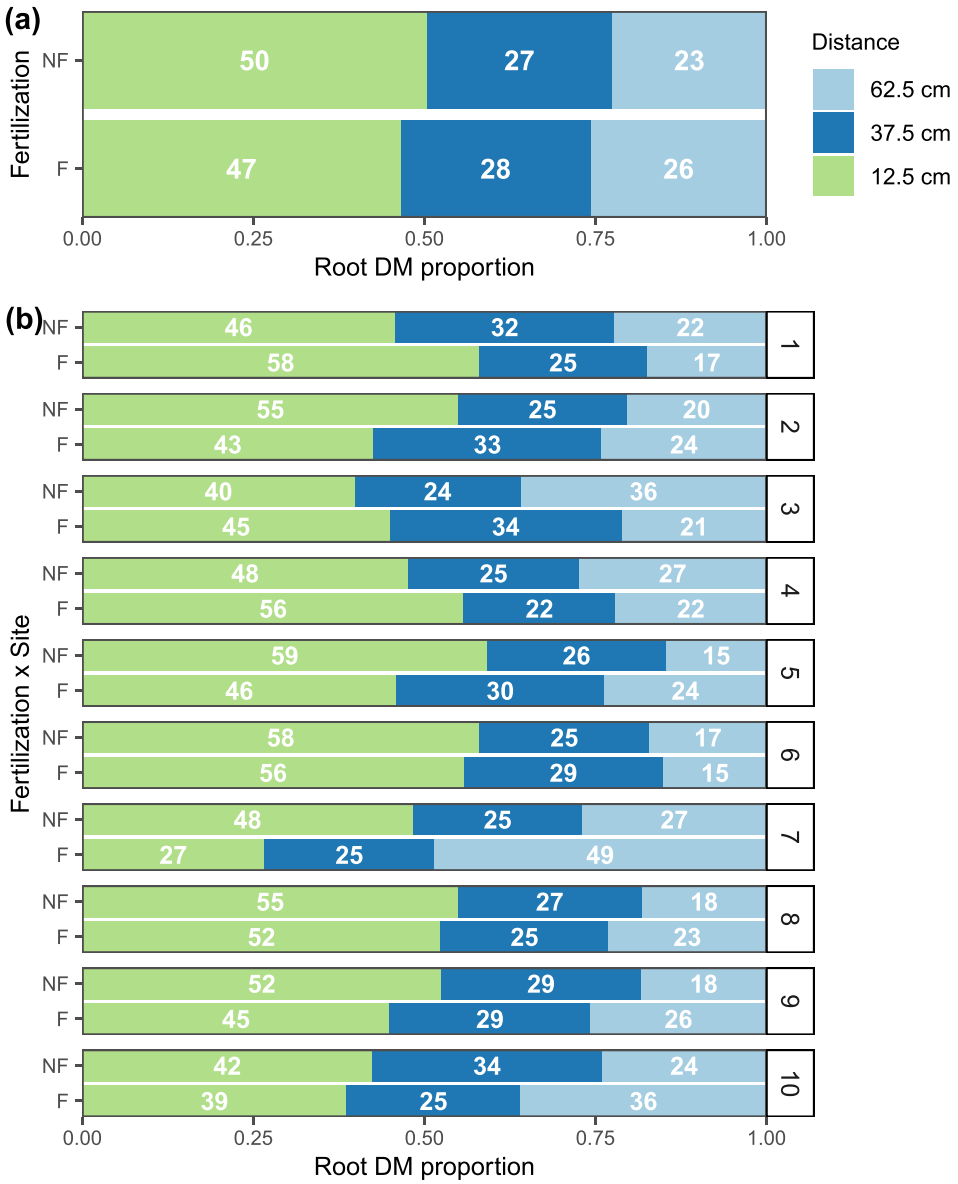

Fig. 3. Proportion of root dry mass (DM) depending on (a) nitrogen fertilization conditions (F nitrogen fertilization, NF no nitrogen fertilization) and distance from the row (12.5, 37.5, and 62.5 cm); (b) N fertilization, distance, and site (1 to 10). Numbers in white indicate the proportions as a percentage.

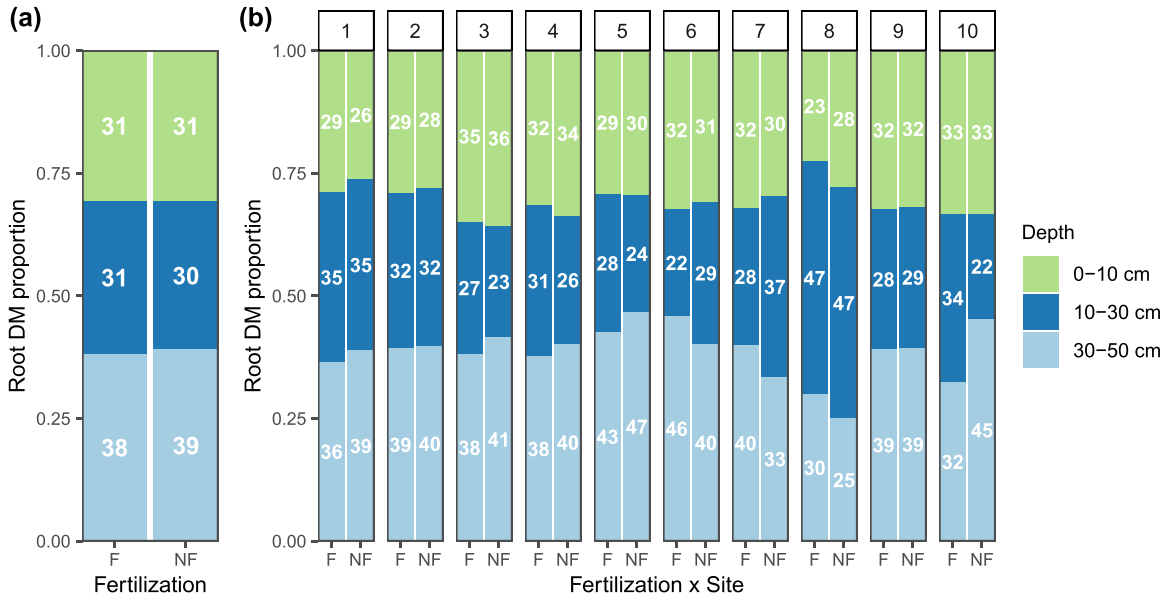

Fig. 4. Proportion of root dry mass (DM) of sugarcane depending on (a) nitrogen fertilization conditions (F: nitrogen fertilization, NF: no nitrogen fertilization) and the depth of the soil layer (0–10, 10–30, 30–50 cm); (b) N fertilization, depth, and site (1 to 10). Numbers in white indicate the proportions as a percentage.

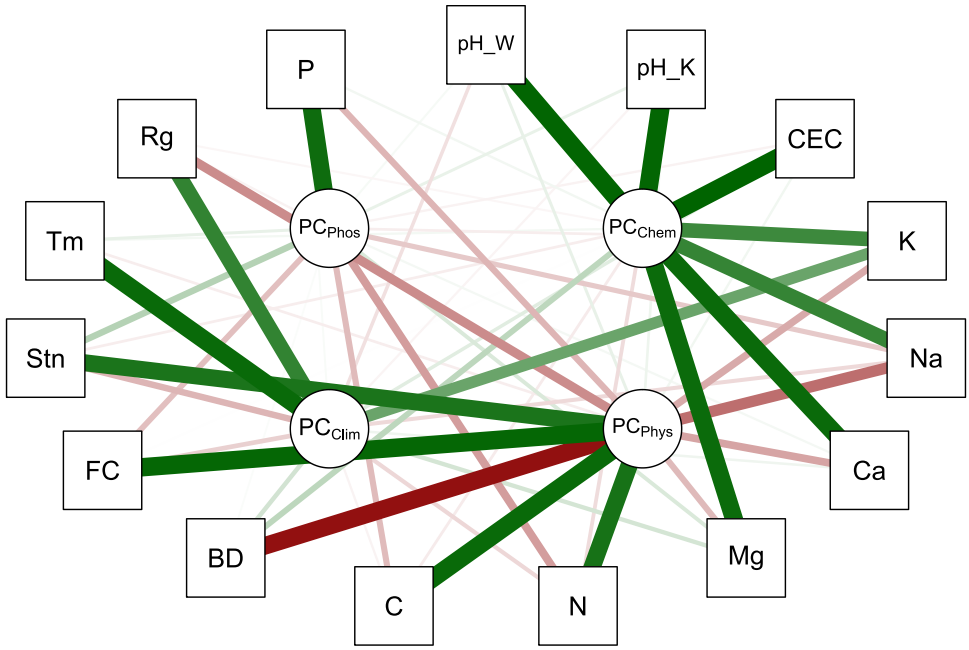

Fig. 5. Correlation between soil and climatic variables and the four principal components: PC_{Chem}: chemical characteristics; PC_{Phys}: physical characteristics; PC_{Clim}: climate; and PC_{Phos}: phosphorus. The green lines indicate a positive correlation, the red lines a negative correlation. The width of the lines represents the strength of the correlation. The variables include pH measured with water (pH_W) and KCl extraction (pH_K), carbon exchange capacity (CEC), K^+, Ca^{2+}, Mg^{2+}, Na^{2+}, N, and C content, bulk density (BD), field capacity (FC), stoniness (Stn), mean daily temperature (Tm), mean global radiation (Rg).

decreased with increasing PC_{Phos} values, the faster decrease in RDM also induced a decrease in the RS DM. Finally, the soil physical component PC_{Phys} induced highly non-linear SDM, RDM, or RS DM responses. The proportion of sugarcane roots in the 0–10 cm soil layer (%R10cm) decreased with the soil physical component PC_{Phys}, increased with the soil mineral component PC_{Chem}, and decreased to a lesser extent with the climate component PC_{Clim} (Fig. 6h).

4. Discussion

4.1. Effect of mineral N fertilization on root biomass and N content

Our study confirmed our first hypothesis that fertilization reduces the growth of sugarcane root biomass, with an average 15 % reduction in fertilized conditions. However, evidence for the effect of N fertilization on root growth in the literature is contradictory. For example, (Reynolds and D'Antonio, 1996) found that N fertilization reduced root biomass in 75 % of cases across 129 species, whereas more recent reviews suggest that, in the majority of cases, N fertilization increases root

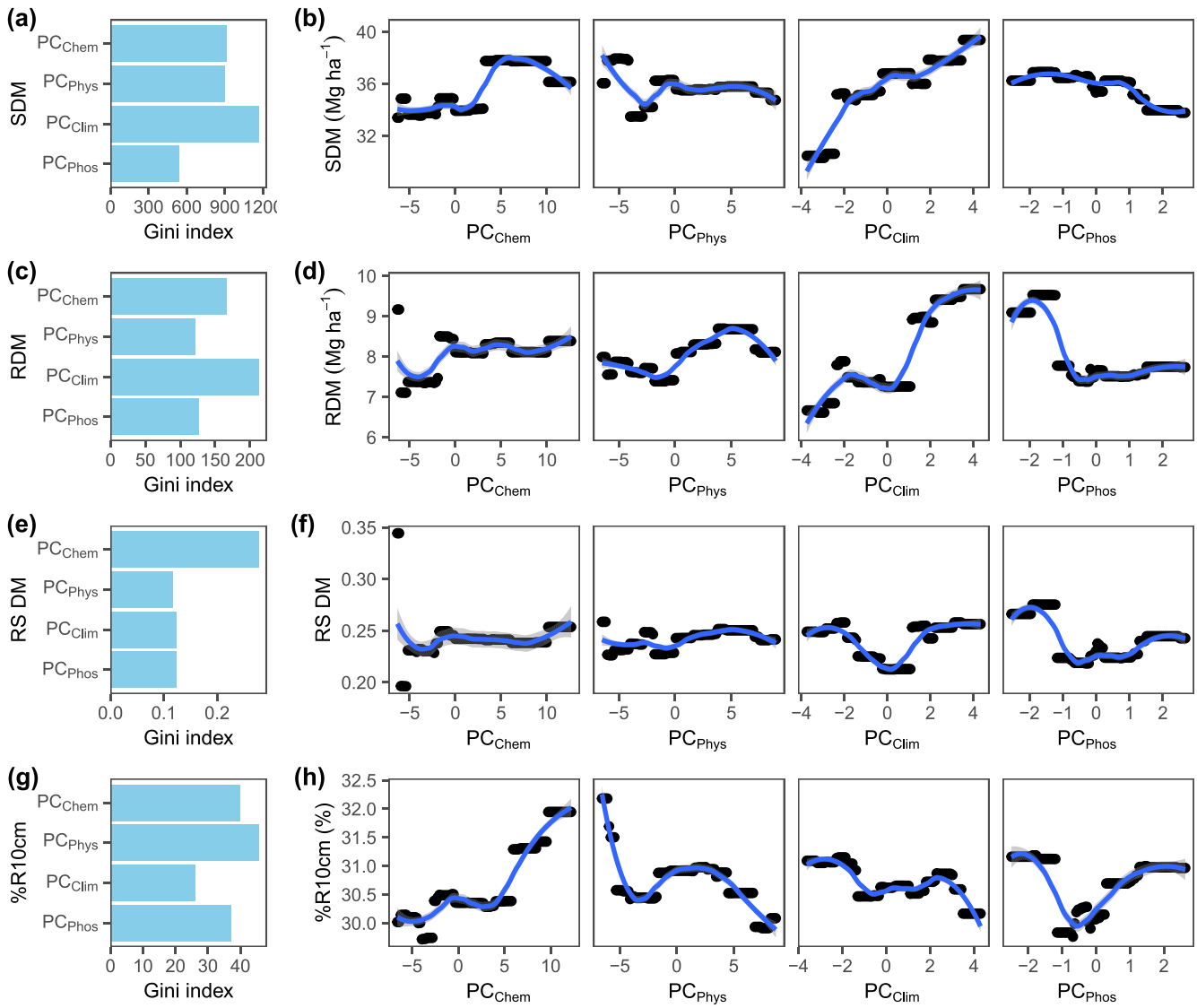

Fig. 6. Relative importance of variables (Gini index) and partial correlation plots in the random forest models for shoot biomass (SDM, a,b), root biomass (RDM, c,d), root-to-shoot dry mass ratio (RS DM, e,f), and proportion of root dry mass in the 0–10 cm soil layer (%R10cm, g,h). Partial correlation plots of each variable in response to the four principal components are presented (PC_{Chem}: Chemical characteristics, PC_{Phys}: Physical characteristics, PC_{Clim}: Climate, and PC_{Phos}: Phosphorus). Predicted variable responses were smoothed with a loess function (blue line).

biomass (e.g. Lopez et al., 2023). One possible scenario in fertilized conditions is that the plant receives sufficient mineral N for growth, and prioritises shoot development at the expense of root systems, resulting in reduced root biomass in fertilized (F) compared to in unfertilized (NF) conditions. However, the opposite trend has been reported in studies on cotton (Chen et al., 2019), maize (Oikeh et al., 1999), and wheat (Hirte et al., 2018). In these cases, fertilization was reported to significantly boost shoot growth, and to enhance photosynthesis because root biomass increases due to greater carbon availability. Our study suggests that sugarcane is more likely to follow the first scenario, where the crop diverts resources from the root system to support shoot growth. Yet previous studies have also reported diverse responses in sugarcane. For instance, a previous study in Brazil found no effect of fertilization on sugarcane root biomass down to a depth of 60 cm (Otto et al., 2009), while other authors observed an increase in root biomass (Otto et al., 2014; Sampaio et al., 1987). Hirte et al. (2018) found no impact of fertilization on root biomass, highlighting the variability in responses across different studies and conditions.

The variability in root biomass response to mineral fertilization, whether in our study or in the literature, is likely influenced by environmental or management conditions that are specific to each site, as suggested by previous studies (Hirte et al., 2018; Otto et al., 2014). Research on sugarcane suggests that the crop's likelihood of not responding to fertilization may be linked to the type of soil (Sanches and Otto, 2022). In the sites studied by these authors, the significant supply of nutrients provided by the soil itself could explain the lack of response to N fertilization. In such cases, both shoot and root systems may not respond to additional fertilizer, making it challenging to conclude on root responses. In our experimental network, our unresponsive sites showed shoot and root biomass were unresponsive, yet the overall data still showed a response to fertilization. We hypothesize that soil type, fertility, and climate are key factors that influence root biomass variability depending on the site.

In addition to soil type, fertility, and climate, the age of the sugarcane may also influence root responses to fertilization, and a key limitation of our study is that root biomass measurements were only made at harvest, potentially disregarding temporal variations that occur during the crop cycle. Some authors have shown that the root-to-shoot ratio, as

well as root biomass, can vary significantly over the crop cycle, with higher root biomass and root-to-shoot ratios often observed at earlier growth stages in both plantation and ratoon crops (Otto et al., 2014; Smith et al., 2005; Versini et al., 2020). These dynamics suggest that the timing of observations during the crop cycle could affect the interpretation of the effects of fertilization on root systems. Future studies should account for these temporal variations to better understand the responses of root biomass and their implications for sugarcane management and carbon sequestration.

Whereas root biomass decreased and shoot biomass increased in F conditions, the sugarcane root-to-shoot dry mass ratio decreased with fertilization (from 0.31 in the NF to 0.21 in F conditions in our study). Similar results have been reported in other studies on sugarcane, showing a ratio of 0.29 for four-year-old sugarcane under F condition (Silva-Olaya et al., 2017) and ratios of 0.39 for NF and 0.23 for F at harvest for three-year-old sugarcane (Versini et al., 2020). Studies on other crops also indicate a decrease in the root-to-shoot ratio in F conditions, such as those by (Reynolds and D'Antonio, 1996), and (Anderson, 1988) on maize, and (Hirte et al., 2018) on wheat. However, in some cases, fertilization can increase the root-to-shoot dry mass ratio at the beginning of the sugarcane cycle before it stabilizes (Otto et al., 2014).

Due to opposing trends in root biomass and root N concentrations, fertilization did not influence root N mass in our study. Studies on N concentration and root N mass in sugarcane are scarce, but a review of 56 studies on other crops showed a reduction in root N concentration without fertilization (Gordon and Jackson, 2000), in line with our observations in sugarcane. Regarding root N mass, our range of values between sites is in line with observations made in Reunion Island (62 kg N ha^{-1} in roots, Versini et al., 2020) and in Brazil (24 kg N ha^{-1} in root and stool, Otto et al., 2014). Unlike root N mass, shoot N mass increased with fertilization, decreasing the root-to-shoot N mass ratio from 0.84 to 0.55. Information on the root-to-shoot N mass ratio in the literature is limited, and a review by (Gordon and Jackson, 2000) indicates that this value varies significantly across species. In sugarcane, two studies reported similar trends in the root-to-shoot N mass ratio, one in Reunion Island (Versini et al., 2020) and the other in Australia (Robinson et al., 2009).

As highlighted in recent studies, the sugarcane root system represents a significant N sink, as it contains up to half of the plant's total N (Poultney et al., 2024; Versini et al., 2020). A greenhouse study using ^{15}N demonstrated that N is gradually transferred from the leaves to the roots over the course of the year (Chevalier et al., 2023), a pattern also reported in other studies (Courtaillac et al., 1998; Kwong and Deville, 1994; Poultney et al., 2020). The N stored in the roots, which remain in the soil, is then used during regrowth to produce new shoot biomass (Chevalier et al., 2023). Two months after cutting, 50 % of the ^{15}N initially stored in the roots was found in different plant compartments (stem, leaf, stool, root), and half of this N was present in the leaves (Chevalier et al., 2023). These factors can significantly influence calculations of N-use efficiency (Poultney, 2021). The data provided in this article will help clarify crop requirements defined by fertilization decision-support tools based on the "nitrogen budgeting" method (COMIFER, 2013), thereby providing more appropriate doses of N fertilizer.

4.2. Effect of mineral N fertilization on root distribution

Our results did not confirm our second hypothesis that fertilization influences root biomass distribution by promoting root biomass production close to the row and concentrated in the topsoil. Our root distribution was consistent with the distribution reported in previous studies (Blackburn, 1984; Christina et al., 2023; Otto et al., 2011, 2009). However, a key limitation of our study is that root biomass was only measured down to a depth of 50 cm, while sugarcane roots are known to grow much deeper, consequently the influence of fertilization on deeper root systems may have been underestimated (Chopart et al., 2010; Evans, 1936).

(Otto et al., 2009) suggested that fertilization increases root growth at the soil surface and decreases growth at depth, hypothesizing that roots are concentrated near the surface where the fertilizer is applied. Conversely, (Versini et al., 2020) observed an increase in root growth at the surface without fertilization, and hypothesized that in NF conditions, the roots of sugarcane are concentrated in the upper layers where most N available to plants is found. Our study across ten sites cannot confirm either hypothesis (Otto et al., 2009; Versini et al., 2020). Other studies of sugarcane of different ages reached similar conclusions, suggesting that site-specific conditions have more influence on vertical root distribution than fertilization (Hirte et al., 2018; Otto et al., 2014). Our results concerning the influence of chemical fertility (PC_{Chem} component) suggest that roots are concentrated where nutrients are most available. Contradictory results may be due to the influence of other factors, such as physical fertility (PC_{Phys} component) or climate (PC_{Clim} component). The potentially weaker effect of mineral fertilization on root distribution may be due to its shorter period in the soil, given potential losses, compared to the more stable, ongoing influence of inherent soil chemical or physical fertility. Indeed, some studies have shown that other phenomena such as water availability can affect the rooting depth of sugarcane (Laclau and Laclau Battie, 2009). Similar observations have been made in many crops (Kalra et al., 2024; Kätterer et al., 1993; Lindh et al., 2014; Pace et al., 1999), thereby highlighting the impact of climate on root development.

4.3. Effect of soil fertility on root biomass and distribution

In the present study, all plots were managed conventionally before the experiment began, including annual applications of urea. It seems unlikely that the absence of fertilization for a single year would have significantly affected soil fertility compared to fertilized plots. Our theory is supported by the absence of an interaction effect between fertilization and site in the present study. This suggests that the mineral fertilizer applied during the year of the experiment did not interact with the inherent fertility of the soils sufficiently to influence root development. Moreover, it is important to note that the NF condition does not necessarily imply a nitrogen deficiency for sugarcane. The natural fertility of the soils, combined with mineralization of organic matter may have provided sufficient N to sustain plant growth (Lopez et al., 2023). Consequently, the observed differences between F and NF conditions may not only reflect N availability but could also be influenced by other site-specific factors such as climate, soil physical and chemical fertility.

We hypothesized that soil chemical and physical fertility would decrease total root biomass while increasing the proportion of roots in the topsoil. The effects of soil fertility on root development have rarely been studied in sugarcane. Our PC_{Phys} component, representing soil physical fertility associated with the pedogenetic stage of development of these volcanic soils, was negatively related to the proportion of roots in the 0–10 cm soil layer. Studies on other crops have mainly focussed on the effect of bulk density and resistance to soil penetration on root growth parameters, with mixed results. For instance, increased bulk density in maize and mangroves increased root biomass (Himmelbauer et al., 2012; Ola et al., 2018), while in sugarcane, it reduced root elongation (Otto et al., 2011). Studies on soil penetration resistance have consistently shown that root growth declines rapidly with

increased soil penetration resistance, plateauing at around 2–3 Mpa (Boone, 1994; Pardo et al., 2000). In the present study, our models showed that higher bulk density and soil penetration resistance were correlated with lower root biomass, aligning with these findings. On the other hand, in our study, the models showed that higher bulk density promotes superficial roots in the 0–10 cm soil layer meaning that even if high apparent density reduces root biomass, it promotes the development of superficial roots. Boone (1994) reported similar results in maize: higher soil resistance to root growth led to more horizontal root growth and less branching. Conversely, (Himmelbauer et al., 2012) found deeper growth under higher soil resistance.

Regarding mineral soil fertility, we observed that cation exchange capacity (CEC) and exchangeable cations (K^+, Ca^{2+}, Mg^{2+}, and Na^{2+}) positively influenced root and shoot biomass and the proportion of roots in the 0–10 cm soil layer. Nutrients K^+, Ca^{2+}, Mg^{2+}, and Na^{2+}, are essential for plant growth and development (Hodge, 2009, 2004; Pandey, 2018). Our model showed increased root and shoot biomass when these nutrients were present, underscoring their importance for sugarcane growth. The effects of phosphorus (P) on roots where small quantities of P increased root biomass, were similar to the effects of N fertilization,. Other authors have reported similar results (Hermans et al., 2006; Liu, 2021; Rao et al., 2016). Linkohr et al. (2002) observed a decrease in root elongation with high N or P inputs. While the overall trend was the same, root system responses varied depending on the deficiency concerned. Under N limitation, root growth increased, and lateral root growth was stimulated upon encountering N (Hermans et al., 2006). In the case of P deficiency, a highly branched root system has been reported to develop near the soil surface, thereby decreasing primary root elongation and increasing lateral root growth (Hermans et al., 2006; Rao et al., 2016). This last information is in line with our results, which showed that the proportions of superficial roots increases beyond a certain P threshold.

To sum up, enhanced soil fertility increases the quantity of superficial roots at low P values and high bulk density. However, the variables we studied did not explain much of the variability in root biomass. Bulk density is not the best parameter to assess the force necessary for root growth in the soil; using a parameter like soil penetration resistance would be more accurate. Additionally, more than ten sites with mixed soil and climate effects are needed to draw definitive conclusions.

5. Conclusion

This comprehensive study across diverse soil types and climatic zones on Reunion Island provides valuable insights into the complex relationship between nitrogen fertilization, soil fertility, and sugarcane root development. Our findings demonstrate the remarkable plasticity of sugarcane root systems in response to nutrient availability and soil conditions, with higher root biomass but lower nitrogen concentration in roots in unfertilized plots. The spatial variability of root biomass, primarily concentrated in the upper soil layers and closer to the sugarcane rows, highlights the plant's adaptive strategy to optimize nutrient acquisition in nutrient-limited environments. Given the critical role of roots in carbon sequestration, these results have direct implications for improving fertilization practices by considering the nitrogen requirements of both aboveground plant parts and roots, as well as remobilization of nitrogen from dead roots. The aim of using this approach was both to optimize sugarcane production and promote sustainable soil management. By refining their fertilization strategies to account for soil fertility and root dynamics, sugarcane growers can improve productivity while contributing to long-term sustainability.

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CRediT authorship contribution statement

Daniel Poultney: Writing – review & editing, Investigation. **Versini Antoine:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Chevalier Léa:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mathias Christina:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **Amélie Février:** Writing – review & editing, Resources, Methodology, Funding acquisition. **Christophe Jourdan:** Writing – review & editing, Methodology, Funding acquisition. **Marion Ramos:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Benjamin Heuclin:** Writing – review & editing, Formal analysis.

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

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.eja.2025.127549.

Data availability

I have shared the link to my data in the manuscript

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