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RESEARCH ARTICLE

Optimizing soil and plant functions: combinatory design of fertilizing resources assemblage for rainfed rice in Madagascar

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Summary
The lack of affordable mineral fertilizers and scarcity of organic materials cause decline in soil fertility for smallholder farmers and producers in the highlands of Madagascar, challenging crop productivity. To fulfill plant growth and nutrition, we explored the effect of 132 combinations of 17 different fertilizing resources, both organic and mineral, on rice growth and nutrition using a greenhouse experiment. Two clustering approaches were used to evaluate the effects of fertilizing resources: elemental clustering and functional clustering. Elemental clustering grouped resources based on their elemental intrinsic composition, while functional clustering grouped resources based on their effect in improving plant growth and nutrition when combined in soil. We found that some resources closely grouped based on their elemental composition exhibited different effects on plant growth and nutrition when combined in soil. Zebu horn emerged as a particular organic resource in elemental clustering, and a key resource in functional clustering by promoting plant growth and nutrition when combined with other resources in soil. Its unique elemental composition played a significant role in driving positive interactions with other resources. We proposed to extend the concept of 'assembly motif' within soil fertilization strategy, suggesting that the combination of functional groups of resources determines better their fertilizing effect than their elemental composition. Resources inducing high interaction effects should be combined with those having high elemental composition to optimize crop productivity.

Keywords: soil fertility management; elemental clustering; functional clustering; Ferralsols

Introduction

Soil fertility decline is one of the main constraints to sustaining crop productivity in Africa (Sanchez and Leakey, 1997; Vanlauwe *et al.*, 2015). Most smallholder famers cannot afford expensive mineral resources, or only at low amounts, while organic fertilizing resources are scarce in most areas and offer insufficient nutrients to support crop yields (Palm *et al.*, 2001; Vanlauwe and Giller, 2006). Furthermore, organic fertilizer usually offers a particular nutrient in high amount but exhibit imbalance macronutrients not suitable to fulfil plant nutrients requirements. As a result, most agrosystems export more nutrients than are provided by external inputs or from the soil (Sanchez and Jama, 2001), leading to negative soil nutrient balances and nutrient soil mining (Cobo *et al.*, 2010). Consequently, nutrient deficiencies are common in many crop production systems (Raminoarison *et al.*, 2020). Optimizing tropical soil fertility using appropriate management strategies from both organic and mineral resources is necessary to increase crop productivity sustainably (Chen *et al.*, 2018).

Several studies conducted in Africa have shown that the combined application of fertilizing resources (FR), both organic and mineral, is a promising solution to improve soil fertility compared to using only organic or mineral fertilization (Vanlauwe *et al.*, 2014; Andriamananjara *et al.*, 2019; Gram *et al.*, 2020). Combining FR improves system nutrient use efficiency, reduces nutrient losses, and enhances overall soil fertility (Dapaah *et al.*, 2008; Opala *et al.*, 2010; Palm *et al.*, 1997; Rietra *et al.*, 2017). The composition and interactive benefits between resources, referring to the positive complementary effect and synergies on plant function respectively, supply both macro- and micronutrients for plants, being regulated by the rate of mineralization of the added organics (van Zwieten, 2018). The application of FR whose nutrients are readily available for plants creates high levels of available nutrients that exceed plant demand early in the season, potentially leading to nutrient losses, while organic resources release nutrients slowly during periods of plant demand, leading to temporary nutrient deficiencies (Myers *et al.*, 2014). Combining FR can help match the rate of soil nutrient supply with the rate of plant nutrient uptake. In addition, combining FR can increase soil organic matter content and improve soil biological functions and soil moisture regimes (Sanginga and Woomer, 2009). This is particularly true for Ferralsols characterized by high phosphorus (P) sorption, where P management is complex and can be improved by a combination of organic and mineral FR (Andriamananjara *et al.*, 2019).

Many questions arise when considering the most efficient combination of FR. The hypothesized interactive benefits of combining FR are likely to be influenced by residue properties, particularly the nitrogen (N) content, the C-to-N ratio, and other biochemical characteristics of the resource (Nicolardot *et al.*, 2001; Morvan *et al.*, 2006; Lashermes *et al.*, 2010). FR are usually grouped based on their quality, i.e. their biochemical properties such C:N ratio or lignin content, using hierarchical clustering based on the elemental intrinsic properties of FR. This approach has proved invaluable in predicting mineralization rates of individual fertilizers taken one by one (Palm *et al.*, 2001). However, this approach is inadequate for studying the effects of FR combinations on soil–plant system functioning. Another approach suggests clustering FR based on their effect (e.g. biomass production or plant nutrition), when they co-occur in different combinations (Jaillard *et al.*, 2018a; Jaillard *et al.*, 2018b). Importantly, this functional clustering does not consider the elemental properties of FR, but only the effect of their combinations.

In this study, our aim was to identify the FR combinations that optimize plant growth and nutrition for rainfed rice cultivated in a Ferralsol from Madagascar. To achieve this, we conducted a greenhouse experiment using various FR combinations. We then clustered FR based on their elemental properties (elemental clustering), as well as based on the effect they exhibit when combined in soil (functional clustering). The null hypothesis posits that the composition of functional groups reflects the elemental composition of FR. In others words, the two clustering methods converge in the composition of FR groups. Conversely, the alternative hypothesis would be that the functional clustering of FR does not depend on their composition but on their agronomic effect in soil.

Materials and Methods

Organic and mineral fertilizer resources (FR)

We collected seventeen fertilizer resources (FR) from local farmers and from commercial producers in Madagascar (Table 1). Some of these FR meet the standards NF U42–001 and NF U44–051, which correspond to the designations of 'fertilizers' and 'organic amendments', respectively. The term 'fertilizers' is used for products that contain at least 3% of a major nutrient, whereas the term 'organic amendments' is used for products in which the organic matter content is at least 20%, and the content of a major nutrient is less than 3% of the raw product (Table S1). Following collection, all FR underwent a range of physicochemical and biochemical analyses. Details of the analytical methods and the characteristics of the FR can be found in Raminoarison *et al.* (2022).

Table 1. Description and origin of seventeen organic and mineral fertilizing resources available in the highlands of Madagascar

Code	Classe	Type	Norm	Description	Manufacturer	Equivalent application rate	N added	P_2O_5 added	K_2O added
ManI	Organic amendments	Manures	NF U44–051	Fermentation of raw cattle dejections (excrements + urine) collected over plant residues mainly constituted of rice straw and prepared in outside rudimentary park	Itasy farmer	6 t DM ha^{-1}	129.60	13.19	32.53
ManV	Organic amendments	Manures	NF U44–051	Fermentation of raw cattle dejections (excrements + urine) collected over plant residues mainly constituted of rice straw. The product is prepared and stored in closed place and collected in a specific recipient	Vakinankaratra farmer	6 t DM ha^{-1}	112.08	40.68	159.76
KM	Organic amendments	Animal dejections without residues	NF U44–051	Kraal manure: non-fermentable mixing of soil and cattle dejection accumulate on the floor of outdoor park and stored in the open air	Vakinankaratra farmer	6 t DM ha^{-1}	61.92	21.58	49.73
ComM	Organic amendments	Household fermentable composts	NF U44–051	Fermentable composts from the dumpsite of Mahajanga municipal solid waste landfill under natural composting	Madacompost company	6 t DM ha^{-1}	81.42	65.28	38.02
ComT	Organic amendments	Household fermentable composts	–	Fermentable composts from the dumpsite of Andralanitra municipal solid waste landfill under natural composting	AKAMASOA Association	6 t DM ha^{-1}	35.88	51.12	18.80
VermT	Organic amendments	Plant and animal composts	NF U44–051	Vermicompost of mixing of farmyard manure and various plant residues, with imported earthworm species (*Eisenia foetida*)	TATA association	6 t DM ha^{-1}	119.94	51.53	123.25
VermV	Organic amendments	Plant and animal composts	NF U44–051	Vermicompost of mixing of farmyard manure: soil, rice straw and legumes (mainly *Melia azedarac*), with imported earthworms species (*Eisenia foetida* and *Eisenia andrei*)	Vakinankaratra farmer	6 t DM ha^{-1}	70.38	27.49	26.17
Tar	Organic amendments	Plant and animal composts	–	Bacterial leaven fixed on a rich organic plant support, certified organic by Ecocert, commercially known as Taroka phosphaté	STOI Agri Company	6 t DM ha^{-1}	24.60	52.50	34.92
HornZ	N organic fertilizer	Crushed zebu horn	NF U42–001	Product obtained by crushing and grinding zebu horns of different diameters: flour, semolina, shavings	Madacompost company	6 t DM ha^{-1}	929.88	16.22	3.76
AshE	Fertilizers	Plant ashes	NF U42–001	Ash derived from combustion of *Eucalyptus* branches	Itasy farmer	0.5 t DM ha^{-1}	0.24	44.74	50.89
AshH	Fertilizers	Plant ashes		Rice husk ash obtained after burning out the husk in air	Itasy farmer	0.5 t DM ha^{-1}	0.96	1.42	4.17
DroG	Entirely animal-based NP fertilizer	Bat guano droppings	NF U42–001	Dried droppings of bats. Product formed by accumulation and ageing of those dropping birds, cave in the Southeast Region	Guanomad company	0.5 t DM ha^{-1}	6.29	78.41	1.33
DroP	Entirely animal-based NP fertilizer	Dried poultry droppings	NF U42–001	Desiccated product obtained by the accumulation and drying of poultry excrement for the production of commercial broilers	Itasy farmer	0.5 t DM ha^{-1}	10.55	17.75	7.23
SheF	N organic fertilizer	Shell fish flour	NF U42–001	Product obtained by fine grinding of crab shells.	Madacompost company	0.5 t DM ha^{-1}	5.67	13.73	2.05
Hyp	Phosphorus fertilizer	Rock phosphate + volcanic black soil	–	Organo-mineral product obtained from mixing micronised apatitic rock and volcanic black soil, known commercially as Hyperfos	Prochimad Company	0.5 t DM ha^{-1}	0.19	94.88	0.19
Dol	Fertilizer providing Ca, Mg, Na, and/ or S	Dolomite	NF U42–001	Natural product essentially containing double carbonate of Ca and Mg, deposit in Ibity. Vakinankaratra Region	SEPCM Company	0.5 t DM ha^{-1}	0.01	0.02	0.03
NPK	Fertilizer $N_{11}P_{22}K_{16}$	Synthetic fertilizer	NF U42–001	Synthetic ternary fertilizer in the granular form	Prochimad Company	0.15 t DM ha^{-1}	1.65	6.18	1.27

Soil and plant materials

The soil used for this study was collected from the Eastern part of Itasy region, near the locality of Imerintsiatosika (19°05'40"S; 47°25'65"E; 1480 m asl). The soil was classified according to the WRG Soil taxonomy as Ferralsol (WRB-FAO I, 2015). It is very acidic (pH = 4.7) and exhibits low Olsen P content (3.76 mg P kg^{-1}), a low cation exchange capacity (1,7 cmol+ kg^{-1}), and very low levels of exchangeable cations (K^{+}, Ca^{2+}, Mg^{2+}). The soil shows low total N content (2.1 g kg^{-1}), and the soil organic carbon content was 29.2 g kg^{-1}. Its texture was dominated by fine fractions (clay + silt = 86.6%). Soil sample was taken from the upper layer (0–20 cm) of a farmer's field, which was naturally covered by savannah vegetation known as 'bozaka,' primarily consisting of Aristida sp. grasses. The soil was air-dried, with a portion passed through a 2-mm sieve for laboratory analysis, and a 5-mm sieve for the mesocosms experiment. The soil samples were then stored at room temperature in the dark before analysis. For the experiment, the Chhomrong Dhan rice cultivars, locally used by farmers, was employed. Chhomrong Dhan is an upland rice cultivar well suited for cold and high-altitude regions (Raboin *et al.*, 2013). The seeds for this cultivar were provided by the agronomic station of the local governmental agronomic institute of Madagascar, FOFIFA, based in Antsirabe.

Experimental design

We conducted a combinatory trial in the greenhouse of the Laboratory of Radio-Isotopes (LRI), University of Antananarivo, Madagascar during the 2017–2018 growing season (from November to April). In this trial, we designed 132 different combinations of three FR each (Figure 1). This selection represents 19% of 680 possible combinations of three FR. The chosen combinations were subject to two main criteria: they needed to be both agronomically plausible and statistically unbiased. Specifically, the selected combinations were required to reflect realistic agricultural scenarios and also ensure a fair distribution of each FR, thus maintaining equitable representation of all FR frequencies in the experiment. Because the farmers always use volume or mass as a unit of reasoning for fertilization choices, we preferred to standardize the rate base on the mass, closed to actual input rate done by the farmers in Madagascar when the information was available (Ravonjiarison *et al.*, 2023). Importantly, the application rate remained constant regardless of the combinations tested, i.e. when the FR were combined, the nutrient contents resulting from a combination of three types of organic amendments were three times higher than those obtained from each FR alone. These rates were determined based on surveys conducted in the selected commune for soil sampling within the SECURE project, which involved over 170 farming families (Razanakoto *et al.*, 2021).

Ultimately, each FR was utilized in a range of 50 to 205 combinations, with a median of 100 out of the 132 FR combinations. Among the organic amendments, ManI, ManV, KM, ComM, ComT, VermT, VermV, Tar, and HornZ, each was applied at an equivalent rate of 6 t dry matter ha^{-1} (Table 1). These organic amendments were included in a varying number of combinations, ranging from 50 to 100, with a median of 90 combinations. Conversely, the fertilizers, including AshE, AshH, DroG, DroP, SheF, Hyp, and Dol, were applied at an equivalent rate of 0.5 t dry matter ha^{-1} (Table 1). These fertilizers were found in at least 105 and up to 205 combinations, with a median of 135. The ternary fertilizer NPK was applied at a rate of 0.15 t dry matter ha^{-1} and was included in 105 combinations (Table 1). The total amounts of FR added in the pots were 36 g, 3 g, and 0.16 g dry matter for organic amendments, fertilizers, and NPK, respectively, in order to obtain the agronomic rates related to the size of the pots. Indeed, the application rate was applied according to farmers' practice in the zone, i.e. 3.7 to 13.2 t MS. ha^{-1}, and whose apply FR in terms of volume or mass unit rather than in nutrient equivalent (Ravonjiarison *et al.*, 2023). Accordingly, the quantity of nutrients applied varied across the combinations, N was applied at a range of 24 to 1113 kg.ha^{-1}, P was applied at a range of 6 to 80 kg. ha^{-1}, and K was applied at a range of 3 to 191 kg.ha^{-1}. The impact of each of

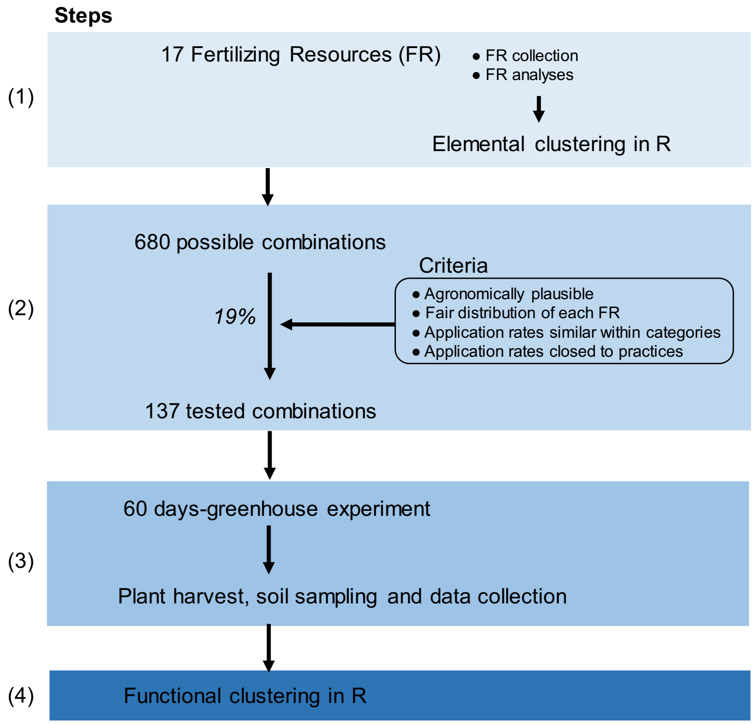

Figure 1. Graphical description of the different steps of the study. Step (1): Collection and analysis of 17 fertilizing resources (FR) from local farmers and from commercial producers, following by elemental clustering in R. Step (2): Selection of FR combinations based on two main criteria: agronomically plausible and statistically unbiased. Step (3): Greenhouse experiment and data collection. Step (4): Computation of functional groups in R.

the 17 FR individually was examined. They were applied at the same quantity as used in the combinations

The experiment was set up in 30 cm high by 16 cm diameter PVC (polyvinyl chloride) cylindrical pots in which 5 kg of 5 mm sieved dry soil was added. The soil was previously mixed with the FR. Each pot corresponded to one FR combination. All pots were randomly placed in the greenhouse and watered two times per day to reach 70% of the water-holding capacity, i.e. 26 g water per 100 g dry soil (temperature 23°C and 65.4% humidity). One rice seed was sown in each pot after soil fertilization and watering. The greenhouse trial lasted 60 days.

Plant and soil measurements

During the experiment, the numbers of tillers and plant heights were recorded for each combination at weekly intervals from sowing until the end of the experiment. After 60 days of growth, the above-ground parts of the plants were cut, and the roots were gently extracted from the soil and washed with water. The dry biomass of the shoots and roots was determined after oven-drying at 60°C for 48 hours. The C and N contents of the plants were analysed through dry combustion using a Flash 2000 CHN analyzer (Thermo Fisher Scientific GmbH, Dreieich, Germany). The P content was measured using colorimetry (molybdenum blue) after dry-ashing (4 h at 600°C) and extraction with 6 M HCl. The Ca and Mg contents of plants were determined using an atomic absorption spectrophotometer (Ice 3000 Series AA Spectrometer,) with lantana reagent after digestion (Okalebo *et al.*, 2002). The element amounts were calculated by multiplying element contents by the shoot or root biomass.

Statistical analyses

All statistical analyses were done using the R software (Team RC, 2016)

Hierarchical clustering of fertilizing resources (FR)

We first performed a hierarchical clustering of properties of FR using the hclust function (method = 'ward.D2') from the *stats* R-package. The distance matrix was built on the basis of all elemental properties of FR using *dist* function (method = 'euclidean') and was referred to 'elemental clustering'.

Partitioning the global effect (i.e. performance) of combinations of fertilizing resources

Then, for a given variable, we partitioned the global effect, called hereinafter 'performance', of FR multiplicatively into composition and interaction effects (Wilson, 1988; Jaillard *et al.*, 2018a). The interaction effect was obtained by dividing the observed performance of each FR combination, $Y_{observed}$, by the expected performance, $Y_{expected}$. $Y_{expected}$ is computed as the average performance of FR that compose the FR combination. Second, the composition effect was obtained by dividing the expected performance $Y_{expected}$ by Y_{alone} computed as the average performance of each FR used in the experiment:

$$Yobserved = \frac{Yobserved Yexpected}{Yexpected\ Yalone} Yalone$$

The first quotient of this equation is the interaction effect, the second quotient is the composition effect, and the last term is the scale factor of the experiment. The interaction effect integrates all nonlinear effects induced by interactions among FR within an FR combination on combination performance. The composition effect corresponds to linear effects induced by the FR within a combination on combination performance: the more performant the constitutive FR, the greater the composition effect.

Functional clustering of interaction effect, composition effect, and global performance

Lastly, we conducted functional clustering using the fclust function from the functClust R-package. A functional clustering relies on the performance (e.g. the global effect of FR combination on plant growth and plant N content) of FR combinations with composition of FR combinations, without any information on fertilizer resource properties. The functional clustering analysis proceeds in two steps: a calibration step followed by a validation step (Jaillard *et al.*, 2018a, 2018b). Briefly, functional clustering searches for the FR clusters that best account for the observed variations in a given performance, that is, the cluster model that minimizes the intracluster variance and maximizes the intercluster variance. The explanatory ability of the clustering model is determined by its coefficient of determination, R^2, and the predictive accuracy was measured by the model efficiency, E. The Akaike information criterion (AIC_c) was calculated to select the optimal number of clusters without overfitting. Once the model indicated the optimal number of clusters, all the combinations of which the effects were observed are grouped into 'assembly motifs', i.e. a given combination of FR clusters. In sum, the model provides a FR hierarchical tree indicating the optimal number of clusters and displays in a decreasing order the performance of assembly motifs. The best FR combinations will thus be identified by assembly motif.

Regarding performances, we focused on three primary plant functions, i.e. (i) plant growth, (ii) shoot nutrition, and (iii) root nutrition. To achieve this, the following variables were employed for each plant function: (i) plant growth encompassed shoot biomass, the number of stems and tillers, and the number of leaves, (ii) shoot nutrition included total shoot nutrients amounts (N, P, Mg, K, and Ca), (iii) root nutrition encompassed the same nutrients but in the roots. These

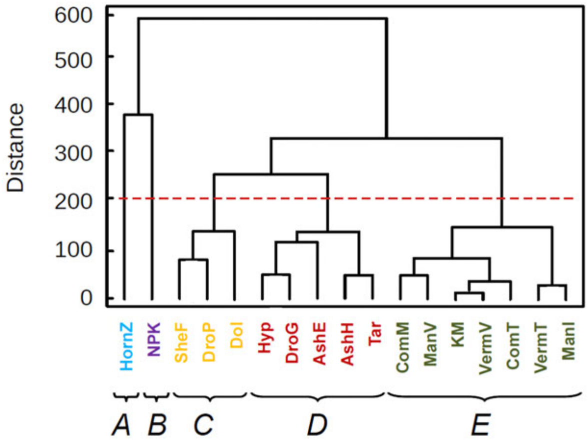

Figure 2. Elemental clustering of fertilizers based on their intrinsic properties. The fertilizers are manures (ManI and ManV), kraal manure (KM), fermentable compost (ComM and ComT), vermicompost (VermT and VermV), Taroka (Tar), zebu horn (HornZ), ash (AshE and AshH), guano (DroG), poultry droppings (DroP), shell fish flour (SheF), hyperfos (Hyp), dolomite (Dol), and synthetic ternary fertilizer (NPK). The different colors and letters (*A*, *B*, *C*, *D* and *E*) correspond to the five clusters retained. The description of each fertilizer is presented in Table 1.

variables were treated as pseudoreplications in the *fclust* function, meaning that each variable was independently analyzed, and the reported overall statistics are the medians of the variable statistics. The resulting clustering is this one that corresponds to the overall statistics. Each variable was given equal weight for each performance. For more detailed information, the clustering analysis based on multiple data is extensively explained in Jaillard *et al.* (2021).

Results

Elemental clustering of FR

A hierarchical clustering analysis based on the mineral composition of FR indicated five main clusters (Figure 2), namely: A = [HornZ], B = [NPK], C = [Dol, DroP, SheF], D = [Tar, AshH, AshE, DroG, Hyp], and E = [ManI, VermT, ComT, VermV, KM, ManV, ComM]. A variance analysis using the clusters as main factor showed that the [HornZ] in cluster *A* had higher C and N contents, while the [NPK] in cluster *B* had larger N and P contents (Table 2). FR in clusters *C*, *D*, and *E* have both lower N and P contents, but differed by their C and K contents. More precisely, FR in cluster *E* had relatively intermediate C contents while those in cluster *D* had almost the lowest C contents. Higher K contents were also observed in FR in cluster *D*. Thus, this elemental clustering was mostly driven by differential C, N, P, and K contents among FR.

Functional clustering of FR based on the performances of fertilizing resources combinations

Plant growth

We first explored the performance of each FR when applied alone on plant growth. The individual effect of FR defined as organic amendments, i.e. all composts (ComM, ComT), vermicomposts (VermV, VermT), and manures (KM, ManI, ManV), had higher plant growth performances compare to the other FR (Figure 3a). The remaining FR had then the following plant growth performances: SheF, DroP, DroG, Hyp, AshE > HornZ, NPK > Dol, AshH.

We then explored the clusters (Figure 4). The functional clustering of FR applied to plant growth had a coefficient of determination R^2_{tree} of 0.68 and an efficiency E_{tree} of 0.34 (E_{tree}/R^2_{tree} = 0.496) (Figure 4a and b). The FR are optimally clustered into four functional groups: A = [HornZ]

Table 2. Variance analysis of properties of fertilizing resources with clusters resulting from the elemental clustering as main factor (p value<0.001)

	Cluster	Ash	C	N	P	S	K	pH
ManI	*E*	*a*	*b*	*b*	*b*	*a*	*b*	*a*
ManV	*E*	*a*	*b*	*b*	*b*	*a*	*b*	*a*
KM	*E*	*a*	*b*	*b*	*b*	*a*	*b*	*a*
ComM	*E*	*a*	*b*	*b*	*b*	*a*	*b*	*a*
ComT	*E*	*a*	*b*	*b*	*b*	*a*	*b*	*a*
VermT	*E*	*a*	*b*	*b*	*b*	*a*	*b*	*a*
VermV	*E*	*a*	*b*	*b*	*b*	*a*	*b*	*a*
Tar	*D*	*a*	*c*	*b*	*b*	*a*	*ab*	*a*
HornZ	*A*	*a*	*a*	*a*	*b*	*a*	*ab*	*a*
AshE	*D*	*a*	*c*	*b*	*b*	*a*	*ab*	*a*
AshH	*D*	*a*	*c*	*b*	*b*	*a*	*ab*	*a*
DroG	*D*	*a*	*c*	*b*	*b*	*a*	*ab*	*a*
DroP	*C*	*a*	*bc*	*b*	*b*	*a*	*b*	*a*
SheF	*C*	*a*	*bc*	*b*	*b*	*a*	*b*	*a*
Hyp	*D*	*a*	*c*	*b*	*b*	*a*	*ab*	*a*
Dol	*C*	*a*	*bc*	*b*	*b*	*a*	*b*	*a*
NPK	*B*	*a*	–	*a*	*a*	–	*a*	*a*

Cluster *A, B, C, D* and *E* : names of clusters resulting from the elemental clustering of fertilizing resources properties.
Letters *a, b, c* indicate significant difference according to variance analysis among clusters.

in a singleton, *B* = [ManV, ManI], *C* = [SheF, Hyp, ComM, NPK, VCT], and *D* = [AshH, AshE, Dol, DroP, DroG, KM, Tar, ComT, VCV] (Figure 4a). It was observed that the relative effects of group *A* and *B* were 26% and 19% respectively ($P < 0.001$), meaning that the occurrence of *A* or *B* with other groups in assembly motifs had a significant effect of 26% or 19% compared to the overall mean. The co-occurrence of *A* and *C* with other groups induced also an additional positive effect of 24% ($P < 0.001$) compared to the overall mean. The observed assembly motifs corroborate these relative effects, and the highest plant growth values were observed with the assembly motifs: *ABC*, *ACD,* and *AC* (Figure 4b).

The functional clustering analysis applied to the interaction effect on plant growth indicates an optimum number of four functional groups of FR, which are: A in a singleton =[HornZ], B= [AshH, DroG, ComT], C= [SheF, Hyp, ManI, KM, Tar], and D= [ManV, DroP, NPK, Dol, VermV, ComM, VermT, AshE] (Figure 5a). The [HornZ] has the highest interaction effect that is the co-occurrence of [HornZ] with the other groups in assembly motif induced generally an additional plant growth of 49% (Figure 5a). Moreover, [HornZ] interacts positively with the clusters B and D. On the other hand, the functional clustering analysis applied to the composition effect separated the FR into five groups, namely: *A* = [ManI, ManV, SheF], *B* = [ComM, VermT, VermV, Tar, KM], *C* = [DroG, Hyp, DroP, AshE], and *E* = [ComT, AshH, HornZ, Dol] (Figure 5c). The functional groups *A* and *B* are associated with a high composition effect, with respectively 32% and 15% additional effects ($P < 0.001$).

To summarize, the functional clustering on plant growth showed that [HornZ] needs to interact with other groups in assembly to be used optimally (FR with the highest interaction effect, Figure 5b) while the application alone of other FR which have high compositional effects is sufficient to improve plant growth. Generally, FR with higher composition effect regroup FR as 'organic amendments', namely [ManI], [ManV], [ComM], [VermT], [VermV] and [KM], except [ComT] (Figure 5d).

Shoot and root nutrition

Again, we first explored the shoot and root nutrition performances of each FR when applied alone. We observed the same trend as for plant growth for both shoot and root nutrition (Figure 3b

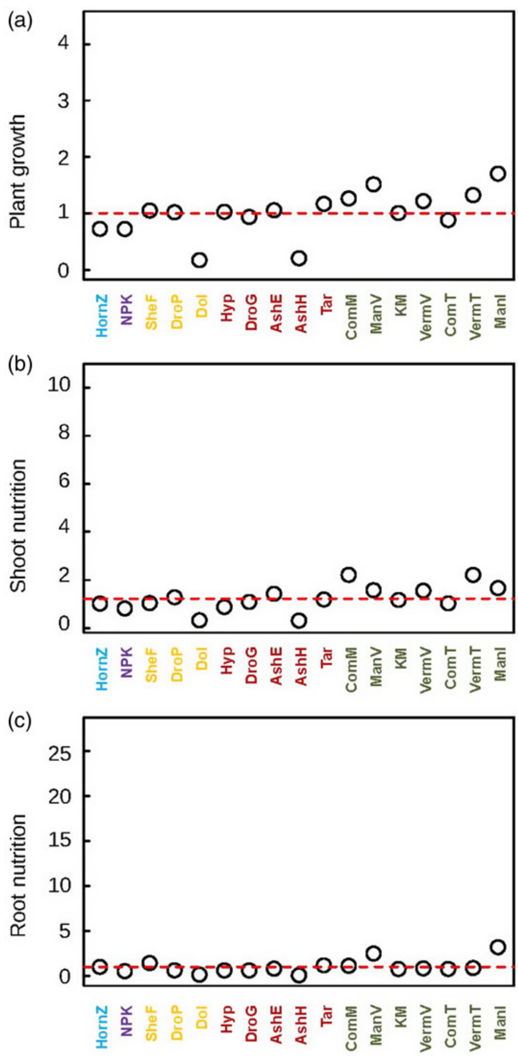

Figure 3. Individual effect (dimensionless) of the fertilizer resources (FR) on plant growth (a), shoot nutrition (b), and root nutrition (c). The dotted red lines indicate the mean values. The color of each FR refers to the cluster resulting from the elemental clustering of fertilizing resources properties (see Figure 2).

and 3c). Namely, the individual effect of FR defined as organic amendments had higher shoot and root nutrition performances compare to the other FR, but these differences were less pronounced.

The functional clustering on shoot nutrition accounts for 87.4% of the total variance, and its efficiency is 72.4% ($E_{tree}/ R^2_{tree} = 0.828$) (Figure 4c, d). [HornZ] is first isolated in a singleton, then the others are split into three groups. The functional groups are namely: *A* in a singleton = [HornZ], *B* = [Hyp, SheF, NPK, VermT, ComM], *C* = [Dol, AshH, DroP, KM, ComT], and *D*= [ManI, ManV, VermV, DroG, Tar, AshE]. Again, the association of the group *A* = [Hornz] with other groups in assembly motifs induces a significantly the higher positive effect on shoot nutrition (+79%, $P < 0.001$). The co-occurrence of *A* and *B*, of *A* and *C*, and the presence of *D*, with other groups in assembly motifs increase also the shoot nutrition but in a lesser additional effects (+22%, +11% and +17% respectively, $P < 0.001$). Conversely, the co-occurrence of C is associated with a negative effect (-27%, $P < 0.001$). AD, ABD, ACD, and AC are then the assembly motifs exhibiting

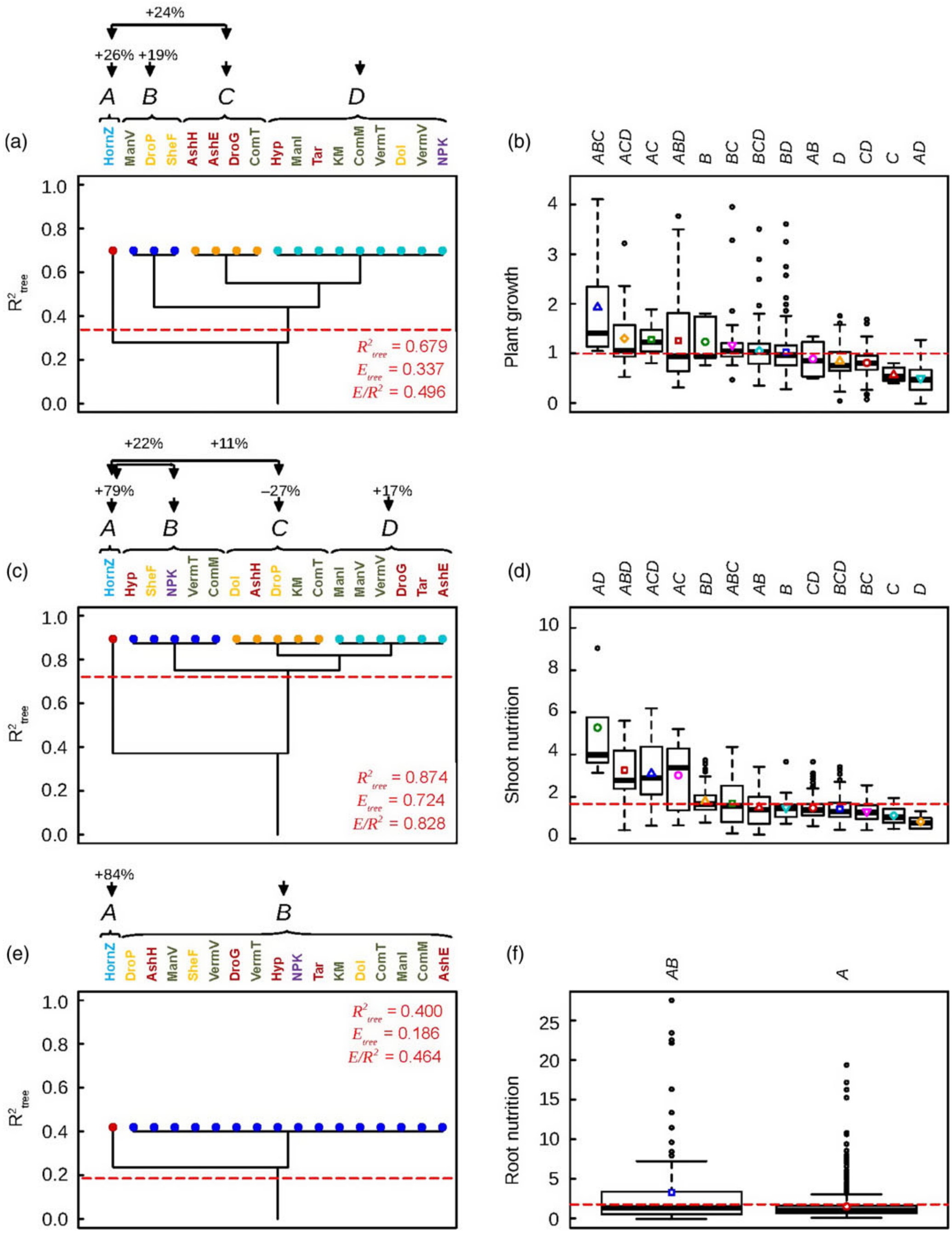

Figure 4. Functional clustering of the fertilizer resources (FR) effects on plant growth, on shoot and root nutrition. Trees of FR clustering for plant growth (a), shoot nutrition (b) and root nutrition (e). Optimal number of functional groups is indicated by Akaike information criterion. Functional groups are noted *A*, *B*, *C*, and *D*. R^2_{tree} is the tree coefficient of determination. The dotted red line in (a), (c) and (e) corresponds to tree efficiency E_{tree}. Boxplots of plant growth (b), shoot nutrition (d) and root nutrition (f) for each assembly motif. The dotted red line in (b), (d), and (f) corresponds to mean values. The black arrows indicate the average positive effect of the group compared to the overall mean. The different colors associated with fertilizer names refer to the hierarchical clusters based of FR properties. See Figure 2 legend for code details.

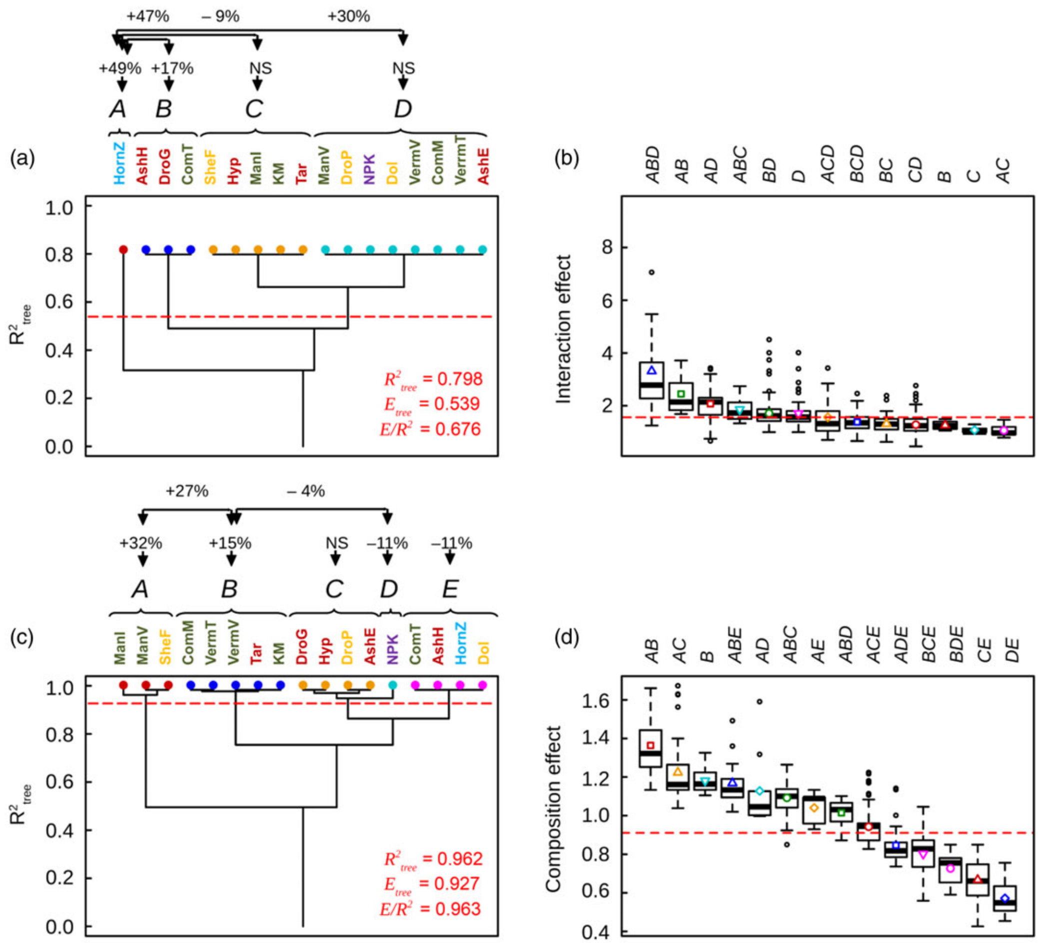

Figure 5. Functional clustering of interaction effect (a and b) and composition effect (c and d) of fertilizer resources (FR) on plant growth. Hierarchical trees of FR clustering for interaction effect (a) and composition effect (c). Optimal number of functional groups is indicated by Akaike information criterion. Functional groups are noted *A, B, C, D,* and *E*. R^2_{tree} is the tree coefficient of determination. The dotted red line in (a) and (c) corresponds to tree efficiency E_{tree}. Boxplots of interaction effect (b) and composition effect (d) of fertilizer resources (FR) on plant growth for each assembly motif. The dotted red line in (b) and (d) corresponds to mean values. The black arrows indicate the average positive effect of the group compared to the overall mean. The different colors associated with fertilizer names refer to the hierarchical clusters based of FR properties. See Figure 2 legend for code details.

the highest effects on shoot nutrition. For root nutrition, the functional clustering generates lower coefficient of determination R^2_{tree} and efficiency E_{tree} (0.400 and 0.186, respectively, $E_{tree}/R^2_{tree} = 0.464$). The FR are split only into two groups namely: *A* in a singleton = [HornZ] and the remaining FR are grouped in one group *B* (Figure 4e).

The functional clustering applied to the interaction effect on shoot nutrition separated FR into three functional groups (Figure 6a). The groups are: *A* in a singleton = [HornZ], *B* = [SheF, Hyp, VermT, KM], and *C* = [DroG, AshH, AshE, ManV, NPK, Tar, Dol, ComT, ManI, VermV, ComM, DroP]. Again, the zebu horn [HornZ] has the strongest interaction effect and the co-occurrence of [HornZ] with other groups in assembly motifs is associated with a positive effect (a relative effect of +98%, $P < 0.001$, Figure 6a and 6b). Besides, the functional clustering applied to the composition effect separated FR into five functional groups, namely: *A* = [VermT, ComM], *B* = [SheF, KM, Tar, VermV], *C* = [ManI, ManV], *D* = [HornZ, AshE, DroP] and *E* = [ComT, Hyp, NPK, Dol, AshH].

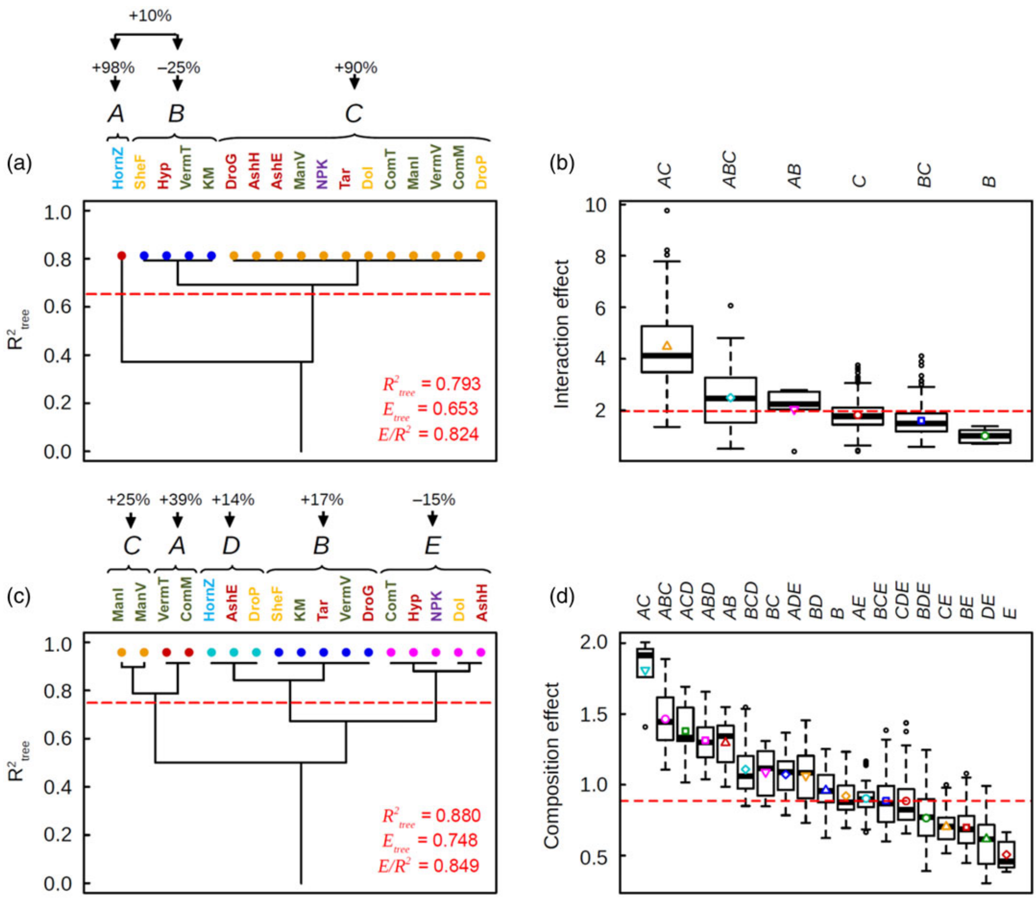

Figure 6. Functional clustering of interaction effect (a and b) and composition effect (c and d) of fertilizer resources (FR) on shoot nutrition. Hierarchical trees of FR clustering for interaction effect (a) and composition effect (c). Optimal number of functional groups is indicated by Akaike information criterion. Functional groups are noted *A, B, C, D,* and *E*. R^2_{tree} is the tree coefficient of determination. The dotted red line in (a) and (c) corresponds to tree efficiency E_{tree}. Boxplots of interaction effect (b) and composition effect (d) on shoot nutrition for each assembly motif. The dotted red line in (b) and (d) corresponds to mean values. The black arrows indicate the average positive effect of the group compared to the overall mean. The different colors associated with fertilizer names refer to the hierarchical clusters based of FR properties. See Figure 2 legend for code details.

The co-occurrence of *A* or *C* with other groups is associated with the highest composition effects (+39% and +25%, respectively, $P < 0.001$) (Figure 6c and 6d).

For root nutrition, the functional clustering model applied to the interaction effect has generated only one functional group (Figure 7a). On the other hand, the clustering model applied to the composition generated seven functional groups, and the functional groups *A*, *B*, *C*, *D,* and *E* are singletons. The groups are namely: *A* = [ManV], *B* = [SheF], *C* = [HornZ], *D* = [Tar], *E* = ManI], *F* [AshE, ComM, VermT], and *G* = [AshH, Dol, DroG, DroP, NPK, KM, ComT, Hyp, VermV] (Figure 7c).

Ranking the farmers' fertilization practices

The functional clustering allows to situate the assembly motif corresponding to commonly practices of farmers' fertilization against all observed assembly motifs. Among these practices,

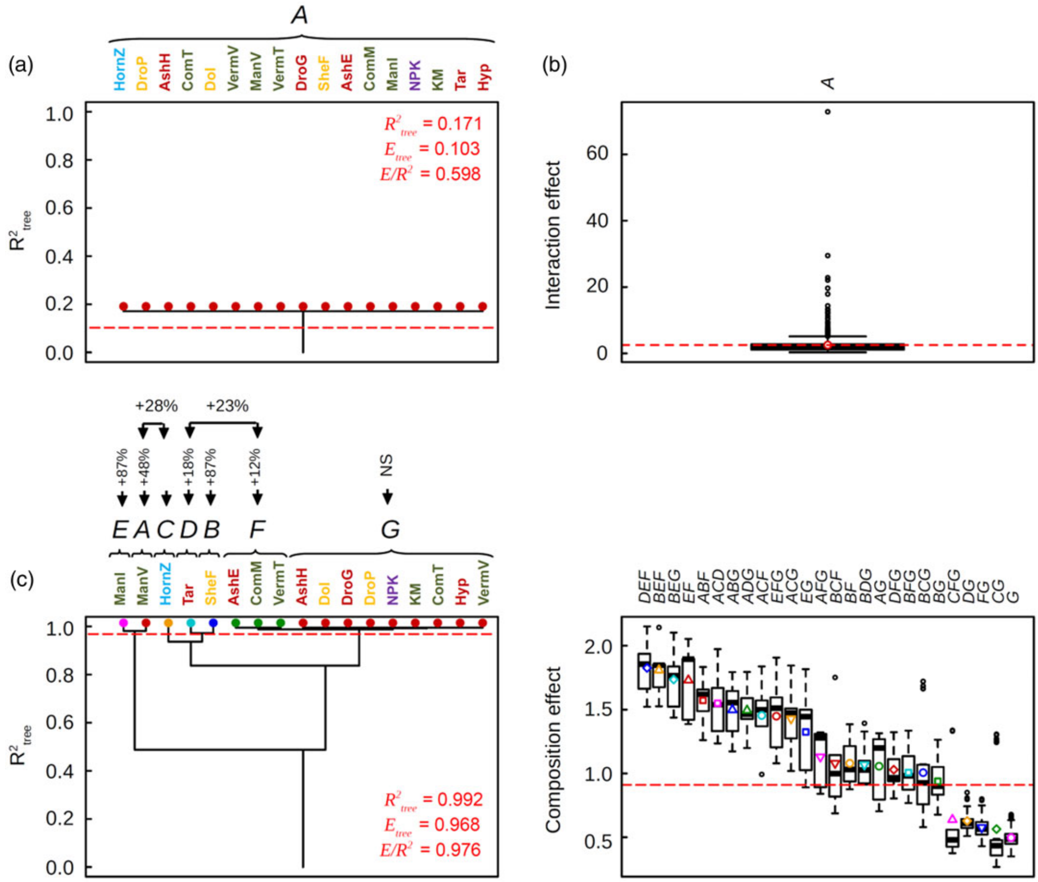

Figure 7. Functional clustering of interaction effect (a and b) and composition effect (c and d) of fertilizer resources (FR) on root nutrition. Hierarchical trees of FR clustering for interaction effect (a) and composition effect (c). Optimal number of functional groups is indicated by Akaike information criterion. Functional groups are noted *A*, *B*, *C*, *D*, *E*, *F*, and *G*. R^2_{tree} is the tree coefficient of determination. The dotted red line in (a) and (c) corresponds to tree efficiency E_{tree}. Boxplots of interaction effect (b) and composition effect (d) on shoot nutrition for each assembly motif. The dotted red line in (b) and (d) corresponds to mean values. The black arrows indicate the average positive effect of the group compared to the overall mean. The different colors associated with fertilizer names refer to the hierarchical clusters based of FR properties. See Figure 2 legend for code details.

farmers commonly combine manure (ManI) and rice husk ash (AshH) (Razanakoto *et al.*, 2021). The combination [ManI, AshH] corresponds to *CD* assembly motif on both plant growth and shoot nutrition (Figure 4a and 4c). For both plant growth and shoot nutrition, *CD* assembly motif belongs to the motifs with lowest effects on these variables (Figure 4b and 4d).

Discussion

Discrepancies between elemental and functional clustering of the fertilizing resources

The elemental and functional clustering of fertilizing resources did not align. Because the effects of FR on plant functions are assumed to reflect their biochemical quality, our expectation was that the composition of the cluster resulting from functional clustering would match the elemental clustering. This assumption was our null hypothesis. This alignment was expected, especially in highly weathered ferrallitic soils with pronounced nutrient deficiencies where fertilizers were anticipated to directly influence plant functions through nutrient supply, independent of interaction effects (Raminoarison *et al.*, 2020). Conversely, the alternative hypothesis proposed that functional grouping does not depend solely on the composition of fertilizing resources, but incorporates possible interactions between fertilizing resources that modify, for better or worse, agronomic plant growth, shoot and root nutrition performances. Our study strongly supports the alternative hypothesis.

Many fertilizing resources grouped in the elemental clustering were dispersed across different clusters in the functional approach. This means that resources with similar properties can behave very differently in combination with other resources. This is evident in the case of synthetic fertilizer NPK and zebu horn (HornZ), where the latter is the sole resource with consistent behavior in both approaches. Therefore, zebu horn warrants special attention due to its unique behavior.

Zebu horn, a key ally to considerably improve plant growth and nutrition in Madagascar

Zebu horn was isolated as a singleton in both elemental and functional clustering. This trend persisted across all three plant functions, wherein the combination of zebu horn with other functional groups in assembly motifs yielded the highest plant growth, shoot and root nutrition performances. This can be attributed to the distinct composition of zebu horn, characterized by higher contents of carbon (C), nitrogen (N), and sulfur (S) compared to other fertilizing resources (Raminoarison *et al.*, 2022). Zebu horn is rich in recalcitrant protein, namely keratin, and acts as N source for growing plants (Ichida *et al.*, 2001; Zoccola *et al.*, 2009) by supplying mineral N in a diffusive way, i.e. little but continuously. By the way, N is available throughout the plant growth. Notably, the application of zebu horn is strongly recommended, if available, for N fertilization in organic farming systems (Commission Regulation (EC) 2007, No. 834/2007). N is one of the most limiting factors of agricultural productivity in the majority of agrosystems (Cassman *et al.*, 2002), since it plays a vital role in biochemical and physiological functions of plant among them enzyme, chlorophyll, and nucleic acids constitutions (Harper, 1994). Enhanced N supply enhances growth and consequently increases the demand for other nutrients (Fageria, 2001).

The alignment between the two clustering approaches was limited to this singleton. Indeed, zebu horn and synthetic fertilizer NPK showed similarity in the elemental clustering which was not the case for the functional clustering. The divergence is attributed to the different forms of N in these resources: synthetic fertilizer NPK provides readily plant-available mineral N, while zebu horn supplies N in a more diffusive manner. Additionally, the application doses differed based on farmers' practices, with 6 t dry matter per ha for zebu horn and 150 kg dry matter per ha for synthetic fertilizer NPK. Unlike biodiversity-ecosystem functioning experiments, where functional clustering relies on consistent species ratios (Tilman *et al.*, 2001), the application doses for functional clustering of fertilizing resources should be tailored to farmers' practices. Interestingly, organic amendments such as manures, composts, and vermicomposts, initially grouped together in elemental clustering, were divided into distinct groups based on functional clustering. This categorization occurred for both plant growth and shoot nutrition, indicating intrinsic variations among these resources. Together, our findings suggest that, while functionally diverse, the co-occurrence of these resources in fertilizing combinations produces similar effects on agronomical performance.

Zebu horn acts by interacting with other fertilizing resources

Notably, zebu horn, when applied alone, displayed lower plant growth and shoot and root nutrition performances. However, an interesting phenomenon emerged when zebu horn was combined within assembly motifs, leading to much higher performances. This recurring pattern is evident despite zebu horn consistently appearing as a singleton. Functional clustering, applied to interactions, emphasized that zebu horn invariably remains in a singleton, signifying its pivotal role in driving interaction effects. Positive interaction effects were observed when zebu horn co-occurred with rice husk ash (AshH), guano droppings (DroG), and compost from the

Andralanitra dumpsite (ComT), particularly in terms of plant growth. Zebu horn's organic C and N content complement other resources, which likely contain higher levels of P and other nutrients, as seen in guano droppings (DroG). This synergetic effect is in line with the increased plant growth (+24%) when zebu horn co-occurs with other resources. Given that Ferralsols are deficient in multiple nutrients, such as P, N, Ca, Mg, and micronutrients (Kihara *et al.*, 2020; Raminoarison *et al.*, 2020), and in soil organic C (Sanchez and Jama, 2001). The combination of nutrient-rich resources like animal droppings with diffusive-nutrient resources can enhance nutrient availability, thus influencing (im)mobilization processes (Gentile *et al.*, 2009; Gentile *et al.*, 2011; Gram *et al.*, 2020).

On the other hand, all manures (ManI, ManV, KM), composts (ComM) and vermicomposts (VermT, VermV), drive the composition effect, that is when organic amendments co-occur with other resources in functional groups in combinations, the composition effect is high, and their role varies over the combination performances but in a lesser extent. Application of organic amendments alone was sufficient to address nutrient limitations on Ferralsols and sustain plant growth and nutrition. The significant impact of organic amendments on soil fertility and plant growth arises from their influence on physico-chemical properties, microbial activity, and carbon availability (Zingore *et al.*, 2008; Chivenge *et al.*, 2011). Decomposing organic amendments provide a source of inorganic nutrients and organic resources and are well known to reduce P sorption in Ferralsol by competition or enhanced pH (Andriamananjara *et al.*, 2019).

However, the compost from the Andralanitra dumpsite (ComT) behaves distinctly from the other organic amendments. This compost is not classified within the same functional group as the organic amendments, whether under functional clustering based on overall performance (plant growth and nutrition indices) or under functional clustering based on interaction and composition effects. Consequently, it can be inferred that compost from the dumpsite is of lower quality. This divergence in quality is likely due to elevated pollutant levels and the presence of trace elements. This can be attributed to the dumpsite's management lacking specific recycling systems (Tella *et al.*, 2010; Andrianisa *et al.*, 2018).

Implications for innovative agriculture: towards the use of the assembly motif concept in fertilization strategy

Numerous researchers have emphasized the synergistic combinations of FR as a means to overcome soil fertility limitations faced by smallholder farmers in Sub-Saharan Africa (Palm *et al.*, 1997; Vanlauwe *et al.*, 2015). Successful management of these resource combinations hinges on consistent clustering of FR that result in positive and advantageous interactions. The prevailing decision support tool for FR management primarily relies on the elemental attributes of these resources. However, this elemental clustering rests on assumptions that might not always hold true; specifically, the notion that interactions among fertilizing resources can be entirely explained by their elemental properties. In our study, when elemental clustering was contrasted with functional clustering, it became evident that this assumption does not hold. Biological and chemical processes tied to nutrient mineralization, plant nutrient uptake, and soil functioning are integrated within functional clustering, aspects that elemental clustering may not adequately account for. Moreover, initial elemental properties used for clustering might continually change during the decomposition of fertilizing resources in soil, thus potentially distorting the conventional clustering approach.

Our findings highlight the concept of 'assembly motif' within soil fertilization strategy. By definition, an assembly motif is a combination of functional groups of resources; in essence, FR combinations sharing the same assembly motif exhibit similar performance on targeted functions such as plant growth and nutrition. Each assembly motif corresponds to a specific level of performance. Leveraging the assembly motif concept, functional clustering can situate conventional practice performance levels relative to all observed assembly motifs. In the Imerintsiatosika zone, where our soil samples were collected, farmers commonly combine farmyard manure (ManI) with rice husk ash (AshH) for rainfed rice fertilization. This combination corresponds to *CD* assembly motif with regard to plant growth. Consequently, all assembly motifs surpassing the *CD* motif are more productive. This opens up the possibility of intensifying rice productivity by selecting the most effective combinations.

Furthermore, our study underscores that optimal performance depends on specific interactions between resources, rather than the number of functional resource groups in a combination. Although the combined application of fertilizing resources can certainly enhance rice plant growth and nutrition compared to conventional practices, achieving positive interactions is limited and most effective when the role of each resource is discerned. Thus, unravelling interaction and composition effects become particularly crucial. Resources co-occurring with high and positive interaction effects should be combined with other functional resource groups, as their association yields positive complementarity. Conversely, resources governing composition effects are inherently productive, making their individual application sufficient for improving soil fertility. Hence, the most effective approach for proposing a fertilization strategy with farmer-available resources is to combine functional resource groups with high interaction effects and to individually apply functional resource groups with high composition effects.

Limits and perspectives

In this study, we must note that the measures of interaction or composition effect encompass both the effects of application rate and the effects of interactions or composition effect *per se*. Specifically, the application rates for testing the individual effects of each fertilizing resource were set at 6 t DM. ha^{-1} for organic amendments, 0.5 t DM. ha^{-1} for fertilizers, and 0.15 t DM. ha^{-1} for the synthetic fertilizer NPK. Throughout our experiment, these application rates remained constant regardless of the combinations tested. Consequently, when these resources were combined, the nutrient contents resulting from a combination of three types of organic amendments were three times higher than those obtained from each FR alone. This nutrient content was more significant than that from a combination of three types of fertilizers. We posit that comparing the plant growth, shoot and root nutrition performances of FR when applied individually against their performance in combinations might not be suitable for this protocol experiment. Instead, for meaningful comparison, after determining how each fertilizing resource performs when applied individually, i.e. identifying the resources with the lowest and highest performances, we then assessed whether the same behaviour is retained in combinations. The insights provided by interaction and composition effects serve to corroborate the roles played by each fertilizing resource. Here, we focused mostly on the agroecological effectiveness and not efficiency (availability, price, and risks) of the combined FR application. However, the efficiency of each practices should be evaluated with farmers, according to their choice within each functional groups based on efficiency criteria.

Moreover, it is important to acknowledge that our present study was conducted under controlled greenhouse conditions, with regular watering during pot experiments. Consequently, the fertilizing resources were integrated into soil with optimal water conditions, ensuring continuous organic matter decomposition and N mineralization throughout the plant experiment. However, it is highly plausible that under more challenging field conditions, particularly concerning water availability, the composition of clusters could shift due to the slower decomposition of diffusive resources, notably exemplified by zebu horn. Replicating a similar combinatorial experiment under field conditions emerges as the primary path for future development.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0014479724000103

Data availability statement. The datasets generated during the current study are available from Figshare (10.6084/m9.figshare.24099552). The R codes used are available from the corresponding author on reasonable request.

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Author contributions. Conceptualization, EB and JT; material preparation and methodology, BJ, EB, JT, and MR; data acquisition, MR and KR; data analyses, BJ and MR; funding acquisition, EB and JT; supervision, EB, JT, and TR. The first draft of the manuscript was written by MR and BJ, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. The study was conducted in the Laboratory of Radio Isotopes supervised by TR.

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