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Leaf-cutter ants: spatial modification of the chemical and physical properties of the soil in a native forest in Argentina

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Abstract
The aim of the present investigation was to determine the spatial modification of the chemical and physical characteristics of an Alfisol Soil affected by *Atta vollenweideri* nests in a semixerophite native forest of the Espinal Ecorregion. The study was conducted in north of the province of Entre Ríos (Argentina) in July 2015, selecting 10 nests. In each nest composite samples of surface soil were taken in five positions. The textural components of soil and nine chemical variables were evaluated and used parametric and non-parametric analysis of variance techniques. The OC content increased significantly as the distance to the nest increased, from 3.20 mg C kg^{-1} in the crest of the nest, to 15.04 mg C kg^{-1} at 60 m. There was a significant increase in pH, CEC, Na, EC and PENa in the crest of the nests with respect to the base, at 15, 30 and 60 m from the nest. The soil on the ridge of the nest showed a slight salinity (3.61 ± 1.55 $dS.m^{-1}$) and slight sodicity (12.42 ± 3.65%) with respect to the adjacent soil. Nests of *A. vollenweideri* in Alfisols soils, negatively alters the chemical and physical properties of the soil in the first 15 meters from the base of the nest.

Keywords: *Atta vollenweideri*, soil, ecosystem engineers, bioperturbation, *Attini*

1. Introduction
Ants are the most abundant social insects in the world [1], inhabit a large variety of habitats, being considered as engineers of the ecosystems [2]. In particular, leaf cutter ants (LCA) of the genera *Atta* and *Acromyrmex* are found in subtropical and temperate climates, being fully known for their activity of cutting different plant fragments and their ability to grow fungi [3].
The dynamics of the nutrients in the soil can be significantly affected by the activity of the edaphic fauna, among which are the ants and termites, produce a bioperturbation of great importance for the processes of the soil and the spatial availability of the trophic resource of the ecosystem. LCA can participate in these processes by creating large-scale biogenic structures and nests, an essential feature for which they are included within the 'ecosystem engineers' [4, 2, 5, 6, 7].
Building their nests improves the penetration of plant roots, the cation exchange capacity of the soil and nutrient removal thereof; resulting in an increase in fertility that facilitates forest recovery in degraded areas [8]. Taking into account what has been said, this species could benefit soil conditions and contribute to the set of strategies used for the improvement of soil ecosystems.
In Costa Rica it was determined that the presence of LCA has been an important modifying element in soil evolution [9, 10], altering drainage conditions [11]. It has been reported that, in tropical soils, the construction of LCA nests increases the content of nutrients and organic matter of the adjacent soil [12, 13] by the processes of mineralization and decomposition of food, and the accumulation of faeces and cadaver inside the internal chambers of the nest [14, 15, 16, 17].
The genus *Atta* presents the peculiarity of building large nests. The nests of *Atta laevigata* caused a major change in the first 20 cm depth on the chemical properties of the soil [18]. Similar studies with *Atta sexdens* show that the activity of LCA not only modifies the superficial horizons, but also in depth, causing changes in the properties of large volumes of soil [19].

Atta vollenweideri Forel 1893, is a species of LCA that presents the peculiarity of constructing cone-shaped nests, with an aerial part that can reach a meter in height and six meters in diameter, and an underground part that can reach five meters in depth [20, 21]. Due to the enrichment of nutrients generated in the soil, it has been recorded that over dead nests in the Paraguayan savanna colonized species of the genus *Prosopis* spp. because of the enrichment of nutrients in the soil [22, 23]. However, in Argentina it was found that after the death of the colonies, there is a loss of soil fertility due to the inversion of the soil profile caused by the activity of the nest [24]. The northern center of the province of Entre Ríos presents very characteristic agroecological conditions, which allow the presence of this species in xerophilous forests on soils Alfisols with vertic characteristics [25], where it has been reported on the modification of the physical properties as a result of the construction of these nests [26]. So far the effect on the physico-chemical characteristics of the soils that make the nests of this species of LCA is unknown.

In this sense, the aim of this work was to determine the spatial modification of the chemical and physical characteristics of an Alfisol soil affected by *Atta vollenweideri* nests in a native semixerophite forest of the Argentine Espinal. The hypothesis is based on the negative alteration in the nutrient content due to the construction of the nests in natural conditions, a native forest, its effect being less as far from the nest.

2. Material and Methods

2.1. Work Area

The study was carried out in the Protected Area and Multiple Use Nature Reserve –PA-MUSR- called Estancia 'El Carayá' (30°40'S, 58°50'W), located in Atencio district (south of Feliciano department) in the north of the province of Entre Ríos, Argentina (Fig.1). According to Rojas and Saluso [27], this region has a humid temperate climate typical of plains. Average annual temperature is 18.9 ºC, average maximum temperature is 24.8 °C, and average minimum temperature is 12.0 ºC [28]. Average annual rainfall is 1,300 mm, rains being concentrated between October and March. The study is located 64 meters above sea level.

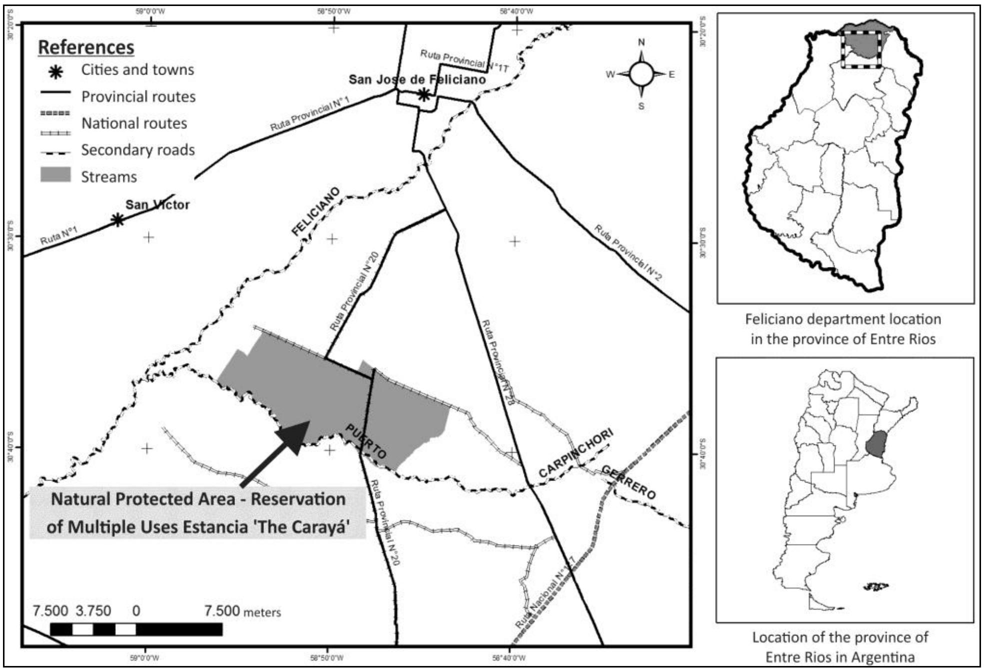

Fig 1: Location of the study area in the province of Entre Ríos (Argentina)

According to Cabrera [29], the study area corresponds to successional forests of the Espinal ecoregion, which is characterized by xerophilous forests dominated by *Prosopis nigra* Griseb., *Prosopis affinis* Spreng., and *Vachellia caven* Molina. In addition, there are 'Riverside Forests with Shrud Jungle' corresponding to the Paranaense ecoregion [33]. Native forests are heterogeneous as regards appearance and structure of tree and shrub strata development, depending on soil diversity and the profuse hydrographic network across the region [30]. In general, the current state of the native forest of the region is characterized by the position of a plant succession, and it is possible to identify: virgin or pristine forests that constitute the final stage of the succession (climax); successional forests that correspond to intermediate stages, where diversity is richer but the native forest is not yet stabilized; and renewable forests at the beginning of the succession after deforestation, where the usually dominating species belong to the invasive type [31].

Soils are imperfectly drained because of the irregular surface that fluctuates from flat to very gently undulating areas, where rainwater is excessively retained and accumulated on the surface. They have a loam epipedon, below 10 cm, which is followed by a waterproof horizon and is impenetrable by roots [32]. According to Sabattini [31], the dominant soil cartographic unit in the study area is Grecco (Vertic Epiaqualfs), located in well-defined small plains which are relatively higher within the landscape of long and slight slopes. Those areas are dominated by the native forest with thick and short species such as *T. campestris*, *B. yatay* and *A. quebracho-blanco* and significant areas without natural grassland.

2.2 Sampling Design

In July 2015, 10 nests of *A. vollenweideri* developed on an Alfisol soil (Vertic Epiaqualfs) were selected. In a 60-meter transect, a composite sample of soil was made up of 15 sub-samples of the surface horizon (00-20 cm) in five positions: nest crest (central part), nest base (periphery of the anthill), 15 m, 30 m and 60 m from the base of the nest. This last position is considered the reference situation without nests. At the time of extraction, the soil moisture content was 26%.

The following edaphic variables were determined: pH by potentiometry in a soil suspension in water with ratio of 1:2.5 [34], organic carbon (OC) and extractable phosphorus (P) quantified according to the IRAM-SAGyP standards 29571-2 [35] and 29570-1 [36] respectively. The cation exchange capacity (CEC) and calcium (Ca^{++}), magnesium (Mg^{++}), and sodium (Na^{+}) exchange cations were determined using the SAMLA standardized methodology [37], using the acetate method for extraction of ammonium of $NH4^{+}$ 1M pH 7; the determination of the CEC was by Kjehldal distillation; Ca and Mg by complexometry with EDTA and Na and K by flame photometry. The percentage of exchangeable Na (PENa) in the exchange complex was determined. The granulometry of the soils analyzed was quantified by the pipette method [38] and the textural class was defined using the USDA classification system [39]. The electrical conductivity (EC) was measured in potentiometric form in a soil: water (volume) ratio of 1: 5 [40].

2.3 Statistical analysis

Subsequently, a statistical analysis of the data was elaborated, and in order to evaluate the normality of the information, the Shapiro-Wilk test was used. To determine significant differences, parametric variance analysis was performed for pH, OC, CEC, Ca and Mg; and non-parametric with the Kruskal-Wallis statistic (Na, EC, PENa, Clay, Silt and Sand). In addition, Principal Components Analysis (PCA) techniques were used to establish a relationship between the variables analyzed and their position. The statistical analysis was performed with the software InfoStat® version 2017 [41].

3. Results

There was a significant increase in the soil variables of pH, CEC, Na^{+}, EC and PENa in the crest of the nests compared to the base, at 15, 30 and 60 m from the nest. The OC content increased significantly as the distance to the nest increased, from 3.20 mg C kg^{-1} in the crest of the nest, to 15.04 mg C kg^{-1} at 60 m (Table 1). The contents of available phosphorus and exchangeable magnesium did not show significant differences in the different positions evaluated ($p = 0.2833$ and $p = 0.9084$, respectively). The soil on the ridge of the nest showed a slight salinity (3.61 ± 1.55 $dS.m^{-1}$) and slight sodicity (12.42 ± 3.65%) with respect to the adjacent soil (Table 1).

Table 1: Average values of the edaphic variables selected in the 5 positions: Crest, base, 15 m, 30 m and 60 m. Stocks with a common letter in the sense of rows are not significantly different (p> 0.05). * H value according to Kruskal Wallis nonparametric test.

Edaphic variables	Crest	Base	15 m	30 m	60 m	R^2	*F*	*P*
pH	$8.81±0.45^{d}$	$8.37±0.41^{c}$	$7.48±0.38^{b}$	$7.07±0.54^{a}$	$6.96±0.27^{a}$	0.77	37.65	<0.0001
OC (g kg^{-1})	$3.20±2.55^{a}$	$7.82±2.13^{b}$	$11.58±3.41^{c}$	$14.20±3.46^{cd}$	$15.04±4.43^{d}$	0.66	22.09	<0.0001
P (mg kg^{-1})	$3.12±0.97^{ab}$	$2.83±0.60^{a}$	$3.60±1.04^{b}$	$3.03±0.82^{ab}$	$3.04±0.38^{ab}$	0.10	1.30	0.2833
CEC (cmol(c) kg^{-1})	$37.85±2.60^{b}$	$34.45±3.17^{a}$	$32.01±3.26^{a}$	$31.70±4.88^{a}$	$31.73±3.88^{a}$	0.32	5.36	0.0013
Ca^{++} (cmol(c) kg^{-1})	$26.45±2.80^{c}$	$25.06±2.15^{c}$	$22.64±2.47^{b}$	$20.46±2.65^{ba}$	$20.16±2.50^{a}$	0.52	11.99	<0.0001
Mg^{++} (cmol(c) kg^{-1})	$4.32±1.01^{a}$	$4.36±1.53^{a}$	$4.70±1.12^{a}$	$4.18±1.23^{a}$	$4.40±1.10^{a}$	0.02	0.25	0.9085
Na^{+} (cmol(c) kg^{-1})	$4.63±1.18^{b}$	$1.81±0.47^{a}$	$1.60±0.54^{a}$	$1.42±0.53^{a}$	$1.46±0.48^{a}$	-	23.70*	0.0001
EC (dS m^{-1})	$3.61±1.55^{c}$	$1.15±0.21^{b}$	$0.85±0.24^{ab}$	$0.79±0.45^{a}$	$0.66±0.10^{a}$	-	33.43*	<0.0001
PENa (%)	$12.42±3.65^{b}$	$5.36±1.69^{a}$	$5.05±1.82^{a}$	$4.56±1.63^{a}$	$4.63±1.61^{a}$	-	19.92*	0.0005
Clay (%)	$35.43±8.65^{b}$	$32.85±2.20^{ab}$	$30.82±3.78^{ab}$	$30.70±2.69^{ab}$	$30.86±4.03^{a}$	-	6.56*	0.1670
Silt (%)	$53.61±9.06^{b}$	$57.80±5.72^{ab}$	$58.03±4.54^{ab}$	$55.66±4.08^{ab}$	$56.63±6.10^{a}$	-	5.31*	0.2567
Sand (%)	$5.48±3.16^{a}$	$4.77±2.49^{a}$	$4.65±3.15^{a}$	$6.30±2.69^{a}$	$5.12±3.17^{a}$	-	2.73*	0.6074

The clay content was higher in the crest of the nest, with significant differences at 60 m distance from the nest, but not in the other distances evaluated. The contents of silt and sand did not significant differences along the transect (Table 1).

From the analysis of principal components it was observed that 88.2% of the variation of the data was defined by the first two components (Fig.2). Component 1 explains a high percentage of the total variability (66%), represented by the variables clay, pH, CEC, Ca^{++}, Na^{+}, EC, PENa that affect it positively, while OC is linked to a reverse effect; for component 2 only the slime was associated in a positive way. The effect of the ants on the changes in the variables of component 1 is manifested with greater intensity in the crest of the nest and at the same time with less influence on the base, with the exception of the OC whose content is associated more from 30 meters. The percentage of silt had a different behavior from the 15 meters of the base of the nest, finding its highest value in this position, although not significant (Table 1). The influence of the activity of the ants on the nest, is reflected in a higher percentage of clay, while as the distance to the nest increases, silt appears as a major component. Finally, the variables Mg^{++}, P and percentage of sand were the parameters that did not show significant differences according to the distance to the nest and therefore they were not related to any of the positions of the transect evaluated.

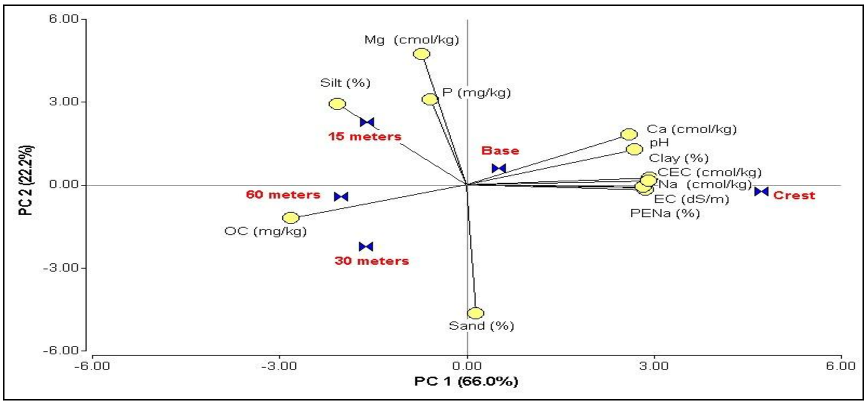

Fig 2: Principal components of the variables evaluated according to the position in the transect.

4. Discussion

The present study work showed that nests *Atta vollenweideri* make a significant alteration in the physical and chemical properties of soils, as stated Farji-Brener [43]. These changes are due to the construction of tunnels and galleries [43] that increase the porosity, drainage and aeration of the soil [44, 11, 45, 10] and also produce a reduction in bulk density [46, 47]. Previous studies have determined that the average area occupied by a nest is 48.7 ± 12.2 m^2, with average dimensions of 8.1 ± 1.0 m for the major axis and 7.5 ± 1.1 m for the axis less; while its average height is 0.4 m.

Due to the structural characteristics of the dominant vegetation, the study site responds to a native forest in its initial stage to intermediate in the plant succession [31]. In this sense, the modifications caused by the construction of the nests, would advantage the colonization of pioneer plants within the process of plant succession [48, 49, 16] accelerating their development to a climax forest [50]. On the other hand, the herbivory relationship of cattle is modified, due to direct competition in the cutting of the natural pasture (Sabattini J, pers. comm.)

The increase of the pH in the crest and the base of the nest, which leads to alkaline conditions, can be explained by the action of the ants that carry to the surface original material that in this soil is very rich in Ca^{++}, since it is a matter of silt calcareous of lacustrine-marsh origin (Fig.2). In addition, a negative correlation (r^2=0.72) was observed between the organic carbon content and the soil pH (Fig. 3). This behavior could be due, on the one hand, to the presence of the active groups in the organic matter that behave as weak acids and tend to decrease the pH, and on the other hand, to the materials present on the nests that are brought from endopedons characterized by a low CO content and the high pH value that the original mineralogy of the soil gives it.

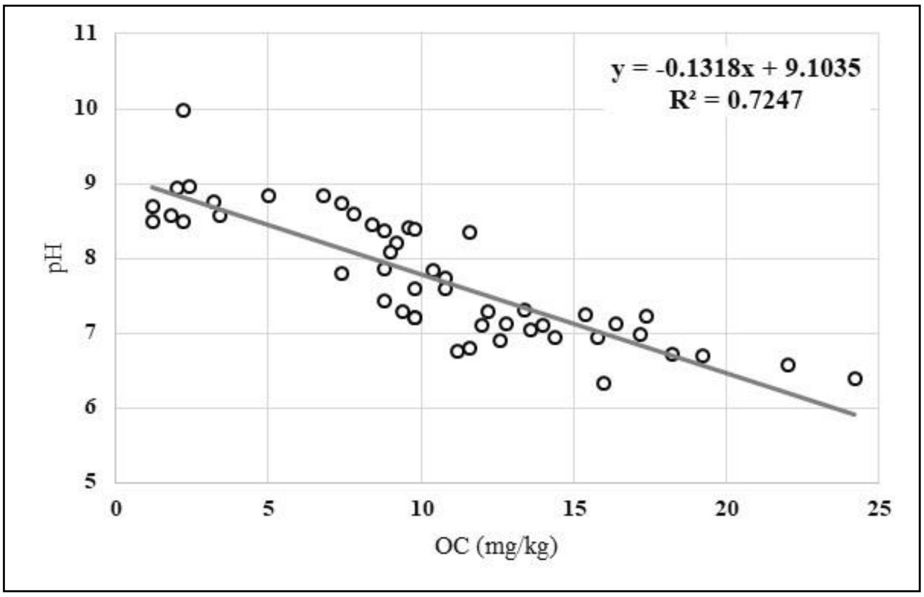

Fig 3: Variation of soil pH as a function of organic carbon content

With other genera of leaf cutter species [51] and in *Atta robusta* on Spodosol soils, increases in pH were recorded over the nest but related to the eluviation of organic matter typical of the forming processes of this soil class [52]. However, in *Atta sexdens* nests of the Brazilian Amazon on Haplustol soils, there was no significant difference in the pH of the nest crest in the first 50 cm depth, but a decrease was observed at 100 cm depth [19]. In general, ants develop at neutral pH, with the particularity of increasing the pH in acid soils and decreasing it in basic soils [53, 54], although this behavior is not entirely clear in the different genera. The effect of pH in the soil increases with the age of the colonies and may be even greater in the periphery of the nests than in the ridge [55]. The increase in pH is often the result of the increase in basic cations, while the decrease is associated with the accumulation of organic matter [16, 54]. This variable is important in the foundation of the colonies by the queens, since the growth of the fungus is done in bare soils, without organic remains [55], which would be less affected by the pH [56].

The organic carbon in the crest of the nests was significantly lower compared to the base and 15 meters away. These results are consistent with those obtained in *Atta cephalotes* [6], and it would affirm the hypothesis that ants substantially reduce the carbon content in the nest from the surface horizon to the deeper layers of soil [57]. Studies conducted in Brazil show a higher percentage of organic carbon in the nests compared to adjacent soils [56], while in Venezuela, no significant differences were found [18].

Regarding the availability of P, the province of Entre Ríos is characterized by a generalized deficiency due to the low contents of this element in the original materials. P can be found in soils in organic forms linked to organic and inorganic matter, and its availability is conditioned by physicochemical and biological reactions [58, 59]. In the soil of this study, the content of P available on the surface was extremely low and was not modified by the action of the ants, because they are soils derived from very poor original material in this nutrient [59].These results are consistent with those obtained in *A. laevigata* [18], *A. sexdens* [19,56] and *A. robusta* [52].Other genera of cutter species, in soils other than this one, can not only increase the phosphorus content on the nest, but also increase its availability; improving fertility conditions [54,60].

The cation exchange capacity is closely linked to the soil texture (Fig.2). In the class of soil evaluated, the motmorillonite dominates in the clay fraction and the results obtained show that on the crest of the nest there is a higher clay content with respect to the adjacent soil. This would explain the increase in cation retention capacity such as Ca^{++}, Mg^{++}, and Na^{+} (Table 1, Fig.4). On the other hand, the accumulation of organic matter inside the waste chambers also contributes to increase the CEC. These results affirm the hypothesis that the ants invert the soil profile, transferring to the surface the original material of these soils. The results are consistent with the observations of van Gils [56] in *Atta sexdens*, and in *Atta cephalotes* [52]. On the other hand, when the physical and structural properties of soil have low CEC, it is further reduced by the decrease in organic matter [52] or no significant differences are observed [18].

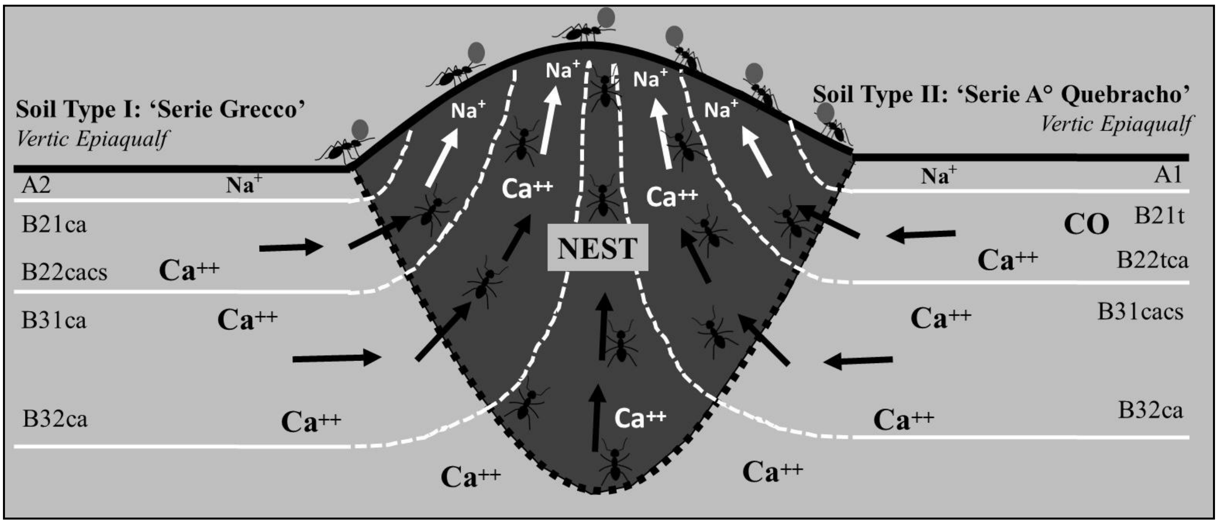

Fig 4: Schematic representation of the modifications made by *Atta vollenweideri* nests in two soil types with Vertic Epiaqualf characteristics

The same behavior was found in the content of Ca^{++} and Na^{+}, where there was a higher concentration in the ridge and the base of the nest (Table 1), due to the inversion of the horizons. Similar results were obtained in *A. sexdens* and *A. laevigata* [18, 56]. The subsurface horizons contain high alkalinity, with Na + contents that sometimes exceed 10% in the exchange complex [28]. For the EC and PENa variables, the highest values in the crest and base of the nest were also observed, given that they are linked to the Na^{+} content (Fig.2); this is important because of the negative effect produced by the high values of these variables, both on plant development and on the physical and chemical quality of the soil. The Mg^{++} did not present variations and associations (Fig.2) depending on the position of the nest, coinciding with the rest of the observations of this element in other regions of the neotropics.

These modifications in the chemical and physical properties of the soil can be beneficial for the installation of plant species with low nutritional requirements, given that in its initial colonization process, it generates environmental conditions that would improve the biological diversity of the forest. In this way, over the years a native forest could be reached with characteristics similar to the climax.

5. Conclusion

The presence of *Atta vollenweideri* nests in an Alfisol soil, produces negative changes on some chemical and physical characteristics of the soil. From 15 m towards the crest of the nest, the activity of the LCA caused a decrease in the OC content, and an increase in pH, EC and Ca^{++}, while in the central part of the nest there was a significant increase in the content of clay, Na^{+} and PENa. In this sense, it is appreciable the alteration in the spatial distribution of the soil characteristics evaluated, which cause high edaphic heterogeneity, being able to affect other variables of the ecosystem, such as the floristic composition of the herbaceous vegetation.

Future research should consider increasing the sampling depth to analyze not only chemical parameters, but also physical ones, such as the apparent density of the horizons and their effect on the composition and modification of the herbaceous, shrub and arboreal vegetation.

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