INFLUENCES OF FOREST REGROWTH AND ANTS ON THE RECOVERY OF SOIL HYDRAULIC PROPERTIES IN A SEMIARID REGION OF BRAZIL

A Thesis

by

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ABSTRACT

Dryland tropical forests are at risk globally because of accelerated deforestation and the consequent losses of hydrological functions. The Caatinga shrublands in Brazil, for example, are dry tropical forests undergoing rapid deforestation, which is often followed by conversion to pasturelands. When overgrazed, these pastures become degraded and are often abandoned, allowing forests to regrow. Studies in the humid tropics have shown that natural regrowth of forest promotes a gradual recovery of soil hydraulic properties and also protect the soil against erosion. One of the mechanisms through which forests might improve soil structure is by the promoting the activity of ecosystem engineers, such as ants. However, there are some knowledge gaps in the literature of tropical dry forests about the effects of forest regrowth on the recovery infiltration and soil loss, as well as on the effects of ants on infiltration.

Soil hydraulic properties and soil erosion were evaluated on a secondary succession continuum in the Caatinga. Rainfall simulation was used to assess infiltrability and susceptibility to erosion, and saturated hydraulic conductivity was determined in the field and in the laboratory using two different methods. A relation between forest age and erosion was not found. However, there was gradual increase of hydraulic conductivity with increasing forest age, and infiltrability was only higher at the older forested site. The results suggest that a complete recovery of soil hydraulic properties might take several decades.

Soil modifications by fauna can critically affect water infiltration, which is particularly important on dryland ecosystems. Modification of soil hydraulic properties by two ant species in the Caatinga– one found at preserved forest and the other at a degraded pasture– were evaluated. Soil bulk density, texture, and infiltration were assessed on their nests and on non-nest soils. Both ants significantly modified these soil properties, but while modifications by the forest species might increase soil water available to plants, the other species had an overall negative effect on soil hydraulic properties. Such modifications could be impacting forest resilience and recovery in opposite ways.

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CHAPTER I

INTRODUCTION

The Caatinga of Brazil is an important representative of the dry tropical forest biome type. It occupies an area of 800,000 km^2, approximately 12% of Brazil's terrestrial surface. It is named for this region's native vegetation cover, which is composed mostly of shrublands and deciduous forests, the latter being dominant [*Sampaio et al.*, 1995]. It is one of the largest and most populated regions of dry tropical forest in the world [*Castelletti et al.*, 2003]; and of the various Brazilian ecosystems, it is among the most threatened by deforestation—with less than 1% of its forests under some kind of IUCN protection [*Leal et al.*, 2005]. A very common land use change in the Caatinga is the clear-cutting of forest for timber and conversion to cropland, often succeeded by planting for pasture. Once the pastureland has been degraded by overgrazing, which commonly occurs, the land is abandoned. In a study looking at land cover changes in the Caatinga, Beuchle et al. (2015) found that between 1990 and 2010 an area of 25,335 km^2 of land was deforested. At the same time, they found a gross gain of 9764 km^2 of forest, which was attributed mostly to regrowth on abandoned land. This and other studies show that the Caatinga vegetation is actually a mosaic of secondary forests of different successional stages [*Coimbra Filho*, 1996; *Leal and da Silva*, 2003]. Therefore, to understand the effects of deforestation and forest regrowth on soil hydrological properties, it is important to consider forest age.

Older forests often have higher abundance of soil invertebrates, such as ants. Ants are present in most terrestrial environments [*Wilson*, 1971] and play important roles in the functioning of ecosystems—as key species in trophic webs, as seed dispersers, and as soil engineers [*de Bruyn and Conacher*, 1990; *Folgarait*, 1998; *Leal et al.*, 2007; *Styrsky and Eubanks*, 2007]. Soil-engineering ants are those that modify or create habitat for other species, including plants, by altering the soil in their colonies and around their nests. In semiarid regions, ants and other soil fauna—such as termites and rodents—have been shown to increase infiltration and to promote islands of soil moisture where plants have increased growth and survival [*Reichman and Seabloom*, 2002]. Ants have also been shown to increase their activity in the latter stages of secondary succession [*Colloff et al.*, 2010], which can facilitate the recovery of disturbed environments [*Brener and Silva*, 1995; *Moutinho et al.*, 2003; *Bonachela et al.*, 2015]. However, not all ant species modify the soil in the same way, and it is important to understand the effect of different species on infiltration, particularly on semiarid environments such as the Caatinga, where water is a limiting resource.

CHAPTER II

INFLUENCES OF LAND USE AND FOREST REGROWTH ON SOIL HYDRAULIC PROPERTIES AND SEDIMENT YIELD IN A SEMIARID REGION OF BRAZIL

II.1. Overview

Dryland tropical forests are important but little-understood ecosystems. These landscapes are at risk globally because of accelerated deforestation and the consequent losses of hydrological functions. An example is the Caatinga shrublands in northeastern Brazil; these dry tropical forests are undergoing rapid change as the land is converted to cultivated cropland and pastureland, then often abandoned after the land is exhausted, allowing forests to regrow. In this study we evaluated how these changes influence soil hydraulic properties and soil erosion in Caatinga landscapes, by examining four sites of different ages: a recently abandoned pasture, a young (7 years of regrowth) secondary forest, an intermediate (35 years regrowth) secondary forest, and an older (more than 55 years) forest. Rainfall simulation was used to assess infiltrability and susceptibility to soil erosion. In addition, we determined hydrological conductivity in the field using the Beerkan method (*Kfs*) and collected samples for laboratory-determined measurements (*Ks*). We found that infiltrability and *Kfs* values were progressively higher as time since land abandonment increased, while *Ks* values were not significantly different across sites. Infiltrability was approximately two times smaller than *Ks* and *Kfs*—possibly owing to the formation of soil crusts from raindrop impact. Soil erosion did not show a progressive improvement with forest age, and was better explained by site characteristics, such as herbaceous cover and slope. In general, our results suggest that in Caatinga landscapes, more than 35 years is required for the recovery of soil hydraulic properties following land abandonment.

II.2. Introduction

Despite an increased emphasis on conservation in recent years, deforestation in the tropics is still widespread [*Lawrence and Vandecar*, 2014; *Spracklen et al.*, 2015], and dry tropical forests are among the most threatened [*Miles et al.*, 2006; *Dirzo*, 2011]. Conversion of forests to croplands and pastures often leads to degradation of the soil, reducing its saturated hydraulic conductivity (*Ksat*) and its infiltrability [*Ghuman et al.*, 1991; *Lal*, 1996; *Nyberg et al.*, 2012]. Infiltrability—defined as the steady-state infiltration rate when water is made fully available at the surface—is strongly influenced by soil surface characteristics (including soil crust and vegetation) and by *Ksat*, which determines how much water will flow through the soil under saturated conditions. In dry regions, soils normally have low *Ksat*; as a consequence, intense seasonal rainfall events often generate overland flow runoff, resulting in erosion [*Wilcox and Wood*, 1989; *Lasanta et al.*, 2000; *Ludwig et al.*, 2005] and increasing the chances of flooding [*Bradshaw et al.*, 2007]. These trends are accentuated when protective vegetation cover is removed, leading to degradation of the soil.

If once-deforested lands are abandoned and there is natural reestablishment of forests, it is expected that the effects would be the opposite: recovery of soil hydraulic properties, resulting in higher groundwater recharge [*Tobella et al.*, 2014], lower flooding risk [*Bradshaw et al.*, 2007], and less erosion [*Cerdá and Doerr*, 2005; *Descheemaeker et al.*, 2006]. However, the time that would be needed for a complete recovery will vary greatly across different landscapes and ecosystems—a major determinant being past land use and land management. Several studies have investigated the effects of land cover type and land use history on soil hydraulic properties (e.g., infiltrability and *Ksat*) [*Lal*, 1996; *Elsenbeer et al.*, 1999; *Descheemaeker et al.*, 2006; *Zimmermann et al.*, 2006; *Yimer et al.*, 2008; *Bonell et al.*, 2010; *Nyberg et al.*, 2012; *Niemeyer et al.*, 2014]. However, fewer studies have looked explicitly at forest age to understand the recovery of these properties under secondary succession [*Zimmermann et al.*, 2006; *Zimmermann and Elsenbeer*, 2009; *Archer et al.*, 2015], and to our knowledge, no studies of this kind were carried out in dry tropical forests.

The Caatinga of Brazil is an important representative of the dry tropical forest biome type. It occupies an area of 800,000 km^2, approximately 12% of Brazil's terrestrial surface. It is named for this region's native vegetation cover, which is composed mostly of shrublands and deciduous forests, the latter being dominant [*Sampaio et al.*, 1995]. It is one of the largest and most populated regions of dry tropical forest in the world [*Castelletti et al.*, 2003]; and of the various Brazilian ecosystems, it is among the most threatened by deforestation—with less than 1% of its forests under some kind of IUCN protection [*Leal et al.*, 2005]. A very common land use change in the Caatinga is the clear-cutting of forest for timber and conversion to cropland, often succeeded by planting for pasture. Once the pastureland has been degraded by overgrazing, which commonly occurs, the land is abandoned. In a study looking at land cover changes in the Caatinga, Beuchle et al. (2015) found that between 1990 and 2010 an area of 25,335 km² of land was deforested. At the same time, they found a gross gain of 9764 km² of forest, which was attributed mostly to regrowth on abandoned land. This and other studies show that the Caatinga vegetation is actually a mosaic of secondary forests of different successional stages [*Coimbra Filho*, 1996; *Leal and da Silva*, 2003]. Therefore, to understand the effects of deforestation and forest regrowth on soil hydrological properties, it is important to consider forest age.

II.3. Objective and hypothesis

Our study was carried out in a Caatinga region of Pernambuco-Brazil. We studied four cover types, each representing a stage on the successional continuum from abandoned land to mature forest: an abandoned pasture, a 7-year-old regrowth forest, a 35-year-old forest, and a forest > 55 years old. Our specific objectives were to (1) quantify and compare soil hydraulic properties (infiltrability and *Ksat*) and sediment yield for the four cover types; (2) compare the three different methods used to obtain our soil hydraulic properties (rainfall simulations for infiltrability, and a laboratory method and a field method for *Ksat*); and (3) correlate infiltrability and sediment yield with site characteristics—i.e., slope, bulk density, soil texture, and soil surface cover (rock, litter, or herbaceous vegetation). With respect to Objective 1, we hypothesize that infiltrability and *Ksat* will be lower at the pasture end of the continuum and will gradually increase with forest age, while sediment yield will follow the opposite trend. This result would support the notion that forest regrowth promotes the recovery of soil hydraulic properties, as shown by other studies in tropical regions [*Descheemaeker et al.*, 2006;

Zimmermann et al., 2006; *Zimmermann and Elsenbeer*, 2009; *Hassler et al.*, 2011], and would be the first demonstration of this trend in the Caatinga. With respect to Objective 2, we expect that the two *Ksat* methods will render comparable values, and that these will differ from the infiltrability values obtained via rainfall simulation, since the latter method also takes into account the effects on infiltration of soil cover and raindrop impacts [*Bowyer-Bower and Burt*, 1989; *Lasanta et al.*, 2000; *D'Odorico et al.*, 2007]. Finally, with respect to Objective 3, we expect that the measured soil and surface characteristics will correlate with infiltrability and sediment yield, explaining in part the variability we are expecting to find across our sites.

II.4. Site description

Our study was carried out during June and July of 2015, in an area within the municipality of Serra Talhada, PE Brazil (07° 56'50"S and 38° 23'29"O), and approximately 400 km inland from Recife, PE. Within this area we selected four sites, each representing a stage in the recovery of forest on abandoned lands (Figure II.1). Site AP is a recently abandoned pasture; Site YF is a young forest that is regrowing on ~~a~~ pastureland abandoned 7 years prior to our study; Site IF used to be a pasture, but was abandoned 35 years prior to our study and now is a secondary forest at an intermediate stage of succession; and Site OF is an old forest that has not been cleared since at least 1960.

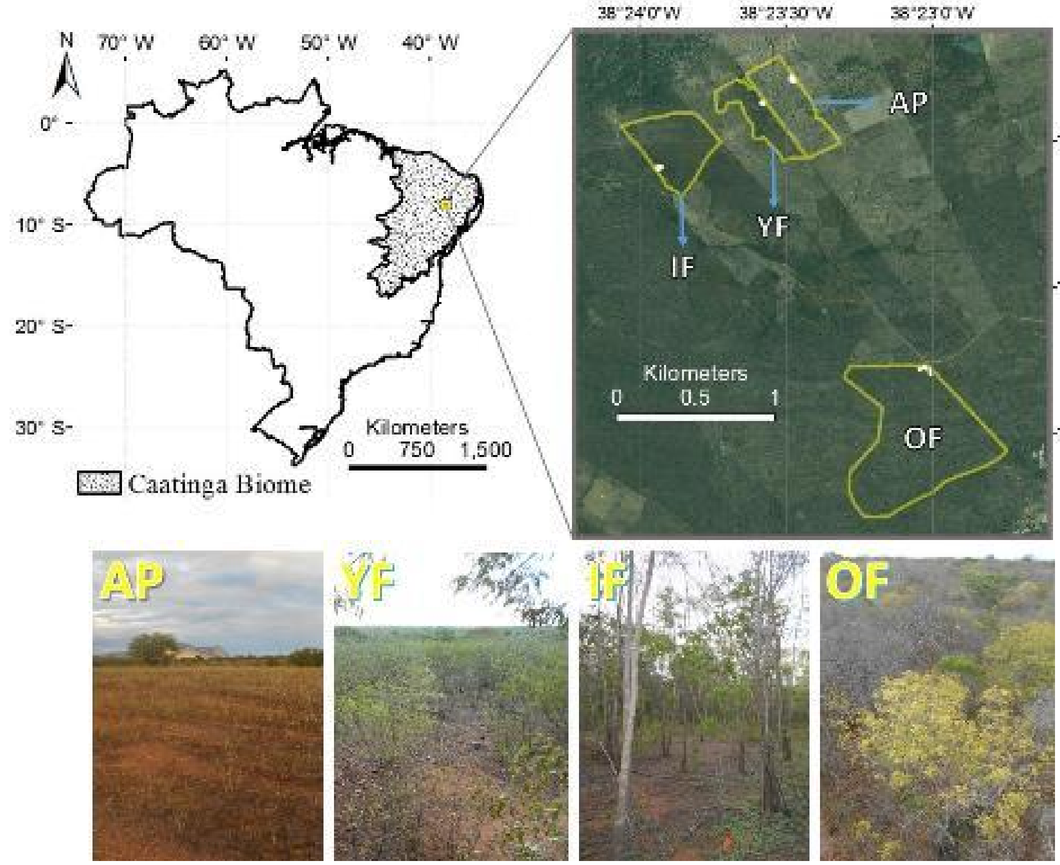

Figure II.1: Map showing the location of our study sites in the Caatinga and pictures showing the characteristic vegetation cover of each site. AP is a recently abandoned pasture; YF is a young, 7-year-old regrowth; IF is an intermediate, 35-year-old forest; and OF is an old forest >55 years old.

The climate in this region is semiarid BSh [*Peel et al.*, 2007], the elevation is approximately 500 m, mean monthly temperatures range between 23°C and 27°C, and mean annual rainfall (based on measurements from the period 2000 to 2014) is 608 mm (see Appendix 1). Approximately 80% of the rainfall occurs between January and May, mostly in the form of a few short events with intensities commonly exceeding 100 mm/h [*Medeiros and de Araújo*, 2013]. The bedrock in this region is crystalline and fairly impermeable, and the soils at our sites are shallow (40 cm), rocky, and sandy loam in texture. The two soil types found in our sites are Alfisol (Luvissolo Crômico) and Entisol (Neossolo litólico) (Figure II.2). Both are shallow soils (<50cm) and comparable in terms of hydrological properties, normally showing low infiltrability and high potential for runoff and erosion [*Sartori et al.*, 2005; *FAO-ISRIC-IUSS*, 2006]. The main difference between these soils is that Entisols are younger soils with a marked presence of rocks close to the surface, while Alfisols are relatively older and normally have an argillic B horizon due to illuviation [*FAO-ISRIC-IUSS*, 2006].

Figure II.2: Pictures of the soil profile trenches cut to identify the soil depths and types. Picture A shows an Alfisol (Luvissolo Crômico) at the abandoned pasture (AP) site, and picture B shows the profile of an Entisol (Neossolo Litólico) at the 35-year-old forest (IF) site.

The original vegetation cover of this area is a seasonally dry tropical forest known as Caatinga, which gives its name to the Brazilian biome in which it occurs.

However, most of the original Caatinga vegetation has been cleared at least once in the past for firewood or agricultural purposes [*Leal et al.*, 2005].

The main physical attributes of the four sites are shown in Table II.1.

Table II.1: main physical attributes of our study sites. The soil types are from the USDA classification, and while the soil from the OF site was not specifically identified, it is believed to be an Alfisol.

	AP	YF	IF	OF
Cleared	1962	1962	1960	–
Abandoned	2015	2008	1980	–
Main cover	50% bare soil, 50% grass and Malvaceae	Shrub layer of 1 to 3 m, 70% *Poincianella pyramidalis*	7 to 10 m trees, 80% *Anadenanthera sp.*	*Croton sp*. shrubs and a diverse arboreal layer of 7 to 10 m
Soil Type	Alfisol	Alfisol	Entisol	–
Texture	Sandy loam	Sandy loam	Sandy loam	Sandy loam

Both sites AP and YF were manually cleared and burned in 1962. They were then plowed and cultivated with cotton until 1982, followed by rotation cultivation of maize and beans until 1993. In 1994 the areas were plowed for the last time and sowed with two types of African grasses, *Cenchrus ciliares* and *Urochloa mosambicensis*. Cattle and goats grazed on site AP until 2014, and were normally allowed to forage intensively for two months right after the rainy season (usually June and July). Currently site AP is extremely degraded, characterized by small patches of vegetation in a matrix of bare soil. The vegetation during our study had a strong predominance of a few weed species (*Sida spinosa and Portulaca sp.*) and the grass *Urochloa mosambicensis*.

At site YF grazing stopped in 2008, when the area was abandoned and native vegetation started to recover. The area is now a shrubland of mainly small (1 to 3 meters) pioneer species, including Marmeleiro (*Croton blanchetianus*), Pereiro (*Aspidosperma pyrifolium*), and Caatingueira (*Poincianella pyramidalis*), the last being dominant. The soil matrix has some herbaceous plants (mostly Malvaceae) and areas covered by a very thin layer of litter, but is mostly composed of bare soil. There are also a few large (ca. 10 m) Brauna (*Schinopsis brasiliensis*) trees that were spared during the initial clearing of the land.

The original forest cover at site IF was manually cleared by slash and burn in 1960, with the sparing of some large Angico (*Anadenanthera sp.*) trees. It was plowed and cultivated with Palma cactus (*Opuntia sp.*), maize, and beans in a rotation system until 1970, when the area was plowed for the last time and planted with the grass *C. ciliaris*. Cattle and goats grazed the area until abandonment in 1980. Subsequently it developed into a tall forest and is currently dominated by *Anadenanthera sp.* (80%) trees of small trunk diameter (15–20 cm) and 7–10 m in height. A few smaller trees and shrubs (2–3 m) are also present, notably *S. brasiliensis* and *A. pyrifolium*, as well as some cacti (*Cereus jamacaru*). The herbaceous layer is strongly dominated by the forb *Commelina agrarian*.

Finally, site OF is an older forest with no known history of clearing. Although we found no records for the history of this site earlier than 1960, it is assumed to be a secondary forest that was cultivated or grazed in the past, like most areas in the Caatinga [*Coimbra Filho*, 1996]. It certainly was not cleared after at least 1960, but selective cutting of small trees for firewood and grazing by goats were common until 1980. Currently this area is affected only by the occasional crossing of a small herd of cattle during 2–3 months of the year. It is characterized by an arboreal layer (7–10 m) with over 30 species of trees of varying trunk diameter, and by a shrub layer dominated by *Croton blanchetianus, Croton sonderianus, A. pyrifolium*, and the cactus species *C. jamacaru* and *Pilocereus sp*. Interestingly, although the diversity of woody plants was the highest at this site, the canopy cover and the density of woody plants was visually lower than at the IF site. The soil matrix is similar to the one at the YF site, with sparse thin layers of litter and herbaceous vegetation and several areas of bare soil.

II.5. Methods

II.5.1 Infiltrability and sediment yield

To obtain data on infiltrability and sediment yield, we delineated five plots (2 m x 1 m) at each site (except AP, where N=7) for rainfall simulations. The plots were selected to represent the site's main characteristics and were bordered by 30-cm-high galvanized zinc sheets installed at a depth of 15 cm. Our rainfall simulator was the same as that used by de Freitas et al. (2008), developed on the basis of the model proposed by *Meyer and Harmon* (1979). It consists of an oscillating Veejet 80-150 sprinkler mounted on four aluminum legs that extend 3 m above the soil and operates under a constant pressure of 41Pa, providing rainfall similar in drop size and kinetic energy to natural rainfall events of intensities greater than 25 mm/h [*McGregor and Mutchler*, 1976]. We carried out a set of two rainfall simulations over each plot: the first on dry soil (dry run) and the second 24 hours later, on the previously wetted soil (wet run), for a total of 10 simulations at each site (except at AP, where we did dry runs only on the two additional plots, for a total of 12).

The duration of each simulation varied from 10 to 37 minutes, and because water supply was limited, we interrupted the simulations when runoff rates were considered constant. Mean precipitation (in mm) was measured by seven evenly distributed rain gauges (Fig. II.3A), and mean rainfall intensity (in mm/h) was obtained by dividing mean precipitation by the duration of the simulation. Runoff was collected every 2 to 5 minutes, and collection time ranged from 15 to 30 seconds. We calculated infiltration rates at each time interval by subtracting runoff (mm/h) from the mean rainfall intensity (mm/h). Infiltrability was defined as the steady-state infiltration rate obtained from the wet runs, and was determined by averaging the last three measurements, when runoff was estimated to be constant. We focused our analysis on the infiltrability derived from the wet runs because these had the same initial soil moisture, and antecedent moisture is known to have a strong influence on infiltration [*Robinson et al.*, 2008].

We estimated sediment load in the runoff (g/L) by filtering, drying, and weighing the first, third, and fifth runoff samples (for our analysis, we used only the fifth samples because we considered those to be the least influenced by the sediment derived from plot installation). We used sediment load, collection time, and plot area to calculate sediment yield, which is expressed in terms of Kg $ha^{-1}min^{-1}$.

For each plot we obtained a set of variables that could be correlated to infiltrability and sediment yield: (i) soil texture, determined with the pipet method [*Klute*, 1986]; (ii) surface bulk density, calculated by drying and weighing cylindrical soil core samples of fixed volumes and dividing dry weight by cylinder volume; (iii) slope percentage, measured at the center of the plot using level meters; and (iv) cover type (herbaceous, including grasses and forbs; bare soil; rock; or litter), visually estimated as percentages using rulers as references, as shown in Fig. II.3C. Although tree and shrub cover are known to influence infiltrability, they were not directly measured in our study.

Figure II.3: (A) Representation of the 2-m x 1-m plots with the seven evenly distributed rain gauges. (B) A rainfall simulation in progress on one of the plots in the AP site. (C) A plot in the YF site, where a researcher is measuring the slope and estimating cover.

II.5.2 Ksat

To determine *Ksat* in the laboratory (hereafter *Ks*), we collected three 5cm in diameter core samples of surface soil (0- to 5 cm depth) from each rainfall simulation plot (N = 15 per site) and applied the constant head method to those samples [*Klute and*

Dirksen, 1986]. This method is based on Darcy's equation and expresses *Ks* (mm/h) as follows:

$$K_s = VL/[At(H_s - H_1)],$$

where V is the water volume flowing through a sample having length L and cross sectional area A during time t, and $(H_s - H_1)$ is the hydraulic difference across the sample.

We obtained *Ksat* in the field (hereafter *Kfs*) following the Beerkan method [*Lassabatère et al.*, 2006; *Bagarello et al.*, 2013; *de Oliveira Júnior et al.*, 2014]. This method consists of a series of infiltration tests done by manually pouring fixed volumes of water (0.1 L) into a single ring of small diameter (we used 127-mm and 150-mm rings) inserted to a depth of approximately 10 mm. We selected four locations from the 2- to 3-m area surrounding each rainfall simulation plot, which included patches covered with grasses and herbaceous vegetation as well as patches of bare soil, for a total of 20 infiltration test locations per site. The presence or absence of vegetation inside the rings was recorded, but firstly plants were clipped at ground level. For each test, at time zero we poured a first volume and started recording the time. Once the first poured volume had completely infiltrated, a new volume was poured. We repeated the procedure, recording the number of volumes and the time elapsed between complete infiltrations until steady state was achieved, which normally happened after 8 to 12 volumes. To estimate *Kfs*, this method also requires initial volumetric soil water content (cm^3/cm^3), bulk density (g/cm^3), and particle density (g/cm^3), which we obtained from samples collected at a distance of 20 cm from the infiltration test locations. We then analyzed the data and calculated *Kfs* using the BEST-*steady* algorithm [*Bagarello et al.*, 2013] with SciLab software.

II.5.3 Statistical analysis

Using the Shapiro-Wilk statistical test, we determined that none of our data were normally distributed, and therefore we used only non-parametrical statistics. We used the Mann-Whitney Rank Sum test to evaluate differences in infiltrability and sediment yield between dry and wet runs; and we used the Kruskal-Wallis analysis of variance to test for differences in infiltrability, sediment yield, *Ks*, and *Kfs* between sites, and for differences between infiltrability, *Ks*, and *Kfs* values within each site. These tests were followed by a Dunn's test on ranks for multiple comparisons. The Mann-Whitney Rank Sum test was also used to detect significant differences in *Kfs* between points with and without vegetation. Finally, to test whether infiltrability and sediment yield were correlated with our soil and surface characteristics (e.g., bulk density and herbaceous cover), we used Spearman's test for non-parametric data. All our statistical analyses were carried out with SigmaPlot13 software, with significance level at p= 0.05.

II.6. Results

Average soil infiltration rates for the four sites, during the dry and wet runs, are shown in Figure II.4. Mean infiltration was initially highest at AP during the dry runs, and runoff began the latest at this site. Counting initial infiltration rates in the analysis is problematic because they directly reflect rainfall intensity, which at the outset was subject to unintentional variations.

Five to seven minutes into the dry runs, infiltration at AP dropped to levels below those measured at the OF site, and after 20 minutes reached a rate similar to those observed at YF and IF (approximately 40 mm/h). By contrast, during the wet runs there was less variation in rainfall intensity, runoff started faster (at 2–3 min for all sites; $p = 0.016$), infiltration was on average 20% lower, and the differences in final infiltration rates between sites were more pronounced, with approximately twice as much infiltration at OF than the other sites ($p = 0.01$). Mean infiltrability values at AP, YF, IF, and OF were 31 mmh-^{1}, 38.6 mmh-^{1}, 31.8 mmh-^{1}, and 65.8 mmh-^{1}, respectively (Table II.2). Variability in infiltrability values was highest at the AP site (100%) and lowest at the OF site (25%).

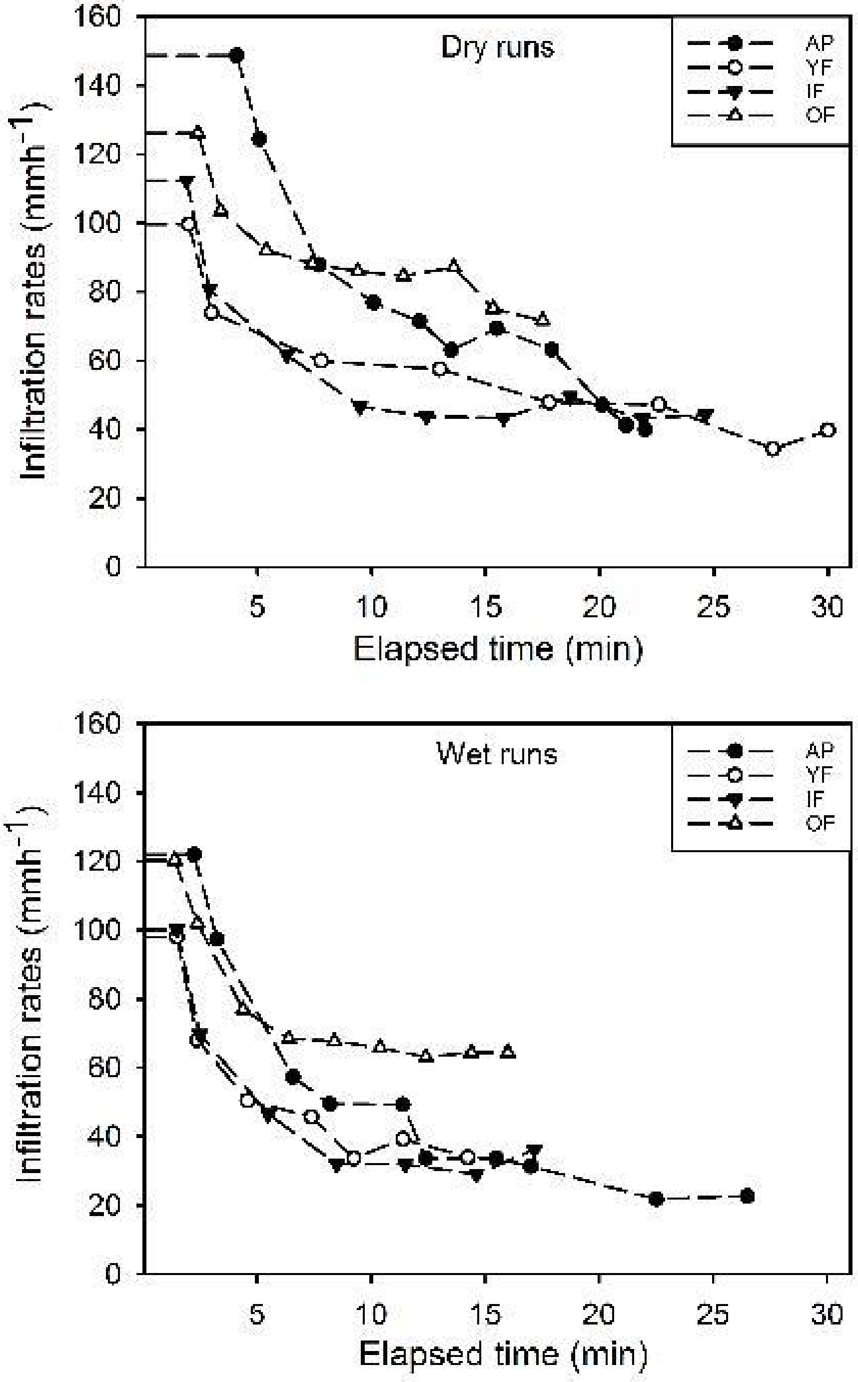

Figure II.4: Average infiltration rates during the dry and wet runs of the rainfall simulation experiments carried out at the four study sites.

Table II.2: Descriptive statistics of infiltrability, *Ks*, *Kfs*, and sediment yield at the four study sites. Different italic letters after site names indicate significant differences at $p<0.05$.

	Site	MEAN	STDEV	MED	MAX	MIN	CV*
Infiltrability (mm h^{-1})	AP *a*	31.00	30.28	19.35	100.11	7.56	1.00
	YF *a*	38.62	19.59	40.03	55.58	7.67	0.51
	IF *a*	31.80	17.40	26.52	57.34	15.60	0.55
	OF *b*	65.75	14.97	69.91	80.96	42.12	0.23
Ks (constant head) (mm h^{-1})	AP *a*	87.45	112.96	66.86	532.73	11.18	1.30
	YF *a*	101.05	72.72	80.31	261.50	28.73	0.72
	IF *a*	92.97	40.30	88.81	165.43	43.63	0.43
	OF *a*	115.44	94.70	73.84	275.68	41.03	0.82
Kfs (Beerkan) (mm h^{-1})	AP *a*	36.75	26.81	27.58	133.36	16.01	0.69
	YF *b*	71.00	39.44	66.28	163.30	17.05	0.81
	IF *b*	100.82	81.28	77.44	365.53	17.64	0.56
	OF *c*	213.60	145.96	153.30	595.46	55.65	0.73
Sediment yield (Kg hec^{-1} min^{-1})	AP *a*	10.73	10.98	5.53	32.78	0.36	1.02
	YF *b*	34.67	30.72	32.04	106.79	6.39	0.89
	IF *a, b*	10.22	2.89	11.70	13.77	6.41	0.28
	OF *a, b*	14.86	12.90	9.85	43.05	2.89	0.87

*coefficient of variance

Within-site variability was high for both *Ks* and *Kfs* values, as shown by the coefficient of variance values in the table. Across the four sites, *Ks* values were not significantly different ($p = 0.43$) and ranged between 11 and 533 mm/h (both the lowest and the highest values were from the AP site). Conversely, *Kfs* values differed significantly among the sites ($p<0.001$), in decreasing order as follows: OF > IF > YF > AP; actual values ranged between 16 mm/h at AP and 595 mm/h at OF (see Table II.2 and Figure II.5). *Ks* and *Kfs* values were, on average, 2.3 and 1.7 times higher than the infiltrability values, respectively. The ratio *Kfs*:Infiltrability was approximately 3:1 at the IF and OF sites, 2:1 at the YF site, and 1:1 at the AP site.

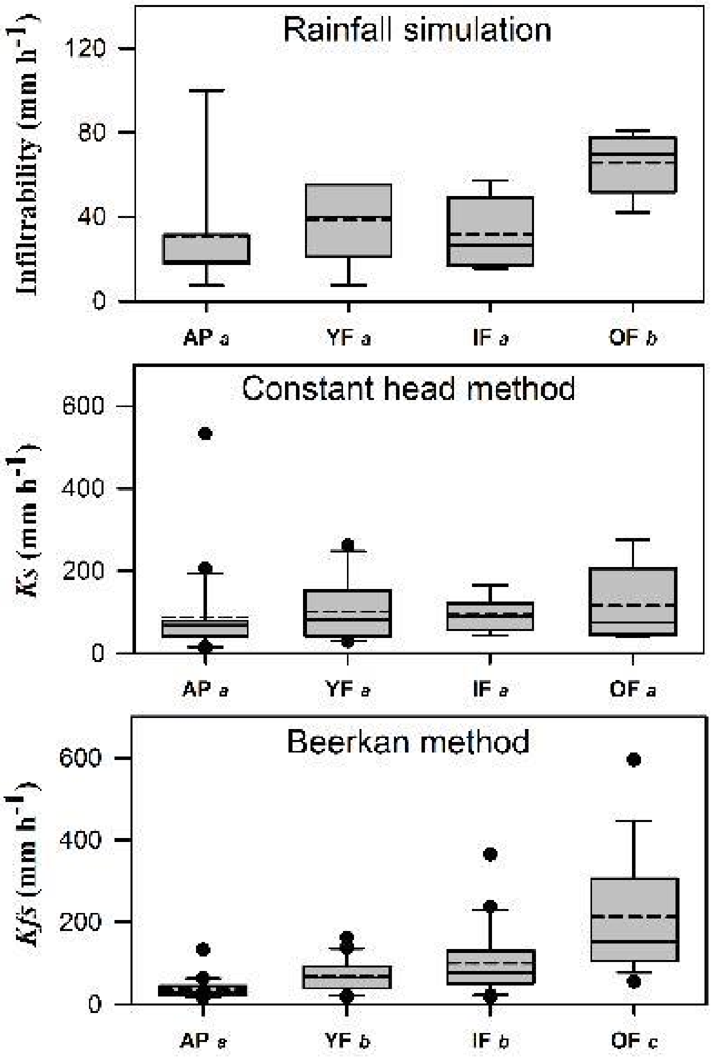

Figure II.5: Box plots showing the infiltrability (steady-state infiltration) and the surface hydraulic conductivity values—the latter obtained both via the laboratory constant head method (*Ks*) and via the Beerkan simple ring method (*Kfs*). Italic letters after site names stand for significant differences between sites detected by the Kruskal-Wallis test ($p<0.05$).

There was no statistical difference in sediment yield between dry and wet runs (p = 0.88). The highest mean sediment yield (34 Kg ha-^{1} h-^{1}) was at the young forest site, and the lowest (10 Kg ha-^{1}h-^{1}) was at the intermediate forest site (Table II.2 and Figure II.6). However, the only significant differences in sediment yield, detected by the Kruskal-Wallis test, were between AP and YF (p = 0.02).

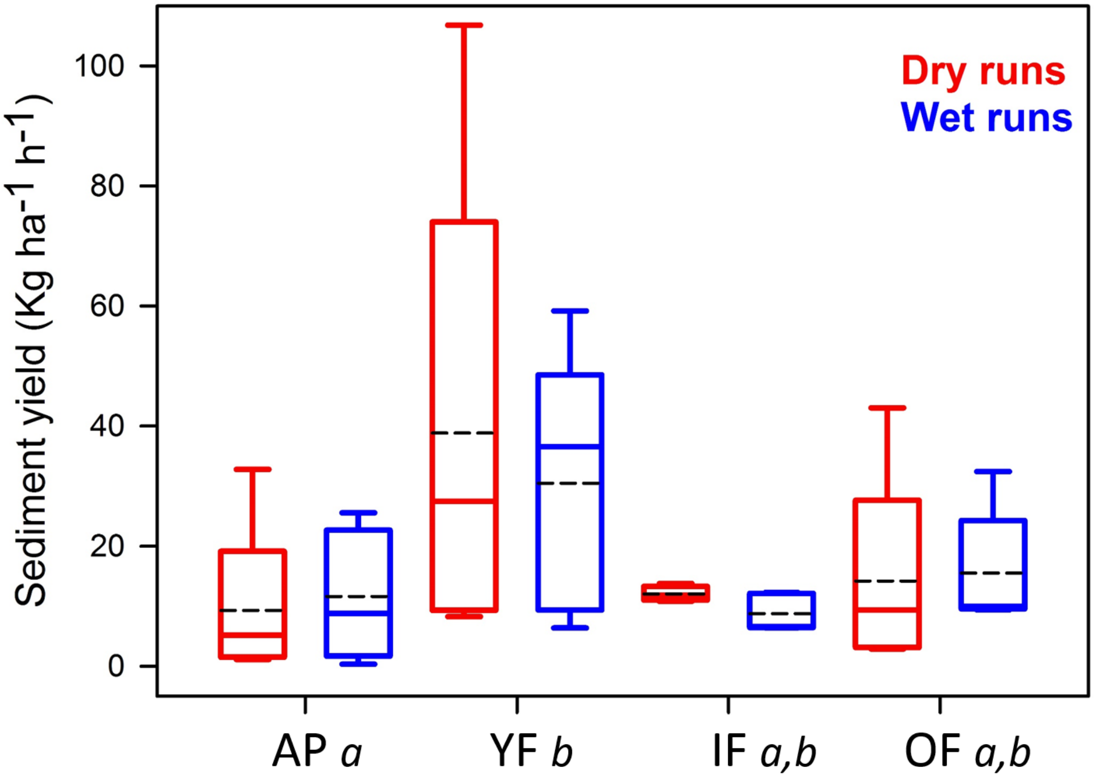

Figure II.6: Box plots showing the sediment yield at each site during the dry runs (red plots) and wet runs (blue plots). Italic letters after site names stand for significant differences between sites detected by the Kruskal-Wallis test (p<0.05).

Kfs measurements done on vegetated patches were twice as high as those done on bare soil (55.5 mm/h and 24.2 mm/h, respectively; p= 0.002). Table II.3 shows the mean value and the standard deviation for each measured variable (slope, bulk density, clay content, clay + silt content, rock cover, litter cover, and herbaceous cover) at each site, as well as the correlation coefficient between each variable and the measured infiltrability and sediment yield values. Infiltrability was not correlated with any of those variables, while sediment yield showed negative correlations with herbaceous cover (r = -0.58, p= 0.009) and bulk density (r = -0.48, p = 0.035) and a nearly significant positive correlation with slope (r = 0.44, p=0.054) and litter cover (r = 0.48, p=0.069).

Table II.3: Mean values and standard deviations for the measured variables (determined from the plot studies) for each site, as well as correlation coefficients between these variables and the infiltrability and sediment yield values obtained via the rainfall simulations.

		Slope (%)	Bulk density (g/cm^3)	Clay (%)	Silt + Clay (%)	Rock (%)	Litter (%)	Herbaceous (%)
Mean ± STDEV	*AP*	3.3 ± 0.6	1.46 ± 0.07	16 ± 4	33 ± 4	–	–	55.5 ± 36.5
	YF	8 ± 3.2	1.38 ± 0.04	16 ± 1	36 ± 3	9 ± 8.4	46 ± 24.3	14.4 ± 15.2
	IF	5.4 ± 2.3	1.39 ± 0.02	11 ± 1	32 ± 4	–	22 ± 10.8	29 ± 21.9
	OF	6.6 ± 1.8	1.40 ± 0.08	11 ± 3	28 ± 3	27.6 ± 10.6	19 ± 16.5	8 ± 4.7
Correlation	*Infiltrability*	0.15 –	0.14 –	-0.161 –	-0.31 –	0.34 –	-0.05 –	-0.05 –
	Sediment yield	0.44 *	-0.48 **	0.03 –	0.26 –	-0.47 –	0.48 *	-0.58 ***

* = P<0.1 (nearly significant difference), ** = P<0.05, *** = P<0.01

II.7. Discussion

II.7.1 Infiltrability and Ksat

Our results support the initial hypothesis that Caatinga forest regrowth promotes a gradual recovery of soil hydraulic properties by augmenting *Ksat* and infiltrability. These findings are in agreement with those reported by several other studies in the wet tropics and in temperate zones (Appendix 2).

As was found by other studies, the *Ksat* values we obtained—regardless of the method used—varied greatly even within the same site. This was expected, since *Ksat* is affected by several surface properties, and even measurements done within a short distance of each other can render very different values [*Zimmermann and Elsenbeer*, 2008; *Hassler et al.*, 2011]. But despite this inherent spatial variability, the *Ksat* values we measured in the field using the Beerkan method (*Kfs*) did reflect differences in land cover: *Ksat* increased gradually with forest age. The laboratory *Ksat* measurements (*Ks*), on the other hand, did not reflect this trend—possibly because there were fewer (15 per site, vs 20 per site for *Kfs*). However, this difference is not large, and we believe that the similar *Ks* values found at all sites are better explained by a limitation of the laboratory method in measuring macropore flow. Although laboratory constant head is a well-established method for determining *Ksat* and is relatively simple and inexpensive [*Klute and Dirksen*, 1986], it has the disadvantage of compacting the soil and truncating macropores during sample collection [*Lee et al.*, 1985; *Mohanty et al.*, 1994]. Field measurement of *Ksat* (*Kfs*) is less disruptive and thus better suited for comparisons between sites having similar soil types but different land-use histories and vegetation cover [*Ankeny et al.*, 1991; *Lassabatère et al.*, 2006; *Zimmermann and Elsenbeer*, 2008].

Small-plot rainfall simulations can be expensive and laborious, but they enable a more realistic analysis of infiltrability than ponded infiltrometers, and are particularly valuable in semiarid regions, where rainfall events are scarce [*Wilcox et al.*, 1986; *Bowyer-Bower and Burt*, 1989]. During our rainfall simulations, runoff was started later and infiltration rates were higher during the dry runs. This is as expected, given the low antecedent soil moisture and the steeper moisture gradient on the wetting front [*Bowyer-Bower*, 1993]. Infiltrability at the older Caatinga forest (OF site) was twice as high as at the other sites. An important difference between *Ksat* values and the infiltration rates and infiltrability values obtained with rainfall simulation is that the latter method takes into account the effects of raindrop impact, which can create physical crusts and partially seal the soil surface [*Meyer*, 1994]. This could explain why infiltrability values were, in general, half of those of *Kfs* and *K*. However, it does not explain why, when comparing infiltrability across sites, only the OF site showed a higher infiltrability values, instead of showing a gradual increase with forest age, as did *Kfs*.

Water infiltration over a larger area is much more complex than at a single point and is strongly affected by surface characteristics [*Seyfried*, 1991; *Wilcox et al.*, 2003]. For example, it can be enhanced by grasses and herbaceous vegetation [*Blackburn*, 1975; *Cerdà*, 1997] and by leaf litter [*Dunkerley*, 2015]. In our sites, *Kfs* values were significantly higher in spots with herbaceous vegetation, but we found no correlation between infiltrability values and herbaceous cover. In fact, our OF plots had the lowest herbaceous and litter covers, but still showed twice as much infiltrability as the other sites—possibly suggesting that other surface and/or soil characteristics of that site are offsetting the negative effect of low vegetation on infiltration. Rock cover and steeper slopes, for example, have been associated with both enhanced and reduced infiltrability [*Wilcox et al.*, 1988; *Brakensiek and Rawls*, 1994]. At our sites, however, infiltrability values did not correlate with any of the measured soil and surface cover variables. We do not exclude the possibility of this result being an artifact of our analysis. For example, because of the limited number of plots, we combined plots from all four sites in our correlation tests; had we instead done individual correlation tests for each site, using a larger number of plots, the results might have been different. At the same time, the fact that we did not find these extensively documented correlations can be seen as an indication that forest age is an important determinant of hydraulic properties. On that basis, we may conclude that the main reason for the higher infiltrability and *Kfs* values found at the OF site is its advanced stage of secondary succession and the longer time it has had to recover from past disturbances.

Recovery of soil hydraulic properties in older secondary forests could be associated with either an improved soil structures due to higher organic matter content [*Blackburn*, 1975; *Franzluebbers*, 2002] or enhanced macroporosity—the latter due to a number of factors, including greater diversity of plants and root systems [*Pohl et al.*, 2009], greater activity of soil ecosystem engineers (e.g., ants and termites) [*Brener and Silva*, 1995; *Colloff et al.*, 2010], and longer periods for macropores to develop [*Lal*, 1996; *Colloff et al.*, 2010].

Practices such as slash-and-burn land clearing, crop cultivation, and grazing are normally associated with soil compaction, loss of organic matter, and reduced soil fauna activity, all of which can decrease macroporosity and infiltrability. The effects of such practices on soil structure can last for several decades after the land has been abandoned [*Arevalo et al.*, 1998; *Zimmermann et al.*, 2006]. In the case of our sites, land use histories prior to abandonment were comparable and therefore land use must account for the differences we found among them. Other important factors known to affect soil hydraulic properties are woody plant density [*Niemeyer et al.*, 2014] and canopy cover [*Bhark and Small*, 2003; *D'Odorico et al.*, 2007; *Magliano et al.*, 2015], which determine the degree of interception of rainfall. Tree and shrub canopies reduce raindrop impact and soil surface sealing, and water flowing down the trunks quickly infiltrates at the base [*Wilcox et al.*, 2003; *D'Odorico et al.*, 2007; *Tobella et al.*, 2014]. We were unable to take such interception into account in our study because of the limited height of our rainfall simulation ~~s~~ apparatus, which was effective only for herbaceous plants and small shrubs. Had our calculations included a value representing interception by larger shrubs and trees during natural rainfall events, they would no doubt have yielded higher infiltrability estimates—particularly at the IF and OF sites. Visually, it was apparent that site YF had the least woody plant density and canopy cover while sites IF and OF had similar density and cover (but infiltrability and *Kfs* values were lower at IF than at OF, which we attribute to the longer recovery time at the latter site).

II.7.2 Sediment yield

Our initial hypothesis that sediment yield would gradually decrease as forest recovery advanced was not corroborated: the lowest values were found at the AP site and the highest at the YF site. In contrast to studies on *Ksat* and infiltrability, few studies have investigated sediment yield in forests at various stages of natural regrowth; studies looking at various types of land cover, including afforestation with native or non-native species, are more common [*Dunjó et al.*, 2004; *Huang et al.*, 2010; *Molina et al.*, 2012; *Navarro Hevia et al.*, 2014]. A study carried out by *Nunes et al.* (2010) compared sediment yield for sites with recovering vegetation of different ages in a semiarid area of Portugal. They found a substantial reduction in sediment yield at their older forested site, which was mainly attributed to higher litter cover. However, another study comparing runoff and sediment yield for abandoned pastures (meadows) with runoff and sediment yield for secondary shrublands in the Aisa Valley, Spain, found that although the abandoned pastures had the highest runoff rates, sediment yield was four times higher for the young shrublands [*Molinillo et al.*, 1997]. The authors attribute the greater sediment yield to a loss of grass cover and enlargement of bare soil areas during early stages of succession. As noted above, a similar pattern was found during our study. Finally, Harden (1996) reported higher runoff but lower erosion rates on pastures than on abandoned lands in central Ecuador. However, neither the vegetation type undergoing recovery nor the period since land abandonment is clear from this paper.

The importance of vegetation in protecting soil from erosion is well recognized [*Stocking*, 1994], and several studies in semiarid regions have found decreased soil loss rates as vegetation cover increases [*Blackburn*, 1975; *Wilcox and Wood*, 1989; *Cerdà*, 1997; *Wilcox et al.*, 2003; *Boer and Puigdefábregas*, 2005]. At our sites we found a strong negative correlation between herbaceous cover and sediment yield. The lower sediment yield values were found at the AP and the IF sites, and were likely due to their greater herbaceous cover (approximately 50% and 30% cover, respectively) and the fact that the grasses and forbs were concentrated in denser patches than at the other sites, thereby possibly acting like a filter—binding soil particles and trapping runoff and sediments [*Cerdà*, 1997]. The stalks and roots of herbaceous vegetation can also increase macroporosity, which in turn enhances infiltration and reduces erosion [*De Baets et al.*, 2006]. Similarly, woody plant root systems can reduce sediment yield by increasing infiltration and decreasing runoff [*Wilcox et al.*, 2003]. Additionally, interception of rainfall by tree and shrub canopies like those found at our IF and OF sites reduces the kinetic energy of raindrops and decreases splash erosion [*Molinillo et al.*, 1997; *Lasanta et al.*, 2000; *D'Odorico et al.*, 2007]. But as noted earlier, our rainfall simulations were not carried out over the canopies of larger shrubs and trees, and therefore this category of interception could not be factored in to the analysis. If it had been, the resulting sediment yield values would probably have been lower, particularly at the sites with higher canopy cover (IF and OF).

The presence of a litter layer also serves to intercept raindrops, reduce runoff speed, and entrap sediment, all of which can lessen soil loss [*Stocking*, 1994; *Nunes et al.*, 2010; *Dunkerley*, 2015]. At all of our sites, however, when litter was present it consisted of a very thin layer of fine woody debris that only partially covered the soil.

The superficial nature of this litter could explain why we even found a nearly significant positive correlation between litter cover and sediment yield [*Wilcox and Wood*, 1989].

At the AP site, sediment yield was relatively low even for the plots having large expanses of bare soil. Possibly there was too little loose sediment readily available for transport via runoff [*Ziegler et al.*, 2000], and/or crusts may have formed over the bare soils, inhibiting infiltration (this would explain the low *Kfs* and infiltrability values) and also lessening raindrop-splash effects (sediment dislocation and erosion) [*Lasanta et al.*, 2000]. Crusting was observed in several of our plots, but was particularly high at the AP site. A common phenomenon at disturbed sites, crusting increases bulk density—which could explain the positive correlation we found between bulk density and sediment yield.

It is well known that erosion rates accelerate as slopes become longer and steeper [*Wilcox and Wood*, 1989; *Renard et al.*, 1997; *Morgan and Rickson*, 2003]. It has been argued that under conditions of small-plot rainfall simulation, overland flow does not attain sufficient energy to detach soil particles, so that sediment yield is mostly a result of splash erosion [*Meyer and Harmon*, 1979; *Lasanta et al.*, 2000]. However, *Wilcox and Wood* (1989) used small-plot rainfall simulations in the Chihuahuan Desert and found higher concentrations of sediment from runoff over steeper slopes, showing that slope is a major factor in erodibility in that region. At our sites, the positive correlation found between slope and sediment yield suggests that in the Caatinga, erosion can be affected by even relatively low slopes (3%–10%), which could partially explain the higher sediment yield at the YF site, where the slope gradient was highest.

Although we did not find a significant difference in sediment yield among AP and our older forested sites, this does not mean that forest regrowth will not reduce erosion in Caatinga landscapes. Since our selected plots did not include larger shrubs and trees it is clear that our results reflect mostly localized splash erosion in the intercanopy zones. At larger scales, the role of trees and shrubs as runoff and sediment sinks is likely to be accentuated, and lower sediment yields can be expected [*Osterkamp and Toy*, 1997; *Wilcox et al.*, 2003].

II.8. Conclusions

Overall, our study shows that forest regrowth promotes a recovery of soil hydraulic properties in the semiarid Caatinga. We found that infiltrability—determined by means of small-plot rainfall simulations—was two times higher in a 55-year-old forest than in a recently abandoned pasture, a 7-year-old forest, and a 35-year-old forest. Because infiltrability across the four sites did not correlate with any of our soil and surface variables, we attribute the higher infiltrability values of the oldest forest to the longer time it remained undisturbed, allowing its soil structure to recover.

Further support for this interpretation is provided by the *Ksat* values we obtained in the field with the Beerkan method (*Kfs*); these values increased gradually as time following land abandonment increased. Conversely, *Ksat* values obtained by laboratory analysis of soil core samples (Ks) were not significantly different across sites. We attribute this discrepancy between *Kfs* and *Ks* to the disruption of macropores during collection of the soil cores for the laboratory method. The infiltrability values were lower than either set of *Ksat* values, probably because during the rainfall simulations, the raindrop impact had a sealing effect on the soil. This effect might have been particularly pronounced at the two older forested sites, where the soil surface is normally protected by the canopy of trees and shrubs.

Surprisingly, the sediment yield values obtained via the small-plot rainfall simulations were not lower for the forested sites than for the abandoned pasture. Site AP, despite having lower *Ksat* and/or infiltration rates, had similar sediment yield as the intermediate age and older forests, and three times lower than the young forest. We attribute the difference in sediment yield between the abandoned pasture and the young forest mainly to the higher herbaceous cover at site AP. Other influencing factors might include (1) a lack of available sediment for transport in the bare soil areas of the pasture, and (2) slope, which was higher in the young forest than in the pasture. Although our small-plot measurements did not show that sediment yield gradually decreases with forest age, this trend would possibly show up on a larger scale, which would take into account the effect of woody plants as sediment sinks.

Conversion of forests to cropland and pastures is the main land-cover change in the Caatinga, and it has a major effect on soil hydraulic properties. Our study shows that when degraded land is abandoned and forest regrows, there is a gradual increase of hydraulic conductivity, and infiltrability might take 55 years or more to recover completely. This is the first time that these relationships have been demonstrated for the Caatinga, and our findings point to the need for ecohydrology studies of tropical dry forests to recognize the importance of forest age.

CHAPTER III

CONTRASTING EFFECTS OF TWO ANT SPECIES ON SOIL PHYSICAL PROPERTIES IN A SEMIARID ENVIRONMENT IN BRAZIL

III.1. Overview

Ants play a crucial role as ecosystem engineers. By building their nests, they modify infiltration and soil moisture patterns, which can in turn strongly influence plant recruitment and distribution. These modifications are particularly important in semiarid environments, where water is a limited resource. In this study, we investigated modifications of soil physical properties by two ant species in the Caatinga, a semiarid region of northeastern Brazil. We assessed infiltration, soil bulk density, and soil texture on (i) 22 active nests of the queenless ant *Dinoponera quadriceps*, located in a seasonally dry, old-growth forest; and (ii) one active and one inactive nest of the leaf-cutter ant *Atta laevigata*, both situated in a degraded pasture. Infiltration around *D. quadriceps* nests was significantly higher than in the other Caatinga soils, and the nests showed significantly lower bulk density and higher clay content. At the pasture site, the inactive nest of *A. laevigata* showed 3 times higher infiltration than the pasture matrix, while the annular zone of both nests, encompassing an area larger than the one covered by the mounds, showed high bulk densities and 3 times lower infiltration than the pasture matrix. Additionally, both the active and inactive mounds had significantly coarser texture than the soils of the pasture. In general, our results suggest that these two ant species are playing different roles in the hydrology of their ecosystems. On the one

hand, *D. quadriceps*, a species sensitive to disturbances, facilitates infiltration and modifies soil physical aspects in ways that can benefit woody plants (which were ubiquitous around their nests), thereby possibly increasing forest resilience. On the other hand, *A. laevigata*, a species that benefits from disturbances, has mixed effects on soil properties and possibly a negative overall impact on infiltration and soil moisture, which can have a detrimental influence on forest recovery.

III.2. Introduction

Ants are present in most terrestrial environments [*Wilson*, 1971] and play important roles in the functioning of ecosystems—as key species in trophic webs, as seed dispersers, and as soil engineers [*de Bruyn and Conacher*, 1990; *Folgarait*, 1998; *Leal et al.*, 2007; *Styrsky and Eubanks*, 2007]. Soil-engineering ants are those that modify or create habitat for other species, including plants, by altering the soil in their colonies and around their nests. Ants and other ecosystem engineers have been shown to increase their activity in the latter stages of secondary succession [*Colloff et al.*, 2010], which can facilitate the recovery of disturbed environments [*Brener and Silva*, 1995; *Moutinho et al.*, 2003; *Bonachela et al.*, 2015]. In semiarid regions, ants and other soil fauna—such as termites and rodents—have been shown to increase the spatial heterogeneity of soil and to promote diversity by creating habitats for disturbance-dependent plants [*Reichman and Seabloom*, 2002].

Soil modifications by ants are often disproportionally large relative to the biomass of the individuals, and can last long after the colony dies [*Baxter and Hole*, 1967; *Jonkman*, 1978; *Bucher*, 1982; *de Bruyn and Conacher*, 1990]. These modifications include: (i) bioturbation, or soil turnover, as the process of nest construction and tunnel digging brings sediment from lower soil layers to the surface, mixing the soil and sometimes even creating a distinct new horizon [*Baxter and Hole*, 1967; *Cammeraat et al.*, 2002]; (ii) modification of soil structure and creation of macropores, which lowers bulk density and thereby can enhance water infiltration [*Eldridge*, 1993; *Cammeraat and Risch*, 2008; *Colloff et al.*, 2010]; and (iii) alteration of soil organic carbon and nutrient content, which can happen either directly (through waste disposal) [*Haines*, 1975; *Brener and Silva*, 1995] or indirectly (through activity that increases soil infiltration and aeration, which then promotes root development and microbial activity) [*Whitford*, 1988; *Dean and Yeaton*, 1993; *Lei*, 2000].

Ant mounds can also act as runoff sinks, altering the distribution of nutrients and water in the soil and sometimes creating islands of fertility and elevated moisture [*de Bruyn and Conacher*, 1990; *Eldridge*, 1993; *Cammeraat et al.*, 2002]. This process is particularly important in semiarid environments, where water availability is limited: soil modified by ants can offer suitable spots for plant germination, growth, and survival [*Briese*, 1982; *Whitford*, 1988; *Carlson and Whitford*, 1991; *Dean and Yeaton*, 1993; *Eldridge*, 1994]. While a number of studies have investigated the effects of ants on soil hydraulic properties in semiarid landscapes, most have focused on one species of ant and one type of cover [*Rissing*, 1988; *Carlson and Whitford*, 1991; *Dean and Yeaton*, 1993; *Eldridge*, 1994; *Cammeraat et al.*, 2002; *Cammeraat and Risch*, 2008], few have evaluated soil modifications by different species and/or considered the effects of these modifications on native cover versus degraded land [*Colloff et al.*, 2010].

Our study investigated the effects of two ant species on soil physical and hydraulic properties under two types of land cover in the Caatinga, a semiarid biome of northeastern Brazil. This region is home to some of the largest areas of tropical dry forest in the world, many of which are threatened by desertification as a consequence of anthropogenic disturbances and climate change [*Araújo et al.*, 2008; *Santos et al.*, 2014]. The first cover type we studied is an old forest; at this site we evaluated how soil properties (bulk density, infiltration, and texture) were modified by the giant queenless ant *Dinoponera quadriceps,* which is a common species in the Caatinga that is highly sensitive to disturbances, especially grazing [*Leal et al.*, 2014b]. The second cover type is a degraded pasture; at this site we evaluated the same three soil properties, comparing the soils of the pasture matrix with those of nests built by the leaf-cutter ant *Atta laevigata*, a species common in disturbed ecosystems such as overgrazed pastures [*Fowler*, 1983].

D. quadriceps, like other queenless ants (Ponerinae), is a mainly carnivorous species that feeds on a large variety of invertebrates but also on specialized seed structures and is an important seed disperser [*Horvitz and Beattie*, 1980; *Leal et al.*, 2007]. This species is abundant in the Caatinga, and while a few studies have examined their trophic interactions and their role as seed dispersers [*Araujo and Rodrigues*, 2006; *Medeiros et al.*, 2012; *Azevedo et al.*, 2014; *Leal et al.*, 2014b], none have looked at their role as soil engineers. The ant *A. laevigata*, like other leaf-cutter ants, can affect plant communities not only as important primary consumers but also by modifying properties of the soils in which they grow [*Leal et al.*, 2014a]. For example, a study by *Brener and*

Silva (1995) in the Orinoco savannas of Venezuela, found that *A. laevigata* nests improved the soil in ways that facilitated the regrowth of woody plant groves in abandoned pastures. Similarly, *Atta cephalotes* have been associated with the recovery of secondary forests in the Amazon of Brazil *Moutinho et al.* (2003).

We hypothesized that the soils in the mounds and annular zones of both the ant species we studied would show lower bulk densities and higher infiltration and would have a finer texture, than non-nest soils. Such modifications would mean higher water availability in and around the ant nests, and therefore a more suitable environment for plants. But the implications of these modifications would be somewhat different under different cover conditions: in the Caatinga forest site, the ant *D. quadriceps* would increase the resilience of the existing vegetation, whereas in the pasture site the ant *A. laevigata* would facilitate plant colonization and accelerate secondary succession.

III.3. Study site description

Our study was carried out during June and July of 2015, in two sites within the municipality of Serra Talhada, PE Brazil (07° 56’50”S and 38° 23’29”O): a degraded pastureland and a Caatinga forest that has not been cleared since at least 1960. The climate is semiarid BSh, with monthly temperatures ranging between 23°C and 27°C and mean annual rainfall (based on measurements from the period 2000–2014) of 608 mm (see Appendix). Most of the precipitation occurs between December and May, mainly in the form of short but intense rainfall events. The soils are mainly Alfisols and Entisols that developed over crystalline rocks during the late Tertiary, through a widespread pediplanation [*Ab’Saber*, 1977]. These soils are normally rocky, shallow, and fairly impermeable [*Sartori et al.*, 2005]. The native vegetation, known as Caatinga, includes areas of shrublands of varying densities and areas of seasonally dry forest (composed mainly of deciduous trees 7–15 m in height and sparsely distributed). The main woody plants are legumes (Fabaceae) within the sub-families Caesalpinioideae, Mimosoideae, and Faboideae, as well as a large number of Euphorbiaceae and Cactaceae [*Sampaio et al.*, 1995]. This vegetation has been modified by centuries of slash-and-burn clearing, normally followed by rudimentary agriculture and/or grazing [*Coimbra Filho*, 1996; *Leal et al.*, 2005].

The degraded pasture site is an area of 5 ha that was cleared of its original forest cover in the 1960s by slash and burn. It was plowed and cultivated with cotton until the 1980s, after which it was plowed one more time, sowed with buffelgrass (*Cenchrus ciliaris*), and turned into a pasture. It has been intensely grazed since then by sheep and cattle and now is extremely degraded, with several areas of bare soil interspersed with patches of grass and forbs (mainly Malvaceae). There are clear signs of erosion, such as the formation of rills and gullies on the lower elevations. We found two leaf-cutter ant (*Atta laevigata*) nests in the area, one active and one abandoned. The two mounds were similar in size—approximately 80 m^2 with an annular zone practically bare of vegetation that extended 3–5 m beyond the mound and covered approximately 170 m^2. The active nest mound had no vegetation cover and had clear signs of crusting (Figure III.1); the inactive nest had some islands of vegetation in a matrix of bare soil resembling that of the surrounding pasture. There were approximately 20 open entrances, 10–20 cm in diameter, in the active nest, whereas most of the entrances of the abandoned nest were collapsed and filled with sediment (only 3 remained open and were about 20 cm in diameter).

The Caatinga forest site is an area of approximately 10 ha that has not been cleared since at least 1960 (Figure III.1). Its developed arboreal stratus stands 7–10 m in height and is composed of more than 30 tree species, including Pereiro (*Aspidosperma pyrifolium*), Caatingueira (*Poincianella pyramidalis*), Brauna (*Schinopsis brasiliensis*), Juazeiro (*Ziziphus joazeiro*), and Umbuziro (*Spondias tuberosa*). The shrub layer is developed as well and is dominated by Marmeleiro (*Croton blanchetianus* and *C. sonderianus*). A number of the trees and shrubs are dead, probably owing to a severe drought prior to our study [Santos et al., 2014]. Finally, there is a thin herbaceous layer, composed mostly of Malvacea, spike mosses (*Sellaginella spp*.), and a creeping species of cactus (*Opuntia sp*.), but most of the areas between trees and shrubs are bare soil. We found over forty active nests of the giant queenless ant *Dinoponera quadriceps* in an area of approximately one hectare. The nest mounds' shape was roughly that of convex discs, varying in diameter from 50 cm to 1 m and in height from 15 cm to 30 cm. All the nests were associated with shrubs and trees—constructed on or around the base of the trunk and in many instances surrounding the whole plant (Figure III.1). Each had 1 to 3 entrances measuring 2–4 cm in diameter, and typically one entrance was located close to the plant's trunk. The annular zones of *D. quadriceps* nests were not as evident as those surrounding the nests of *A. laevigata*; for the purposes of our study, we considered this zone to extend 30 cm from the mound's edge. We selected our study nests on the basis of two criteria: (1) the nest mound must have a reasonably flat surface, to facilitate carrying out of the infiltration tests; and (2) the nest must be associated with live, 2- to 4-m-high Marmeleiro shrubs (the plant species most commonly associated with the nests). Of the more than 40 nests found, 22 met these criteria and were used in our study.

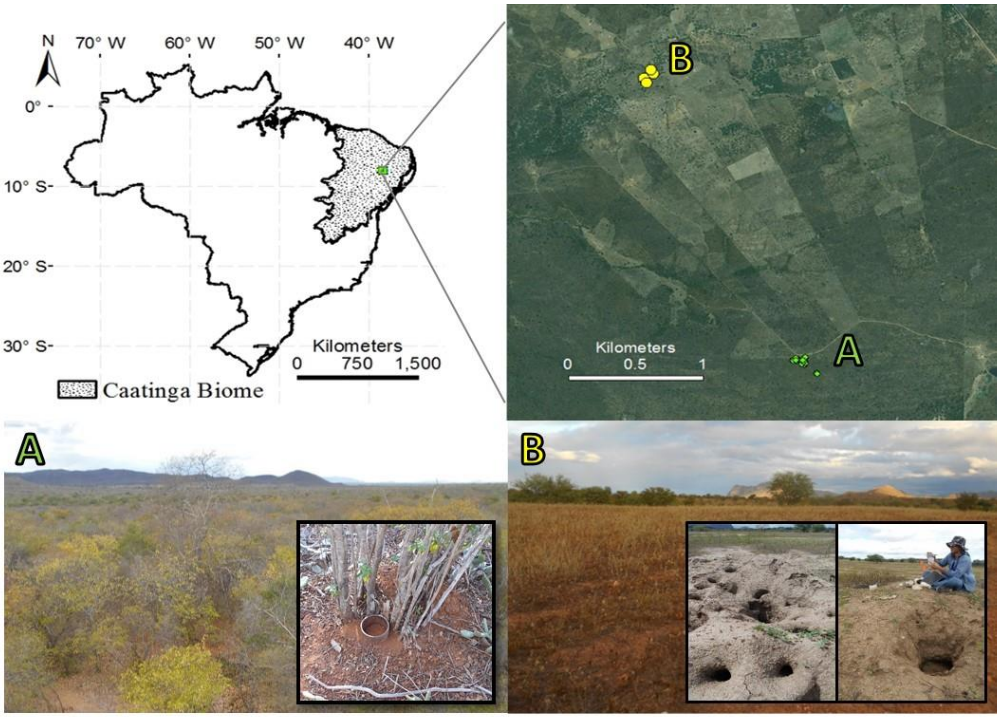

Figure III.1: Map of Brazil, showing the Caatinga region and the location of our two study sites: (A) an old-growth forest; and (B) a degraded pasture. The photo insets show the characteristic cover at each site and examples of the nests of the ant species investigated.

III.4. Methods

III.4.1 Soil measurements

For the bulk density measurements, we carefully collected surface soil (0- to 5-cm) core samples of a constant volume, using metal or PVC cylinders having a diameter of 15 cm. The samples were stored in sealed tin cans and taken to the lab, where they were weighed, dried for 24 hours at 105°C, and then weighed again. We then calculated bulk density (in g/cm^3) by dividing the samples' dry weight by the volume of the cylinder. We also calculated volumetric soil moisture by subtracting the dry weight from the initial weight (but the soil moisture measurements were not used in our analysis because they reflect moisture from precipitation events that occurred during the study, making comparison between nest and non-nest soils impossible).

The infiltration tests consisted of manually pouring fixed volumes of water (0.1 L) into a single ring 150 mm in diameter, inserted into the soil to a depth of approximately 10 mm. At time zero we poured a volume of water and recorded the time it took to infiltrate the soil. Once the first poured volume had completely infiltrated, a new volume was poured. We repeated the procedure, recording the number of volumes and the time elapsed between complete infiltrations, until steady state was achieved (which normally happened after 12 volumes). We calculated the infiltration rates (in mm/h) of each poured volume by dividing the height of the water column by the time elapsed. Finally, we obtained the steady-state infiltration rate (hereafter referred to simply as infiltration) by averaging the last three infiltration rates.

For determinations of soil texture, we used the ABNT method [*Blackburn*, 1975; *Mandel and Sorenson*, 1982; *Eldridge*, 1994; *Lei*, 2000; *Colloff et al.*, 2010][ABNT, 1984]. Loose surface soil samples were collected at several spots within each study site (from mounds, nests annular zone, and non-nest areas). The ABNT method combines sieving and sedimentation techniques to separate soil into three size classes: sand (2 mm to 0.05 mm), silt (0.05 mm to 0.002 mm), and clay (less than 0.002 mm). All texture analyses were carried out at the Soil Physics Lab of the Nuclear Energy Department at Universidade Federal de Pernambuco (UFPE).

III.4.2 Sampling and test design

To obtain data on bulk density, infiltration rates, and soil texture for the pasture site, we took soil samples and carried out infiltration tests in four different contexts: (1) the active *A. laevigata* nest mound, where at 8 points we did infiltration tests and took soil samples for the bulk density analyses, and took four loose soil samples for the texture analyses; (2) the inactive *A. laevigata* mound (same sampling procedure as for the active nest); (3) the annular (border) zones of the two nests, within 3 m of the mounds, where at 4 points (2 around the active and 2 around the inactive nest) we carried out infiltration tests and took soil samples for the bulk density measurements, and sampled 2 points (1 around the active and 1 around the inactive nest) for the soil texture analyses; and (4) the pasture matrix (control soils), at a distance of 40 m from the nests, using the same sampling procedure as for the nests' annular zones (see Figure III.2).

At the Caatinga forest site, we did infiltration tests and took soil samples from 4 contexts, 2 of which were controls (except we did only one control sampling for the soil texture analysis). The first context was nest mounds of *D. quadriceps*; we carried out one infiltration test on the top surface of each of the 22 nests, within 5–20 cm from the shrub trunks, and sampled 11 mounds for analysis of bulk density and soil texture. The second context was the immediate border (annular zone) of the nests, within 10–30 cm from the mound (and 40 cm to 1 m from the shrub trunks); we carried out infiltration tests and took soil samples from the annular zone of 11 nests. To distinguish between the effect of the nests on the study variables and the effect of shrubs, we established a control for each of the study contexts by carrying out parallel sampling and testing close to a Marmeleiro shrub without *D. quadriceps* nests. We selected control shrubs that were 5–10 m away from the nest shrubs and were similar to them in size. The sampling and infiltration test locations within the control zones were at the same distance from the shrubs, and had the same orientation, as those in the nest zones (see Figure III.2). The control sampling for soil texture was done at a location intermediate between the infiltration test locations.

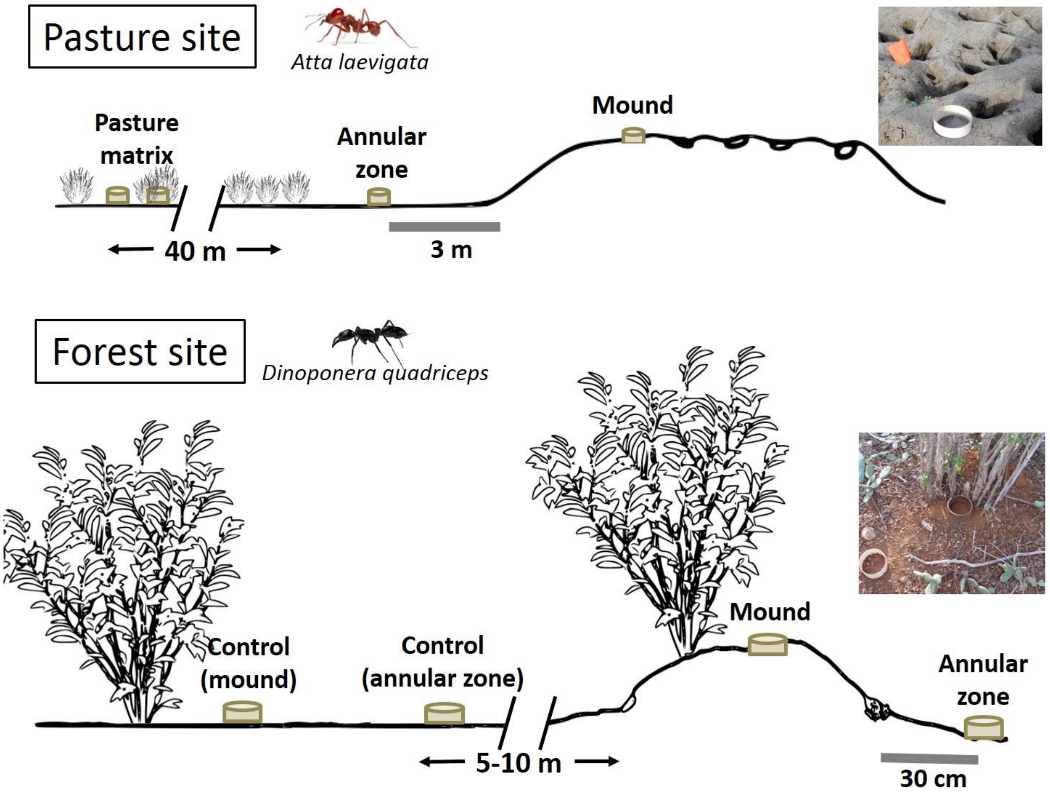

Figure III.2: Representation of sampling and test design at the pasture and forest sites. The gray cylinders represent the infiltration test locations. The pasture representation depicts the active nest, but the same experimental design was used for the abandoned nest. The picture insets show examples of infiltration tests carried at the active mound of *A. laevigata* (at the pasture site) and at mound and annular zone of D.quadriceps nests (at the forest site).

III.4.3 Statistical analysis

We used the Shapiro–Wilk test to determine whether our data were normally distributed, and the Brown–Forsythe test for equality of variance. For parametric data with equal variance we used one-way ANOVA to test for significant differences among means, and for non-parametric data we used the one-way ANOVA on ranks (Kruskal–Wallis) test. We carried out pairwise post hoc comparisons using the Holm–Sidak method as a follow-up to the one-way ANOVA, and Dunn's method as a follow-up to the Kruskal-Wallis test. All analyses employed the software SigmaPlot (Systat Software, San Jose, CA), with a significance level of p= 0.05.

III.5. Results

III.5.1 Forest site

Bulk density values for the Caatinga forest site were normally distributed, and the ANOVA test showed a significant difference between contexts ($p<0.001$). The soils of the mounds and within the annular zones of the *D. quadriceps* nests had the lowest mean bulk densities (1.03 ± 0.09 and 1.04 ± 0.1, respectively), and the Dunn's post hoc test result showed that these bulk density values are significantly lower than those of their respective controls (1.16 ± 0.15 and 1.32 ± 0.12) (Table III.1). The infiltration rates were not normally distributed, and the Kruskal-Wallis test revealed a significant difference ($p=0.019$) between the highest (1002.8 ± 566.9), in the annular zone of the *D. quadriceps* nests, and the lowest (431.9 ± 309.2), in the control zone. Even though infiltration rates showed a high variability, our sampling effort was large enough for the multiple comparison tests to detect a significant difference ($p=0.015$) between the nest annular zones and the control zones (Table III.1 and Figure III.3).

Table III.1: Mean ± STDV values for the three soil variables, the number of samples taken/tests done (*N*) for each context, and the results from the one-way ANOVA and one-way ANOVA on ranks tests. Different italic letters after SDTV values indicate a significant difference ($p<0.05$) as shown by the multiple comparison tests.

Contexts	Bulk density (g/cm^3)	Infiltration (mm/h)	Texture		
			Clay (%)	Silt (%)	Sand (%)
Pasture site					
A. laevigata (active)	1.25 ± 0.1 ***a*** *N=8*	56.3 ± 20.4 ***a,b*** *N=8*	16.5 ± 1.2 ***a*** *N=4*	28.2 ± 0.7 ***a*** *N=4*	55.4 ± 1.5 ***a,b*** *N=4*
A. laevigata (inactive)	1.37 ± 0.1 ***a,b*** *N=8*	120.8 ± 62.7 ***a*** *N=8*	12.5 ± 4.8 ***a*** *N=4*	25.7 ± 2.2 ***a*** *N=4*	61.8 ± 57 ***b*** *N=4*
A. laevigata (annular zone)	1.44 ± 0.1 ***b*** *N=4*	13.4 ± 3.7 ***b*** *N=4*	14.8 ± 1.0 ***a*** *N=2*	40.0 ± 6.8 ***a*** *N=2*	45.2 ± 7.8 ***a,b*** *N=2*
Pasture matrix	1.30 ± 0.1 ***a,b*** *N=4*	37.8 ± 16.2 ***a,b*** *N=4*	20.2 ± 3.4 ***a*** *N=2*	44.6 ± 10 ***a*** *N=2*	35.2 ± 13.2 ***a*** *N=2*
ANOVA	F=3.4,p=0.038	H=17.4,p<0.001	H=5.1,p=0.16	H=8.1,p=0.044	H=9.4,p=0.025
Forest site					
D.quadriceps (nest)	1.03 ± 0.1 ***a*** *N=12*	629.1 ± 365.9 ***a,b*** *N=22*	16.9 ± 2.9 ***a*** *N=11*	27.7 ± 2.5 ***a*** *N=11*	55.4 ± 2.3 ***a*** *N=11*
D.quadriceps (annular zone)	1.04 ± 0.1 ***a*** *N=11*	1002.8 ± 566.9 ***a*** *N=11*	12.8 ± 3.5 ***b*** *N=11*	30.3 ± 1.9 ***a*** *N=11*	56.9 ± 4.8 ***a*** *N=11*
Control (nest)	1.16 ± 0.2 ***b*** *N=11*	530.3 ± 282.1 ***a,b*** *N=22*	9.3 ± 3.3 ***b*** *N=11*	29.1 ± 2.3 ***a*** *N=11*	61.7 ± 5.2 ***b*** *N=11*
Control (annular zone)	1.32 ± 0.1 ***c*** *N=11*	431.9 ± 309.2 ***b*** *N=11*			
ANOVA	F=15.3,p<0.001	H=9.9,p<0.019	F=15.1,p<0.001	F=3.7,p=0.038	H=9.6,p=0.008

F = results from one-way ANOVA tests
H = results from one-way ANOVA on ranks (Kruskal-Wallis) tests

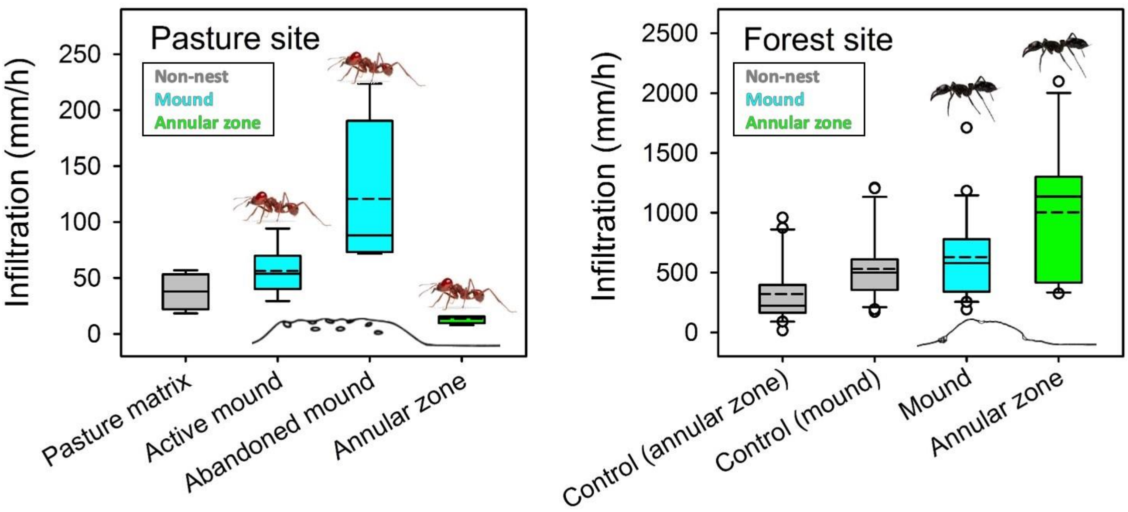

Figure III.3: Box plots showing the median (solid line), the mean (dashed line), the outliers (circles), and the 5th, 25th, 75th, and 95th percentiles of the infiltration values obtained from our two study sites.

The soil texture analyses showed that all the soils of the forest site were sandy loams. However, the *D. quadriceps* mounds and annular zones contained a higher proportion of fine-textured particles. The soils having the highest clay content were those of the mounds (16.93 ± 2.87), followed those of the annular zone (12.78 ± 3.55); the control zones had the lowest (9.28 ± 3.34). The sand content in the non-nest forest soils was higher than that in the soils of the mounds and annular zones. Silt content, although slightly higher in the annular zones, was not significantly so (see Table III.1 and Figure III.4).

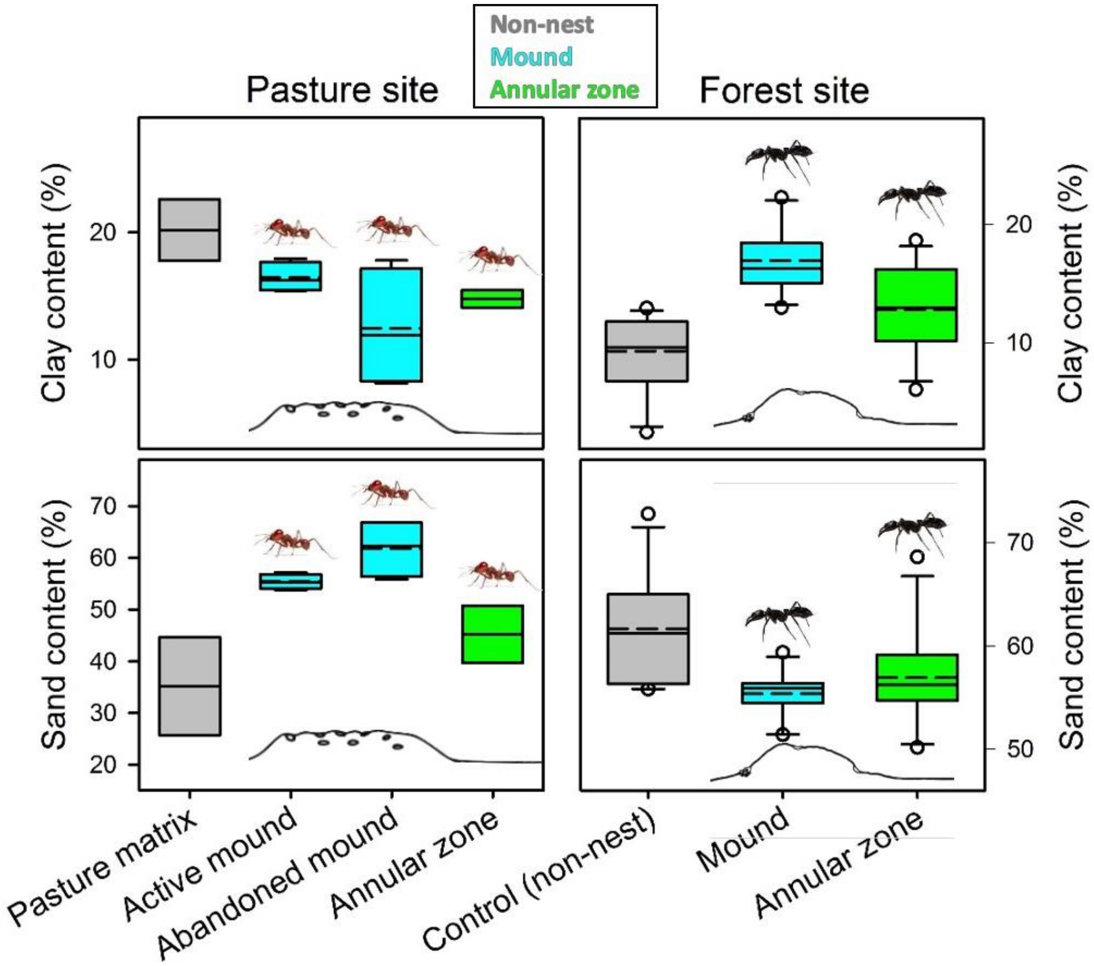

Figure III.4: Box plots showing the median (solid line), the mean (dashed line), the outliers (circles) and the 5th, 25th, 75th, and 95th percentiles of the clay and sand contents of nest soils (mounds and annular zones) and of non-nest soils. To better show within-site variations, we use a different scale for each component, but all scales are spaced by increments of 10.

III.5.2 Pasture site

Bulk density was the only normally distributed variable at the pasture site, and values differed significantly different among the four contexts (p=0.038). In contrast to the forest site, here the annular zones of the A. laevigata nests had the highest mean bulk density (1.44 ± 0.12), and the multiple comparisons showed that it was significantly higher than that of the active nest mound (1.25 ± 0.09; p=0.049) (Table III.1). With respect to infiltration rates, the Kruskal-Wallis test showed a significant difference (p<0.001) among the four contexts. The highest infiltration, found for the abandoned A. laevigata nest (120.8 ± 62.7), was approximately three times higher than the value for the pasture matrix (37.8 ± 16.2). The lowest infiltration was found in the annular zones (13.4 ± 3.7). There was a high variability in infiltration values and the only significant difference between contexts, as shown by the Dunn's post hoc test, was between the abandoned mound and the annular zones (p<0.001) (Table III.1 and Figure III.3). Finally, soil texture within the pasture site varied among the four contexts: the soils of the mounds were sandy, whereas those of the nests annular zones and of the pasture matrix were sandy loam. The pasture matrix soils showed a higher percentage of clay than those of the abandoned mound (20% vs. 12%), but this was not a significant difference and was probably due to our small number of samples. With respect to silt and sand content, however, the Kruskal-Wallis test showed a significant difference (p=0.044 for silt and p=0.025 for sand) among the four contexts. In general, silt content was lower and sand content was higher in both the nest mounds than in the annular zones or in the pasture matrix. On the other hand, the multiple comparison tests showed a significant difference (p=0.049) only for sand content between the inactive nest mound and the pasture matrix, the latter being significantly lower (Table III.1 and Figure III.4).

III.6. Discussion

Our results show that both the ant species investigated in our study significantly modified the soil, affecting its physical properties and the infiltration patterns on and around their nests. This is the first study to directly quantify such soil modifications by ants in the Brazilian Caatinga, and it provides further evidence for the well-documented role of ants as important soil engineers in semiarid landscapes [*Jonkman*, 1978; *Briese*, 1982; *Rissing*, 1988; *de Bruyn and Conacher*, 1990; *Eldridge*, 1993, 1994; *Crist and Wiens*, 1996; *Folgarait*, 1998; *Wilby et al.*, 2001; *Cammeraat et al.*, 2002; *Cammeraat and Risch*, 2008]. Of particular interest, our findings show that the two ant species affect soils and plant water availability in contrasting ways.

III.6.1 Dinoponera quadriceps in the forest site

We found that the nest-building activity of the ant *D. quadriceps* reduced bulk density and increased infiltration and clay content in and around their mounds, which corroborates our initial hypothesis that this ant would improve the physical properties of the soil. The reducing of bulk density is probably the result of increased macro- and microporosity [*Blackburn*, 1975; *Mandel and Sorenson*, 1982; *Eldridge*, 1994; *Lei*, 2000; *Colloff et al.*, 2010]. Increased microporosity generally means higher organic matter content, which binds soil particles and promotes soil aggregation. Although we did not carry out chemical analyses on our soils, other studies have reported higher organic matter content in ant nests [*Whitford*, 1988; *Dean and Yeaton*, 1992; *Frouz and Jilková*, 2008]. Not only does soil organic matter decrease bulk density, it also improves infiltration [*Blackburn*, 1975; *Franzluebbers*, 2002]. *Baxter and Hole* (1967) found considerably lower bulk densities related to high organic matter content in nests of *Formica cinerea montana*, in prairie soils of Wisconsin. Other studies, such as the one performed by *Lei* (2000) in semiarid Nevada, attributed the lower bulk densities of *Pogonomyrmex rugosus* nests to higher macroporosity. Macropore formation can be a direct effect of the ants' digging of tunnels and channels, but it could also be due to increased root growth in and around the nests [*Haines*, 1975; *Moutinho et al.*, 2003].

We found that infiltration rates varied greatly, within both nest and non-nest soils. This can be expected, since infiltration is a complex process, controlled by factors that are highly variable in space and time [*Bergkamp*, 1998; *Mayor et al.*, 2009]. Although mean infiltration for the mounds was higher than for the controls, this difference was not significant. Infiltration tests for both were done very close to shrubs (5–20 cm), a zone where root density is normally high, and the roots' effect on infiltration might have overlapped with the direct effect of the nest-building. However, the nest annular zones in the forest site showed the highest infiltration rates, and these were significantly higher—approximately 2.5 times—than those of their respective control soils. In Australia, *Eldridge* (1994) reported 10 times higher infiltration rates in the annular zones of termites' nests than in their mounds. This difference was attributed to the presence of a thick impermeable layer covering the mounds and to a high macroporosity in the annular zone, enabling the latter to act as a sink for water and nutrients. In our study, the soils in the annular zones of *D. quadriceps* nests appeared to be less densely packed than those of the mounds (personal observation), which could explain the higher infiltration rates. Because Caatinga plants are adapted to shallow soils and to seasonal availability of water, their root systems tend to be shallow and spreading [*Pinheiro et al.*, 2013]— and therefore these plants would likely benefit from the presence of *D. quadriceps* nests, whose annular zones could act as runoff sinks during high-intensity rainfall events.

The results of our soil particle size analysis show that these ants can also modify soil texture significantly. As we expected, clay content was higher and sand content was lower in mounds and annular zone soils than in non-nest soils. This is the most common texture modification by ants in semiarid regions, where clay tends to accumulate in the lower horizons and ants nonselectively bring this finer-textured soil to the surface when building their nests [*Cammeraat and Risch*, 2008]. In another Caatinga region of Brazil, [*Leal et al.*, 2007] analyzed combined soil samples from mounds of multiple ant species, including *D. quadriceps*, and found significantly higher clay content in these soils than in non-nest soils. Finer textured soils, when associated with higher infiltration rates, can improve the retention of water and nutrients and therefore have a positive effect on water availability to plants [*D'Odorico et al.*, 2007].

III.6.2 Atta laevigata in the pasture site

Our results show that the nest-building activity of the leaf-cutter ant *A. laevigata* significantly altered the soils of degraded pasture site. Bulk density was lowest at the active mound and lowest at the annular zones. Infiltration for the abandoned mound was found to be threefold higher than for the pasture matrix, but the annular zones of the both nests had not only three times lower infiltration rates but also significantly higher bulk densities than the pasture matrix. The texture of the abandoned mound soils was sandy, having almost twice the sand content and half the silt content of the sandy loam soils of the pasture matrix.

Other investigations of soil modifications by leaf-cutter ants (*Atta spp.* and *Acromyrmex spp.*) have found evidence of both positive and negative impacts on soil properties. As an example of positive effects, *Moutinho et al.* (2003) found lower resistance to penetration, lower bulk density, and higher root biomass in mounds of *Atta sexdens* in the Brazilian Amazon. Conversely, *Bieber et al.* (2011) found that the plant removal activity of *Atta cephalotes* reduced nutrient availability and compacted the soil on their nests, and that these effects can last for decades after nest abandonment.

Like most Atta species, *A. laevigata* constantly clear their mounds and annular zones of litter and plants [*Corrêa et al.*, 2010; *Meyer et al.*, 2011; *Leal et al.*, 2014a], and contrary to some other leaf-cutter ants, they store their waste in deep chambers instead of disposing of it at the surface [*Haines*, 1975; *Moreira et al.*, 2004]. These activities reduce root density and organic matter, leading to lower macro- and microporosity, which could explain the high bulk density and low infiltration in the annular zones. In addition, vegetation removal by ants constantly exposes the soil surface to the direct impacts of sunlight and rainfall, increasing its susceptibility to crusting and compaction. However, bioturbation might lessen the effects that vegetation removal has on soil compaction, and could explain the lower bulk density and higher infiltration for the mound (the latter could also be related to the coarser texture of the mound soils).

Since in most semiarid regions the soils are weathered and characterized by an accumulation of clays in the deeper portions of the soil profile, the coarser texture of *A.*

laevigata mounds was an unexpected result. It contrasts with our findings for nests of *D. quadriceps* at the forest site, and also with the results reported by most authors, as shown by *Cammeraat and Risch* (2008) in their review paper on soil modification by ants in semiarid regions. One of the few findings of coarser texture in ant nests was presented by *Nkem et al.* (2000) regarding nests of the ant *Iridomyrmex greensladei* in Australian Vertisols. They attribute this finding to the higher erodibility of the clay particles in these soils. They also found few plants growing on the nests and little organic matter in the soils, both of which reduce the ability of soil particles to bind and increase the dispersion of fine particles. As noted above, a similar pattern was found in our study, and these factors could account for the coarser texture of *A. laevigata* mounds. However, we cannot exclude the possibility that deeper layers of our pasture soils may have been richer in sand, which could also explain the different textures found among the four contexts we studied. Regardless of the mechanism, these texture changes could have a negative effect on plant establishment. Since sandy soils tend to retain less water than finer-textured soils, the texture changes on *A. laevigata* mounds could possibly overshadow the benefits of improved infiltration.

III.6.3 Ecological implications

In a recent study, *Bonachela et al.* (2015) show that the presence of termite nests in African savannas can increase the resilience of those landscapes to climate change and also reduce their threshold of recovery from a desertified state. Their results not only show the importance of termites for those landscapes but also point to the key role played by insects as ecosystem engineers in semiarid environments as a whole. On the basis of our findings, we argue that the ant *D. quadriceps* can enhance water infiltration and moisture availability to plants, which suggests that these ants can both enhance primary productivity and increase the survival of plants associated with them. Although nest density is relatively small (approximately 40 nests/ha), the rate of abandonment and construction can be high, and the effects on soil could well be cumulative [*Baxter and Hole*, 1967]. For these reasons, we suggest that the presence of *D. quadriceps* ants in Caatinga forests favors the stability of these environments and can help combat the forces tending to undesirable, degraded states.

Nests of *Atta spp*. are commonly found in higher densities in disturbed ecosystems, such as pastures [*Fowler*, 1983], tree plantations [*Jaffe and Vilela*, 1989], and forest borders [*Wirth et al.*, 2007]. In such environments, they can have a negative impact on plant communities, as primary consumers. In a study on abandoned pastures in the Amazon, [*Nepstad et al.*, 1996] found that *A. sexdens* preferentially clipped seedlings over grasses and shrubs, thereby retarding forest recovery. In another study, *Silva et al.* (2009) showed that the number of *A. cephalotes* nests significantly decreases as the age of secondary stands of Atlantic rainforest increases. It has been argued that leaf-cutter ants not only benefit from early successional stages but also promote their persistence—either by preferentially dispersing seeds of pioneer species or by modifying the physical environment in a way that can favor such species [*Meyer et al.*, 2009; *Leal et al.*, 2014a]. On the basis of our findings, we argue that the leaf-cutter ant *A. laevigata* might also decelerate forest recovery on degraded pastures in the Caatinga, by compacting the soil and reducing infiltration around their nests, and also by increasing the sand content of mound soils—all of which can negatively affect water availability to plants. Further, bioturbation by *A. laevigata*, combined with their removal of vegetation and low infiltration rates, could result in greater overall erosion rates, leading to further degradation.

III.7. Summary and conclusions

Overall, our findings show that in Caatinga forests, the giant queenless ant *D. quadriceps* reduced soil bulk density, improved infiltration, and altered soil texture on and around their nests. Such modifications can increase water availability to plants growing in these soils, which not only would promote higher primary productivity but also could increase the long-term resilience of these forests, favoring the stability of highly vegetated states over undesirable, degraded states. Second, we found that in a degraded Caatinga pasture infiltration was higher for an abandoned mound of the leaf-cutter ant *Atta laevigata*, but both infiltration and bulk density were lower in the annular zone of both active and abandoned mounds. While one might conclude that the modifications to the annular zone soils would hinder vegetation growth (even after colony death), one cannot conclude that the increased infiltration rates in the abandoned mound would have the opposite effect of promoting vegetation growth; because mound soils had twice as much sand as those of the pasture matrix, the positive effects of increased infiltration would likely be offset by negative effects (such as lower moisture retention).

The two ant species investigated in this study are known to differ with respect to sensitivity to disturbances, such as grazing and timber harvesting. On the basis of our study findings, we suggest that further, anthropogenic disturbances will interact negatively with the effects of *D. quadriceps* and positively with the effects of *A. laevigata*—the first accelerating forest degradation and the second slowing down recovery of degraded land. To test these hypothesis, future studies should (1) evaluate the direct effect of the nests of these ants on plants growing on and around them, and (2) examine the ways in which these ants influence large-scale vegetation patterns. Finally, this hypothesis could also be tested in studies of other ant species that modify soil hydraulic properties, and in other semiarid regions.

CHAPTER IV

SUMMARY

Our first study shows that when degraded land is abandoned and Caatinga forests regrows, there is a gradual increase of hydraulic conductivity, and infiltrability might take 55 years or more to recover completely. Such soil recovery could be directly related to vegetation regrowth – due to an accumulation of organic material and increase in root densities on older forests. It could be also due to the increasing activity of soil engineers, such as ant*s*, which can improve soil structure and have positive effect on infiltration. We show in our second study that the ant *D. quadriceps*, in Caatinga forests, improved soil hydraulic properties, which benefits vegetation survival and forest resilience, while the ant *A. laevigata* had mostly negative effects on soil properties, and could slow down the recovery of degraded lands.

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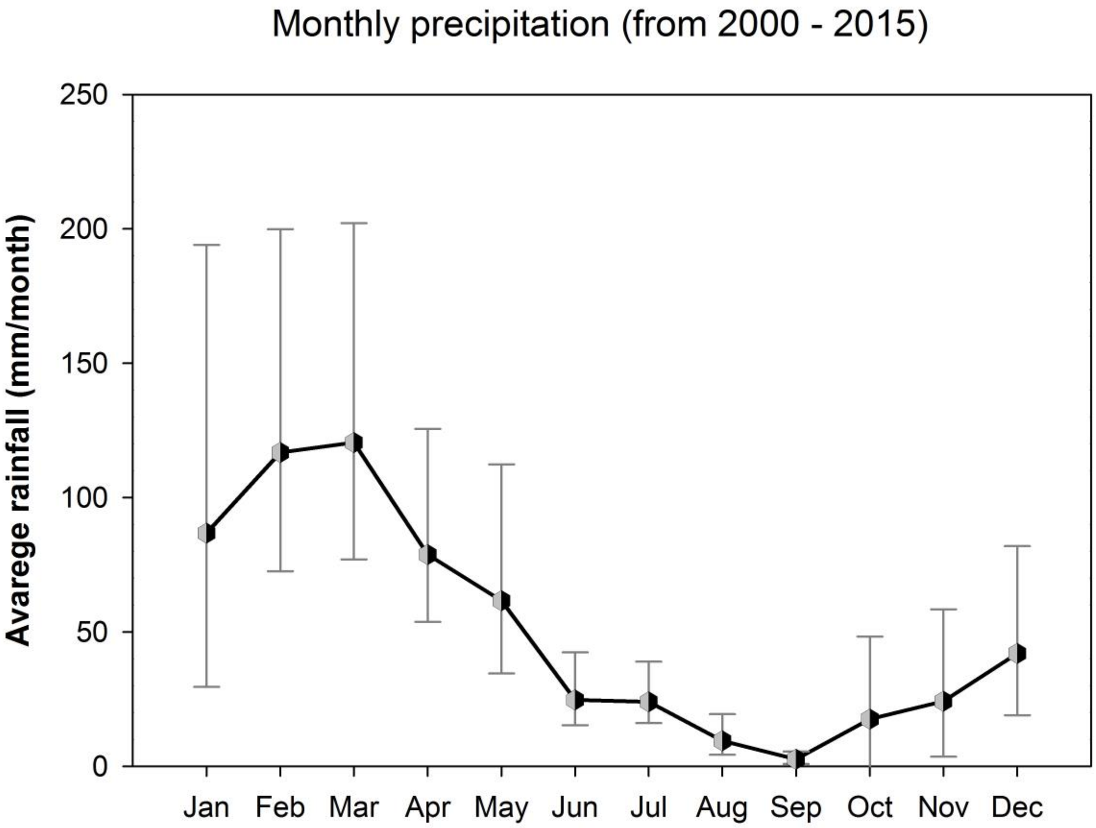
APPENDIX 1



Mean annual rainfall distribution at the study site. We calculated monthly averages from daily rainfall data, obtained from five rain gauges in Serra Talhada-PE, for the period between January 2000 and December 2014. Data available at: http://www.apac.pe.gov.br/meteorologia/

APPENDIX 2

Selected studies that evaluated *Ksat* or infiltrability of soils under different cover types, including at least a degraded site (pasture or abandoned field), a secondary forest (natural regrowth forest or fallow land), and a primary (or older secondary) forest.

Study authors	Study location	Forest type	Precipitation (mm)	Soil type	Physical property/depth/ method	Sites	Age of recovery (years)	Mean *Ksat* / infiltrability (mm h-^{1})
[*Deuchars et al.*, 1999]	Costa Rica	Tropical rainforest	–	Andisols	Infiltrability/ surface/single ring infiltrometer	Older forest	–	2462
						20-yr secondary forest	20	946
						15-yr secondary forest	15	493
						Pasture	0	29
[*Ziegler et al.*, 2004]	Vietnam	Tropical monsoonal	1800	Silty sand/ Kandiudults (USDA)	*Ksat*/surface/ disc permeameter	Older forest	>15	91
						Intermediate secondary forest	7–17	65
						Young secondary forest	2–8	41
						Grassland	2–16	90
						Abandoned field	0-3	27
[*de Moraes et al.*, 2006]	Brazil	Tropical rainforest	1760	Haplustox (USDA)	*Ksat*/5-15 cm/ guelph permeameter	Older forest	–	230*
						Secondary forest	12	14*
						Pasture	0	4*
[*Zimmermann et al.*, 2006]	Brazil	Tropical rainforest	2300	Kandiudults (USDA)	*Ksat*/12.5 cm/ amoozemeter	Primary forest	–	206
						Secondary forest	15–17	201
						Banana/agroforestry	20	227
						Pasture	0	26
[*Zimmermann and Elsenbeer*, 2008]	Ecuador	Lower montane rainforest	2273	Silty/ Inceptisol and Histosols (USDA)	*Ksat*/12.5 cm/ amoozemeter	Older forest	–	738
						Old fallow land	>10	82
						Young fallow land	2	7
						Pasture	0	14
[*Hassler et al.*, 2011]	Panama	Tropical rainforest	2300	Silty clay	*Ksat*/surface/ laboratory constant head	Older forest	100	349
						Intermediate secondary forest	12–15	225
						Younger secondary forest	5–8	113
						Pasture	0	80

APPENDIX 2 Continued

[*Archer et al.*, 2015]	Scotland	Temperate forest	1440	Humic Podzols (USDA)	*Ksat*/4–15 cm/ constant head permeameter	Ancient forest	>1000	224*
						48-yr secondary forest	48	33.8*
						6-yr secondary forest	6	2.3*
						Pasture	0	7.1*

* median values