Earthworms as key actors of self organised systems in soils

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Abstract: Earthworms have co evolved for million years with soil organisms and plants. Adaptive strategies selected in this process allow them to derive significant amounts of energy from decomposing organic matter. This is assumed to be the result of a mutualist digestion system, in association with free soil micro organisms during the gut transit. Part of the energy captured is used in the formation of biogenic structures, macroaggregates (casts), galleries and other types of voids, in accidental or phenotype ecosystem engineering processes. The accumulation of these structures in still poorly described spatial arrays, creates a specific environment that is inhabited by specific communities of micro-organisms and small invertebrates. All these structures, the earthworms of a given population and all the other organisms living in the habitats thus created form the drilospheres, the functional domain of earthworms. This functional domains has all the attributes of self organised systems as defined by Perry (1995). They are the seat of intense biological interactions within physical boundaries that modify constraints outside, with positive feedbacks on the drilospheres and its inhabitants. This chapter describes the organisation and basic function of the drilospheres and considers options for their management in man made ecosystems.

Keywords: earthworm, self organised systems, drilosphere, agroecosystems.

1. Introduction

Earthworms are undoubtedly the most spectacular ecosystem engineers in all soils where neither prolonged drought nor toxic conditions do occur. They are ancient organisms that have inhabited soils for very long periods of time; although the absence of fossiles does not allow a precise dating, we know that they were amongst the first aquatic organisms to colonize terrestrial environments. They can be found from several meters deep in soils up to 20-30m up in some tree canopies. Although they have rarely been acknowledged by traditional cultures the major role they play in soils, scientists has long recognised their importance as "intestines of the soil" (Aristoteles) or key actors of the "formation of vegetable mould" (Darwin, 1881).

During this long evolutionary time, they have developed adaptive strategies in three functional groups and over 10000 species, from tropical to boreal forests (Bouché, 1977). While small brightly pigmented epigeic species specialise in the natural composting of organic debris deposited at the soil surface, large anecics with antero dorsal dark pigmentation inhabit semi permanent burrows in which they shelter most of the time. Anecics get out during wet nights to collect litter that they accumulate close to the burrow entrance as "middens" or drag inside prior to ingesting it admixed with some mineral soil (Subler and Kirsch, 1998; Bohlen et al., 2002). Endogeics, the third large functional group found in earthworms, are unpigmented and seldom get out of the soil. With geophagous feeding habits, they litteraly eat their way through the soil. Some of them, the "compacting" endogeics, transform non aggregated soil particles into solid macroaggregated structures while others, have an opposite "decompacting" effect (Blanchart et al., 1999).

Earthworms are physical ecosystem engineers according to the definition given by Jones et al (1994): "organisms that change the environment of others through their mechanical activities". They are mostly extended phenotype engineers that build structures that maintain optimal conditions for their growth (Jouquet et al., 2006). Some endogeics, however, are rather considered as accidental engineers since the building of structures that they operate does not seem to have immediate positive feedback effects on their growth.

Earthworm effect on soils may be summarised in a few amazing statistics: several hundreds of soil annually transited through their guts in suitable environments (for example, 800 to 1300

Mg ha^{-1} in moist savannahs of Ivory Coast, Lavelle, 1978); surface casts deposits from a few Mg ha^{-1} yr^{-1} to 20-50 Mg (Lavelle and Spain, 2006); the potential to ingest and burry all the leaf litter annually deposited in some forests. Such huge mechanical activities have profound effects on the soil environment and the organisms that live in it. Earthworms also develop chemical and biological engineering effects according to definitions given by Lavelle et al. (2006): they can significantly alter the biology of other species by producing specific energetic or hormone like chemicals or by influencing their dispersal or germination patterns.

This chapter describes the drilosphere defined as an earthworm population, the sum of biogenic structures that they build in the soil and the communities of smaller organisms that inhabit this environment (Lavelle and Spain, 2006). Drilospheres have all the characteristics of Self Organising Systems according to definitions given by Perry (1995)(Lavelle et al., 2006). We first address the interactions with microorganisms and other inhabitants of the drilosphere that allow earthworms to derive energy from decomposing organic matter. We then describe the physical domains created in soils by the accumulation and spatial array of biogenic structures (earthworm casts, galleries, voids and middens), consider the effects of this system on soil environment and the possible positive feedbacks provided in return. We finally discuss the opportunities offered by a proper management of the drilospheres to sustain the provision of soil ecosystem services.

II. Adaptation of earthworms and other organisms to soil constraints: the power of mutualism

Soils are highly constraining environments (Lavelle and Spain, 2006). Movements are restricted since only 50-60%, at best, of the total volume is comprised by pores. This porous space is made of units with greatly diverse sizes, typically in the range of a few mm to microns or less. Their shapes are also greatly diverse and connection is rarely achieved in a way that would allow easy and free movements for relatively large organisms. This porosity is either filled with air or water, in largely variable proportions according to climatic conditions.

Soil organisms have adapted their sizes and respiratory habits to these spatial constraints . Small organisms of the microflora and microfauna, (< 0.2mm on average) live in the water filled soil porosity. They mostly comprise bacteria, fungi, protists and nematodes. Their ability to move is limited and they have developed highly efficient mechanisms to resist dry periods. Invertebrates of the mesofauna (0.2 to 2mm on average) live in the air filled portion of soil porosity and litter layers. Earthworms and a few other groups of larger soil invertebrate ecosystem engineers have developed the ability to dig the soil. This allows them to circulate freely in soils by digging burrows and galleries and creating the voids and ways they need for their sheltering, feeding and reproduction activities.

The other great restriction in soil environments is the generally poor quality of feeding resources. Leaf and root litter and products of their successive stages of decomposition are the main food resource. It is often deficient in nutrients creating important stoichiometric restrictions to their use (Swift et al., 1979: Sterner and Elser, 2002). Blockage of nutrients in complex organic forms and the mere dilution of organic matter in the mineral soil matrix, are further obstacles that require highly specific digestion systems for all soil organisms (Lavelle and Spain, 2006). Bacteria and fungi are the only organisms in soil that can digest any natural organic substrate present in soils. They usually operate in succession processes with different groups involved, generalists or specialists that progressively digest even the most complex organic molecules and make their metabolites available to the rest of the soil organisms. A key component of microbial communities are the white rot fungi, a group of Basidiomycete that has the rare and essential ability to digest polyphenol protein complexes that immobilise over 80% of N contained in decomposing leaves and roots (Toutain, 1987).

Invertebrates seem to have rather limited proper digestive capabilities. A few studies demonstrate that part of the digestive enzymes present in their guts have been actually produced by micro organisms. This is the case for earthworms that have developed mutualist digestion systems in association with free soil bacteria, as hypothesised by Lavelle et al. (1995). When geophagous earthworms ingest soil, they add in their anterior gut an equivalent volume of water plus 5 to 40% of the soil dry weight as intestinal mucus, a highly energetic product of the anterior gut wall (Martin et al., 1987; Barois et al., 1999). This mixture is energetically mixed in the gizzard which frees bacteria from soil micropores where they would be in dormant stages and gets them to full activity and enzymatic capacities within a remarkably short period of time. When the soil gets into the medium part of the gut, mucus that has not been metabolised by bacteria is removed and bacteria start to digest soil organic matter for their own benefit and that of the earthworm. Experiments have actually shown a great increase in microbial activity in the posterior gut of earthworms. Some of the enzymes found in the gut content are not produced by isolated cultures of gut tissues which supports the hypothesis of a microbial origin (Barois and Lavelle, 1986; Lattaud *et al*., 1999; Trigo *et al*., 1999).

This digestion system allows earthworms to make use of very poor soil resources. An extreme case is represented by the endogeic african earthworm *Millsonia ghanensis* that feeds on soil from the deep (20-40cm depth) horizons of sandy soils in savannahs of Central Ivory Coast. This soil only contains 0.6% organic matter on average and it is known that organic matter at such depth in soil is significantly humified and therefore little digestible. The most common species in this savannah, *Reginaldia omodeoi*[1] Czusdi is a rather large animal, 15 to 20 cm in length at the adult stage, that may daily ingest up to ten times its proper weight in soil at maturity, and up to 30 times for recently born juveniles. Overall, worms of this species ingest 500 to 800 Mg soil ha-1 yr-1, with a maximum during the rainy seasons and mostly in the upper 10 cm of soil. Only a few Mg are deposited at the soil surface, the rest being deposited in the galleries that the worms just opened as they moved forward in search of the small organic rich aggregates that they ingest. The energy cost of this behaviour however is enormous. For example, 95% of the energy assimilated by *R. omodeoi* Czusdi, is spent in respiratory activities required by the daily ingestion of 10-25 times their own weight of soil and its further transformation into compact casts (Lavelle, 1978).

Only a long co evolution with soil micro organisms in favourable conditions of moisture and temperature has allowed these tropical earthworms to feed on such poor resources. Comparison of feeding regimes of earthworms across a latitudinal gradient from Western Africa to Northern Europe showed that as soon as temperature decreases, earthworms tend to feed on increasingly richer substrates (Lavelle, 1983), presumably as the mutualist interaction with microflora is less efficient at lower temperatures (Lavelle et al., 1995) which forces them to use better quality material. While endogeic geophages, that live on poor soil organic matter, dominate communities in the wet tropics, anecics that feed on a mixture of soil and litter are the dominant group in grasslands of France or England and epigeics and the small polyhumic endogeics, that feed on leaf litter and soil organic accumulations respectively, comprise most of the communities in Scandinavia and Iceland.

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[1] Formerly known as *Millsonia anomala* Omodeoi

III. The drilosphere as a Self organising system

Earthworms and other major soil ecosystem engineers create physical domains in soils that have all the characteristics of Self Organised Systems as defined by Perry, 1995: : based on strong and rather specific interactions within physical boundaries, these systems change the constraints of their environment with positive feedbacks on their own living conditions (Lavelle et al., 2006) (Fig. 1).

Soil constraints have indeed pushed soil organisms to develop intense interactions along evolutionary time, mostly of a mutualistic type. These interactions have developed within the physical boundaries of the physical domains of the rhizosphere of roots, drilosphere of earthworms and termitosphere of termites and a few other such domains (Lavelle, 2002) that have more or less recognizable limits. These systems in turn have feed back effects on external constraints. Roots and earthworms, for example, significant affect soil structure with known impacts on water availability and their own ability to further penetrate this environment. These systems, finally, are in a metastable state of equilibrium: biodiversity inside these systems, the diversity and intensity of interactions that they develop, the structures that they create in soils are all characteristics linked with the function of the systems that would soon disappear eliminated the ecosystem engineer(s) that maintain their activity.

A large amount of energy is channelled into the drilosphere through the digestion of soil organic matter, in mutualist association with the ingested microflora. Part of this energy is actually invested in the building of solid aggregates and voids that allow soils to provide ecosystem services at a high rate.

We shall first focus on the description of these individual structures before considering their assemblage in soils and their emerging effects on soil properties.

A. Biogenic structures

Earthworm casts may have diverse shapes and sizes. A first classification separates granular casts formed from an accumulation of small, fragile and fine-textured pellets from globular casts comprised of coalescent round or flattened units (Lee, 1985). While soil texture has a great influence over the final shape and structure of casts, some anatomic features of the posterior most part of the earthworm gut also influence the process. Some earthworms produce a continous flow of small independent pellets that rarely stick together to form a globular mass. Others expel at discrete intervals rather large amounts of wet and plastic digested soil material that tend to form units of up to 1 cm depending on the species. These units when wet easily stick to others forming sometimes large and solid structures once they have been dried at least once (Shipitalo and Protz, 1988; Blanchart et al., 1993). When deposited and regularly accumulated at the soil surface globular casts may thus form spectacular tower-shape structures up to 10-15 cm high and several hundred g dry mass (Fig.).

While granular casts tend to form fragile structures easily whipped off by rain when deposited at the soil surface, the other category may persist for very long periods of time, especially when they have been deposited in the soil and stabilised by one or two drying/rewetting cycles (Shipitalo and Protz, 1988; Marinissen and Dexter, 1990). In the African savannah of, Lamto, Blanchart et al (1997) thus showed that large casts that comprise the macro aggregated structure of these soils in the upper 15 cm can still be found almost intact, 32 months after removal of earthworms by a 48h artificial flooding. Dry globular casts deposited at the soil surface can persist for periods of a few days to several weeks or months, depending on their own constitution, the degree of protection by plant cover, and the intensity of rain and other climatic events (alternance of dry and moist periods; freezing/thawing) (Decaëns, 2000 ; Le Bayon, 1999). They may also be crushed by large Mammals or broken by invertebrates that use them as shelter and/or food (Decaëns, 2000). Granular casts are much more fragile and usually do not persist beyond the next rainfall event.

When fresh, casts still are the seat of intense microbial activities and ammonium and other nutrients are found at relatively high concentrations (Lavelle et al., 1992; Blair et al., 1995). In fresh casts of the pantropical endogeic species *Pontoscolex corethrurus*, for example, ammonium concentrations in fresh casts varies from 67 to 1052 µg g^{-1}soil which represents on average 4 to 10% of the ingested organic N (Lavelle and Spain, 2006). Assimilable P concentration is also multiplied by a factor of 2 to 8 in the same casts (Lopez-Hernandez et al., 1993; Chapuis-Lardy et al., 1996). Once dried, casts become a harsh environment for micro organisms. Porosity is often extremely reduced. Casts of *R. omodeoi* for example, have a bulk density of 2.3 as compared to 1.4 on average in soil and a superficial 20µm pellicle rich in clay minerals and polysaccharides seems to isolate the cast environment from the outside and limit water and air penetration (Blanchart et al., 1993). Laboratory incubations have shown that organic matter mineralization was reduced to almost zero in these structures after 30 days while a control non-aggregated soil continued to loose C (Martin, 1991). The quality of organic matter contained in earthworm casts is significantly different from the one in the non digested control soil. Spectral signatures (Near Infrared Reflectance Spectrometry) allow separating them from aggregates produced by other biological or physical processes (Velasquez et al., 2006).

In soils favourable to earthworm activities, subterranean casts tend to accumulate as stable macro aggregates forming >40% of the total soil volume (Blanchart et al., 1999). Persistence and dynamics in time of these biogenic structures are still poorly documented. Highly unstable fresh globular casts can be easily dispersed or included into larger structures made by the addition of a number of similar structures.

The continuous deposition of casts at the soil surface is a response of earthworms to the general trend of soil to compact and a contribution to soil forming processes. The proportion of surface deposition may vary from less than 5% to over 80% depending on species and soil conditions. Surface cast deposition is a very poor indicator of earthworm activity; in the Lamto savannah, overall soil ingestion by endogeic earthworms estimated by a simulation model and surface cast depositions actually had opposite patterns (Lavelle and Spain, 2006).

Both categories of surface casts participate in the soil creeping process, a general mechanism that transfers small sized organic and mineral soil particles from the most elevated parts of the landscapes to low lying areas where they accumulate (Nooren *et al.*, 1995). Surface cast deposition also contributes to the progressive burial of gravels and stones by covering each year the soil surface with a continuous layer of 0.25-0.50mm (Darwin, 1881) to 1-2 mm (Lavelle, 1978).

Gallery networks and burrows made by anecic and a few endogeic species have been studied independently from aggregate assemblages. In a 12 yr-old pasture in France, Bastardie *et al* (2005) made a thorough quantitative description of earthworm burrow systems by applying X-ray tomography to 12 soil cores 25cm in diameter and 60 cm depth. Earthworm mean density was 101+-3 S.D. individuals m² distributed among 8 species. Three were anecic, 4 endogeic and one was epigeic. Total burrow length ranged from 687 to 1212m m^{-3}. Volume represented 13.3 to 24.4 l m^{-3}, which is less than 2.5% of soil volume. Total burrow area represented 1069 to 7237 cm² m^{-2}. Only 9-43% of the volume was connected to the soil surface and large seasonal variations did occur.

Burrow systems seem to have species specific shapes and organisations: diameter of galleries, branching, orientation, continuity of the burrow system significantly vary among species (Kretzschmar,1990; Lamparsky et al., 1987; Lightardt et al., 1993; Bastardie et al, 2005).
Earthworm burrowing activities are highly sensitive to soil compaction (Kretzschmar, 1991) and such soil pollutants as heavy metals (Nahmani et al., 2005) or pesticides (imidacloprid also known as "gaucho"; Capowiez et al., 2005). Galleries may act as preferential ways of circulation for gases and water. Their walls are regularly recoated with cutaneous mucus each time the worm passes through and sometimes with cast deposits. The late process occurs more frequently in deep soil strata than closer to the surface; as a result, continuity between gallery and porosity of the rest of soil is much better achieved in upper soil horizons than in the deeper soil.

B. The topology and dynamics of drilospheric assemblages

Recent studies have demonstrated a significant relationship between soil macroaggregation, especially the abundance and size of biogenic aggregates, and the presence of earthworms and other soil ecosystem engineers. In the Brazilian Amazonian region of Parà, pastures derived from a primary forest cut 6 years ago were planted to 4 different plant species and all possible combinations of them, in a complete randomly designed experiment replicated in 3 blocks. There were two shrub species, the local weed *Solanum nigrum* and the legume *Leucaena leucocephala* and, two herbaceous species, the legume *Arachis pintoi* and the African grass *Brachiaria bryzantha*, the same grass that had been planted 6 years ago when the pasture had been created. Soil macro invertebrate communities significantly responded to the change occurred in vegetation. Soil macro aggregation also changed and co inertia analysis showed a significant relationship of this soil attribute with macrofauna communities. Earthworms, especially endogeic species, were responsible for great part of this aggregation (Fig. 2).
Drilospheres are assemblages of casts, galleries and voids created by earthworm activities, mostly in the upper 20-30 cm of soils. They have physical boundaries that separate them from other comparable systems, for example the termitosphere of termites, or the rhizosphere of plant roots. Theses boundaries that can be seen when examining thin sections of soil showing a discrete array of aggregates of different sizes and shapes; they are also felt when manually

separating soil blocks into different classes of aggregates that further exhibit distinct spectral signatures (Velasquez et al., 2006). However, these boundaries have never been yet directly described and it will be particularly interesting to observe the frontiers of rhizospheres and drilospheres, two systems that otherwise develop very intense interactions.

There is still little knowledge on the topology and dynamics of earthworm structure assemblages. Laboratory and field experiments have described a few basic features that determine the spatial distribution of earthworms and of the biogenic structures that they produce at small scales. They are still rather isolated observations that need to be supported by more field observations and modelling exercises and extended to a larger number of species and situations to be considered as general features.

First, endogeic earthworms do not seem to reingest casts of their own species unless they have been totally disintegrated (Lavelle, 1978). This observation made on endogeic earthworms that produce globular casts has profound implications on the spatial distribution of their populations (Rossi, 2003). In African moist savannahs at Lamto (Côte d'Ivoire), earthworms that produce globular casts (as the "compacting" species) have opposite patterns of horizontal distribution to species that produce granular casts ("decompacting" species). Patches with dominant de compacting populations actually had significantly lower bulk density (hence higher porosity) and a larger density of fine roots than patches predominantly occupied by "compacting" species. Statistical tests (partial Mantel test) showed that the nature of earthworm communities was responsible for these differences, not the opposite. The hypothesis that patches of opposite functional groups should move in time when transformation of soil has been completed has not been tested so far in the field. Modeling exercise predicts a shift in population distribution after 2-3 years of activity (S. Barot, unp. Data).

Second, anecic earthworms seem to have rather sedentary and territorial ways of life. This allows soils that host dense populations to have rather regularly distributed vertical (and sometimes horizontal) drainage networks. A very interesting case was observed in rainforests of Madagascar that led to formulate a hypothesis on the role of anecic earthworms on soil conservation in these environments. The observed forest grows on highly unstable oxisols. Below a A_0 5cm thick holorganic horizon, a 30 cm thick A1 horizon tops a 60 cm deep clayey B horizon. This B horizon has a special prismatic vertical structure that tends to disaggregate in case of physical disruptions like the one created by cutting a slope to create a road (Fig. 4). Any excessive water infiltration in this soil layer is likely to generate horizontal disruptions leading to massive erosion events. Such events are prevented by absorption and drainage of the water in the upper 30cm of soil, maintained by biological activities. The surface humic horizon, an accumulation of invertebrate faecal pellets (mainly Diptera larvae in that case) acts like a sponge able to absorb the equivalent of ca. 100mm rainfall. Below this "sponge" like structure, giant anecic earthworms create a dense network of regularly distributed horizontal galleries that seem to act as a pipe network allowing to store water and convey it by an horizontal transfer to low lying areas and natural effluents. If confirmed, this hypothesis would explain how the destruction of such self organised systems may lead to such spectacular soil destructions.

Another consequence of the relative sedentarity of anecic and some endogeic earthworms is the accumulation over time of surface casts at the same place, that end up making rather large, sometimes tower-like, structures at the soil surface. In predominantly herbaceous fallows in Vietnam, individual cast accumulations may amount several hundred g dry weight and total mass deposited at the soil surface be *ca*. 10kg dry mass m^2 (P. Jouquet, unp. data). Anecics mays also collect litter deposited around the mouth of their burrow creating "middens" colonised by a dense and rather specific fauna and microflora (Hamilton and Sillman, 1989; Bohlen et al., 2002; Subler and Kirsch, 1998). This community is thought to achieve a preliminary decomposition of litter before earthworm ingestion. This process achieves an "external rumen" type of digestion as defined by Swift *et al* (1979).

C. Biological interactions inside the drilosphere

Earthworms have highly intense interactions with organisms within their drilosphere. They ingest microorganisms with the soil and litter that they eat and their gut is a microsite where they strongly interact with microorganisms. Although microbial feeding by earthworms has been claimed by a few authors based on sometimes observed decreases in numbers and biomass between the ingested soil and casts, and laboratory tests, no real proof has been provided so far that this behaviour is widespread. Interaction of earthworms with microorganisms covers a wide spectrum of interactions (Parle, 1963; Barois and Lavelle, 1986; Scheu, 1987; Daniel and Anderson, 1992; Fischer et al., 1995; Karsten, and Drake, 1997; Lattaud et al.,1997; Winding et al, 1997; Zhang, 2000 ; Tiunov et al., 2001; Kersante et al., 2006). With a few exceptions mentioned above, these studies show increased microbial activities in gut contents, fresh casts and burrow walls. This activity is mostly that of soil dwelling mircoorganisms that used to be in resting stages in the soil and take advantage of optimal conditions created by the earthworm in its fore gut to resume their activity. This process has been described as the “Sleeping Beauty” paradigm that states that most microbial activity in soils occurs in specific microsites created by the activities of macroorganisms. Microbial communities in soil are mostly in resting stages, waiting for these “Prince Charmings” to reactivate them (Lavelle et al., 1995). Earthworm guts, gallery walls and fresh casts are the drilospheric microsites where such activations do occur. There is growing evidence that only part of micro organisms are stimulated in this process, and more research is required to know how specific is this interaction and whether activated microbial communities differ among earthworm species and among the different soil functional domains (Lavelle et al., 2005).

As explained earlier, these interactions with micro organisms determine their ability to derive high amounts of energy from low quality feeding resources and invest part of it in the creation of physical structures in soil.

Drilosphere structures are also the habitat of very diverse communities of invertebrates of all sizes while fine roots often concentrate in this specific environment. Decaëns *et al* showed a rather fast colonisation of casts of the anecic neotropical earthworm *Martiodrilus carimaguensis* by fine roots and a diverse community of invertebrates of the macro and mesofauna. Drilospheres are also highly favourable habitats for Collembola and Acari (Marinissen and Bok, 1988; Loranger et al., 1998). In a pasture of Martinique (French West Indies), patches densely colonised by the earthworm *Polypheretima elongata* had 28 instead of 23 species of Collembola; population density was 13000 m^{-2} instead of 9000 outside the patches and the Shannon index of diversity for their communities was 3.53 instead of 2.74 outside the patches.

D. Feedback effects of the drilosphere on soil conditions and other organisms

Feedback effects of biological interaction systems on environment constraints are expected to occur in self organisng systems (Perry, 1995). The accumulation of earthworm biogenic structures in soils has significant effects on soil physical properties that may, or may not, have positive feedback effect on earthworms. Many experiments in laboratory and observations in field conditions have indicated such effects (Chauvel, 1999; Decaëns et al., 1999; Hallaire et al., 2000). Clay mineralogy seems to be one clue to the occurrence of significant effects due to earthworms as earthworm effects are more pronounced and lasting in soils with kaolinitic 1:1 type clays than with smectitic 2:1 clay materials (Blanchart et al., 2004).

The experiment conducted in natural field conditions in Brazilian Amazonia (Fig.3) and observations of Velasquez et al (2006) showed that earthworms may actually be responsible for a significant part of aggregation in the upper 10-20cm of many soils. Soils that have improved biogenic aggregation are less compact and likely present improved hydraulic properties in the upper few cm below surface. This result however largely depends on the diversity and composition of earthworm and other soil engineers communities and the nature of their respective biogenic structures.

Effects of single earthworm species have been assessed in a few studies. *Pontoscolex corethrurus*, a very active endogeic invasive earthworm that produces globular casts has been claimed to be responsible for soil compaction in sweet potatoe cultures (Rose and Wood, 1980), maize crops (Hallaire *et al*., 1990) and recently installed Amazonian pastures following convertion of primary forest to pasture (Chauvel *et al*., 1999). *P. corethrurus* is actually a clear example of invasive engineer as defined by Cuddington and Hastings (2004). Decompacting filiform endogeics, on the opposite, significantly decrease soil bulk density when kept alone in experimental soils (Blanchart et al., 1999). Although more data are clearly needed to conclude, it seems that single earthworm species are not able to maintain alone suitable physical conditions in most cases. They probably need to interact with other earthworm and other invertebrate engineer species, or natural physical processes, in order to achieve this feature. These findings support the view of Jouquet et al that endogeic earthworms may be accidental rather than extended phenotype ecosystem engineers. However, regulations obviously occur at the scale of communities and positive feedback of soil structure maintained by a community may further affect each of the species in the community. Earthworms seem to reingest casts of other species thus converting certain types of structures (e.g., casts of anecics rich in organic residues, or compact casts of large endogeic species) into other types (loose granular casts for example, Mariani et al., 2001) thus exerting regulatory effects on the proportions of each type and preventing the accumulation in excess of a single category of casts.

Feedback effects on direct or indirect competitors comprise the decrease in litter dwelling arthropods when anecic populations increase and adverse effects on communities of plant parasitic nematodes (Yeates, 1981; Lavelle et al., 2004). As regards microbial communities, drilospheres tend to be colonised by bacteria rather than fungi)(Hendrix et al., 1986). Mutualist digestion systems developed in earthworm guts seem to involve only bacteria and there is slight evidence that earthworm cutaneous mucus spraid over litter accumulated in "middens" or in burrow walls might have some fungistatic effects (Tiunov et al., 2001).

E. Chemical and biological engineering effects on plant health and communities

Interactions among earthworms and plants are intense and involve a rather diverse range of mechanisms. Plants grow better and better resist parasites in the presence of earthworms. Their communities may also be affected by the selective effect of earthworms on the germination of the soil seed bank. Several hundreds of laboratory and field experiments have shown significant increases in plant production in over 70% of cases (Brown et al., 1999; Scheu, 2003). The sense and intensity of this effect varies with plant and earthworm species. Shoot and grain productions are generally significantly enhanced while root production remains unaffected or decreases (Brown et al., 1999). Effects are generally greater in poor than in fertile soils which supports the hypothesis that earthworm effects are constant and proportional to their overall activity; their contribution is less visible when plant production is not limited by soil constraints. Five mechanisms likely explain earthworm effects:

- the release of nutrients in fresh casts and their uptake by fine roots;
- favourable effects on soil physical properties;
- enhanced activities of mutualist micro organisms, mycorhizae and N-fixing bacteria;
- direct protection from below ground parasites; indirect protection from above ground parasites;
- hormone like effects on plant growth.

Recently, Blouin et al (2006) have shown that the enhancement of rice growth in the presence of *Reginaldia omodeoi* was not due to an enhanced nutrient availability, nor any change in soil physical properties. Plants received different amounts of mineral-N fertilizer, from 0 to 1600µmol l^{-1}. In the presence of earthworms, a rather constant increase was observed, whatever the mineral N concentration. Since the experiment did not allow parasites of specific root mutualists to act, and that no limitation in water availability or other nutrients was present they concluded that an "hormone like "effect was probably responsible for the observed effects (Fig. 5). This effect first mentioned by Tomati et al. (1988) has been found in *Eisenia fetida* lombricompost extracts (Atiyeh et al., 2002; Arancon et al., 2003).

Earthworm effect is more than a simple indirect effect of their engineering activities on plants. This was shown in an experiment where rice plants *(Oryza* sativa) had been infested with a cyst forming nematode with or without earthworms (*R. omodeoi*) in the soil (Blouin et al., 2005), Earthworm activities changed the expression of stress responsive genes in the leaves of rice plants and allowed them to become tolerant instead of drying out as is observed when earthworms were absent (Blouin et al., 2005). This systemic response of plants to earthworm activities has been recently confirmed with *Arabidopsis thaliana* interacting with the *Lumbricidae Aporrectodea caliginosa* (U. Jana, A. Reppelin, Y. Zuily-Fodil, unpublished data). It is an indication that highly sophisticated communication and interactions among earthworms and plants have been selected by evolution. The exact nature of the interaction, the signal molecules likely involved and their origin (produced by the earthworm or by specific microbes activated by the earthworm) is not known.

Another example of a systemic response of plants to earthworm activities is observed in tea plants restored with the FBO (Fertilisation Bio-Organique) patented method in South China (P. Lavelle, J. Dai, E. Velasquez and N. Ruiz-Camacho, unp. Data). Following the inoculation of earthworms and stimulation of their activities by organic amendments in soil, tea quality evaluated by systematic tasting assessment was significantly improved.

At the larger scale of a pasture plot, several studies have shown that earthworms have significant effects on the germination of seed banks (Decaëns et al., 2003; Milcu et al., 2006). Other examples show how earthworms and other soil organisms may influence the composition of plant communities and their natural successions through different effects (Bernier and Ponge, 1994; De Deyn et al., 2003).

III. Conclusion: Harnessing the drilosphere to restore ecosystem functions in degraded soils

A long co evolution of earthworms with plants and other soil organisms has led earthworms to be key actors through the formation of drilosphere, one of the major self organised systems that regulates soil function. Drilospheres are physical domains that comprise a set of recognizable structures in soils. However, the rules for the assemblage of the structures inside drilospheres and the delineation and patterns of systems boundaries are still largely unknown. Inside these boundaries, earthworms interact with communities of micro organisms and invertebrates that have adapted the environment created by their engineering activities. These interactions allow earthworms to derive large amounts of energy from decomposing organic matter and reinvest part of this energy in the maintenance of structures already created, or the creation of new structures.

As predicted in the Self Organised Systems theory, drilospheres have feedback effects on the external environment, most of them positive. Some feedback effects may be triggered by single species effects, others require a community of earthworms and/or other soil ecosystem engineers with contrasted effects. Earthworms stimulate the production of plants through a number of mechanisms and increased plant production likely improves the amount of resources available to them. The discovery that they may have systemic effects on plant physiology and the expression of plant genes is very important although the mechanisms involved still need to be explained.

The new research field thus opened is highly promising. Surprisingly, the interactions between rhizospheres and drilospheres have been rather poorly addressed so far. It is likely that repetition of the pioneer studies mentioned above will show the extent and specificities of plant earthworm-interactions. It is especially important to evaluate to what extent plant genotype expressions are affected by earthworm activities. Understood these interactions, their adequate management in man made agro ecosystems would achieve such important targets as regulation of plant growth and phenology and the control of plant parasites. Effects of earthworms on plant communities and their successional processes addressed in a few papers also deserve much greater attention.

Drilospheres have significant effects on soil based regulation ecosystem services, especially Carbon sequestration and water infiltration and storage (Lavelle et al., 2006) and the potential for their management in agroecosystems is vast and diverse (Lavelle et al., 1999; Jimenez and Thomas, 2001).

Although drilospheric effects on organic matter dynamics are complex, and may have opposite directions depending on scales and specific organic fractions, there is some evidence that earthworm activities have positive effects on carbon sequestration in the long term (Lavelle and Spain, 2006). Much research is still required however to answer this critical question.

Drilospheric effects on soil physical properties are much better understood. Earthworms are legitimately considered important actors in the maintenance of adequate hydraulic properties in the upper 20 cm of soils where infiltration and most detoxification processes operate.

Earthworms and their drilospheres have long been recognised as resources that should be properly managed in man made ecosystems (Lavelle et al., 1999). Soil degradation is always associated with depletion in earthworm and other invertebrate biodiversity and abundance. Earthworm communities are greatly sensitive to land use intensification. Ploughing and pesticide applications are especially harmful to them (Edwards and Bohlen, 1996). Conversion of forests to pastures and cropped land and habitat fragmentation may eliminate a large proportion of native species, although with variable and still poorly understood patterns (Fragoso et al., 1997; Lavelle and Lapied, 2003). They are partly replaced by communities of exotic species, less than 50 species that form similar assemblages worldwide in comparable environment conditions. We are thus loosing at a very fast rate the extraordinary diversity of native communities generated by exceptional rates of endemism in highly sedentary organisms. In Amazonia, for example, the average ratio of local species richness to regional richness has been estimated at ca. 1% , compared to 20-30% on average for ants and termites and 80% for Sphingidae moths (Lavelle and Lapied, 2003).

Communities of peregrine species or locally adapted species in turn tend to disappear when soil management makes the environment too difficult for them to survive. They mostly suffer from a lack of organic resources to feed, frequent destruction of their populations and habitats by ploughing, poisoning by pesticides and water stress in soils with reduced plant and litter cover. In such soils, most ecosystem services associated to drilospheric activities tend to decline, even plant production that may require increasing amounts of chemical and other inputs to achieve the same crop yield.

Management of ecosystem engineers is an important option in ecosystem restoration (Byers et al., 2006). Reconstitution of drilospheres is an action to consider when recreating or restoring soils. They are key elements of soil function at scales of the functional domains that they delineate in soils, the mosaics of the domains formed by different species of earthworms and other similar ecosystem engineers, plants and their rhizospheres, termites and their termitospheres or ants in their myrmecospheres (Lavelle, 2002). They are sites where the basic soil functions operate allowing the delivery of ecosystem services at higher scales (Lavelle et al., 2006).

Several options have been proposed already to achieve the purpose of drilosphere restoration (Senapati et al., 1999). The FBO (Fertilisation Bio Organique) patented method used in tree plantations creates hot spots of high fertility where organic residues of different qualities are buried in a specific order in the soil and inoculated with appropriate earthworms. Application of this method in India and China has allowed to significantly improve biodiversity of invertebrate communities and soil aggregation while the organic tea thus produced had an significantly improved gustative quality (Pradeep Panigrahi, unp. data; Patrick Lavelle, Jun Dai, Nuria Ruiz-Camacho, Elena Velasquez, unp. data).

In general, such practices first require a restoration of organic inputs that provide adequate and sufficient feeding resources for the earthworms (Lavelle et al., 2001). Maintenance of permanent plant covers and organic amendments are practices that allow to achieve this objective provided the quality and location of organic materials is adequate for the earthworm species present. Such feeding resources will allow local relict populations or inoculated earthworms to develop their digestive interactions with micro organisms.

The quality of biological interactions within the new drilosphere thus created must be considered. In some cases, earthworm inoculation does fail, probably due to the inability of earthworms to adapt a microbial community that is too different from that of their original soil. This has been for example observed by Gilot-Villenave (1994) who showed that adult worms from the species *R. omodeoi* taken from a savannah site would not survive if transplanted in soil of an adjacent gallery forest; young worms issued from cocoons produced in savannah would however survive if they did hatch in the forest soil and interact from the beginning with the local soil microflora.

Once re-established the interactions of organisms inside the drilosphere, the system will start to function and expand as biogenic structures are created. Interactions with other functional domains (drilospheres of other earthworm species, rhizospheres) restore the essential mechanisms that allow soils to provide the large range of functions used by human populations as ecosystem services. Interactions of earthworms with plant roots are another important process to consider at that stage. It is likely that the topology of root systems that greatly differs among plant species has much to do with plant response to earthworm activities. Plants that have dense systems with a large proportion of very fine roots, like e.g., the well known tropical American plant *Bixa orelana* L. used by Amerindians for their traditional face paintings best respond to earthworm inoculations; on the opposite, plants with short systems or rather thick roots, like the palm tree *Bactris gasipaes* Kunth have limited responses (Brown et al., 1999).

The recognition and proper management of drilospheres although highly promising, is still far from being achieved. Just like the different functional domains of the main ecosystem engineers have established interactions in soils along evolutionary time, plant physiologists, soil fertility and soil ecology experts must coordinate their efforts to optimise the production of sustainable ecosystem services from soils. How can the best naturally selected or genetically modified plants grow in a degraded soil? Probably not more than a little productive traditional cultivar grown in the most ecologically active soil…

IV. References

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Captions of figures

Figure 1 : A general model of the drilosphere system as a Self Organised System.

Within the boundaries (large dotted line) of their functional domain, the drilosphere they accumulate macro aggregates, galleries and other pores that constitute the habitat for specific communities of micro organisms and invertebrates; earthworms interact with these organisms. The effect of these interactions affects the external environment, especially hydraulic conditions and organic matter inputs an storage, plant growth and the composition of their communities. + signs indicate positive feed backs.

Figure 2 : Tower-shaped earthworm cast in fallows in Vietnam (Photo P. Jouquet).

This structure is formed after weeks of daily deposition of casts at the top edge of the structure. Note dense colonisation by file roots.

Figure 3: Significant co-inertia among soil fauna and soil morphology parameters in Amazonian pasture soils submitted to all possible combinations of 4 different plants.

Superposition in factorial plan 1-2 of fauna and soil morphology variables shows location in the right half of the figure of earthworm species and biogenic aggregates, suggesting that they are formed by these earthworms.
pm; pl, ps: medium, large and small physical aggregates; bs, bm, bl: biogenic aggregates of small, medium and large size; rs, rm, rl: root aggregates of different sizes
inv: invertebrates found in small soil blocks

Figure 4: Hypothesised role of giant anecic earthworms in soil conservation of Tropical rainforest at Madagascar. Rainfall is first absorbed by a 10 cm thick surface organic layer and then enters deeper soil where a subhorizontal network of earthworm galleries stores and channels water towards low lying areas. This prevents water from penetrating too much in unstable low lying horizons. Cutting a road across the slope by exposing the B horizon (with a prismatic fragile structure) and C made of highly dispersable alterites, eliminates the natural drainage system and accelerates massive soil erosion and the occurrence of major landslides ("lavakas").

Figure 5 : Response of rice (*Oriza sativa*) to increasing inputs of mineral nitrogen, in the presence (dotted line) and absence (solid line) of earthworms.

The effect of earthworms is constant whatever the nutrient status of soil which allows to reject the hypothesis of enhanced mineralization to explain the gain in plant growth observed in their presence.

Figure 1

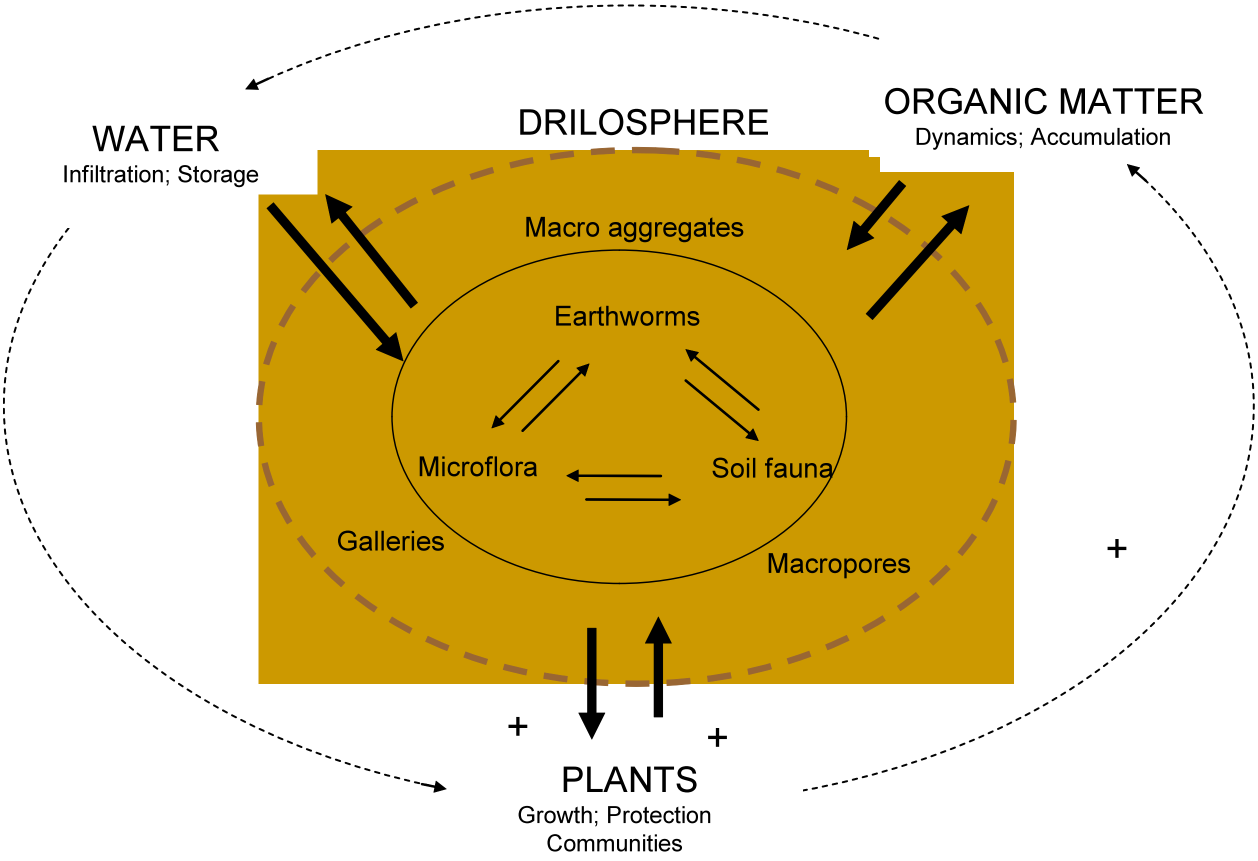

WATER
Infiltration; Storage
DRILOSPHERE
ORGANIC MATTER
Dynamics; Accumulation
Macro aggregates
Earthworms
Microflora
Soil fauna
Galleries
Macropores
+
+
+
PLANTS
Growth; Protection
Communities

Figure 2

Figure 3

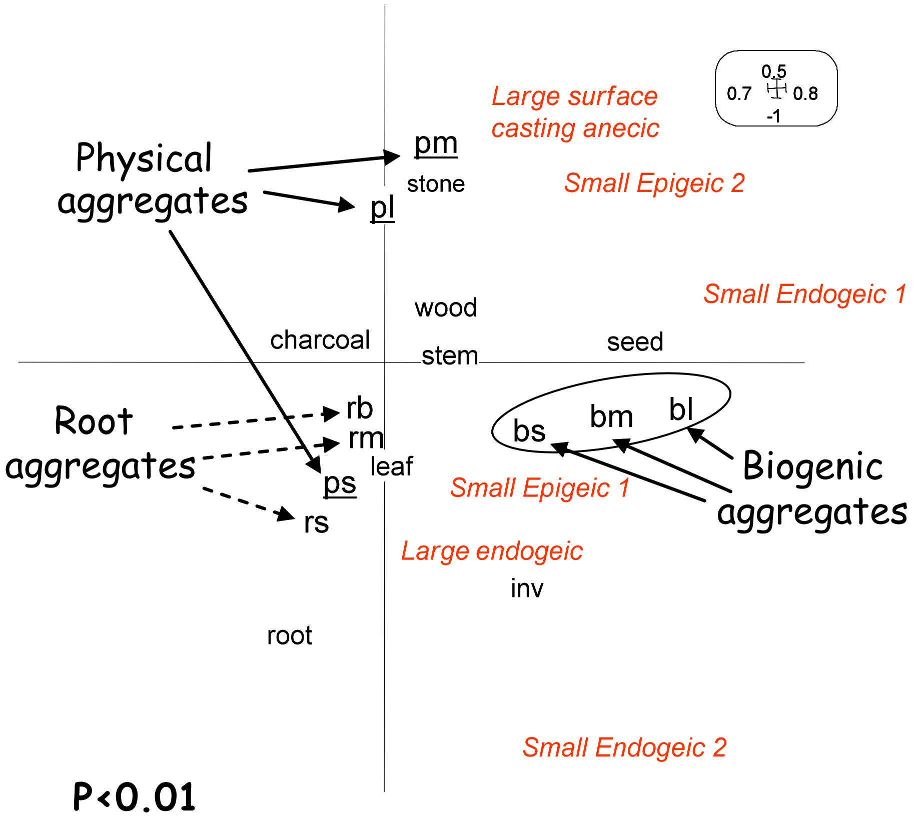

0.5
0.7
0.8
-1
Large surface casting anecic
Physical aggregates
pm
stone
pl
Small Epigeic 2
Small Endogeic 1
wood
charcoal
stem
seed
Root aggregates
rb
rm
leaf
ps
rs
bs
bm
bl
Biogenic aggregates
Small Epigeic 1
Large endogeic
inv
root
Small Endogeic 2
P<0.01

Figure 4:

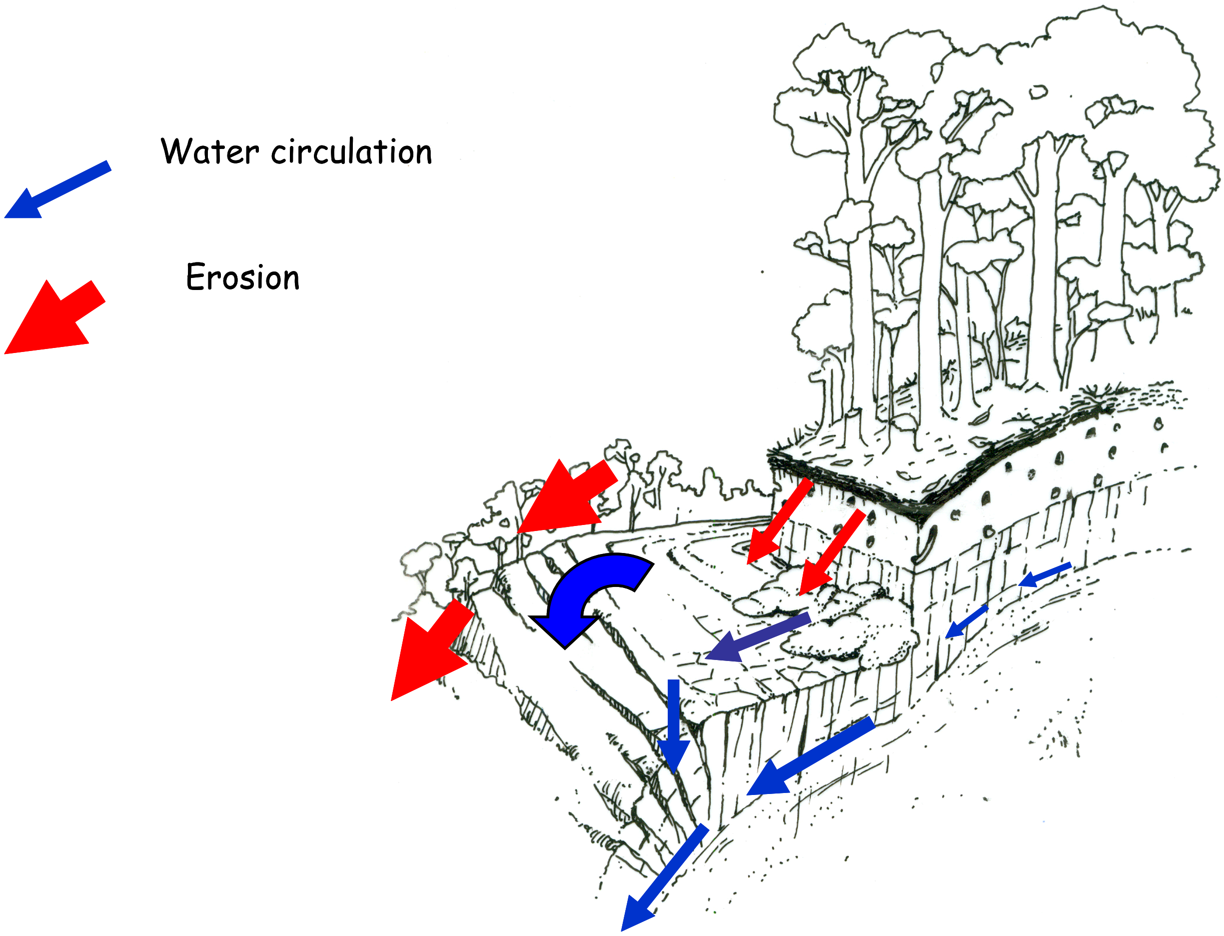


Figure 4 (complete or replace following scheme also refered to as Figure 3)

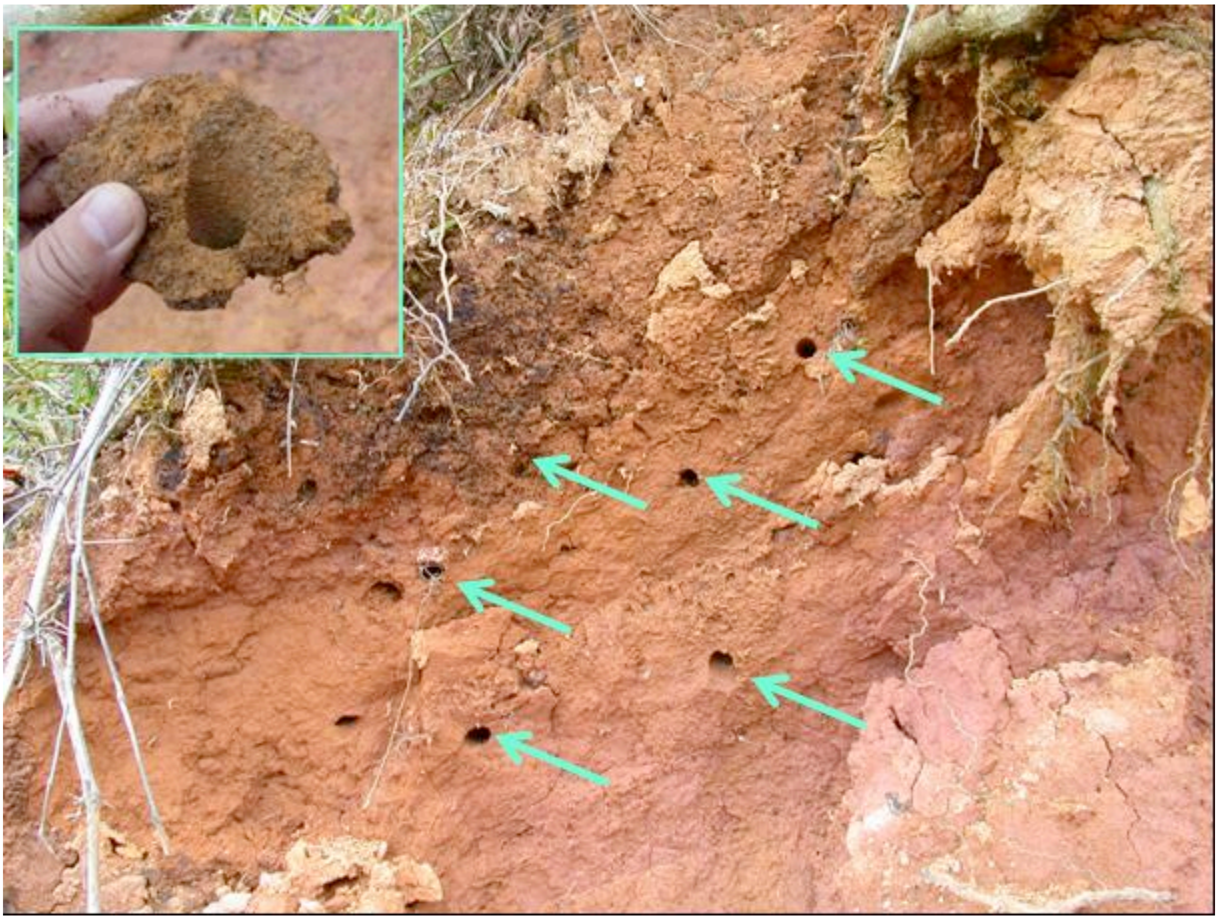
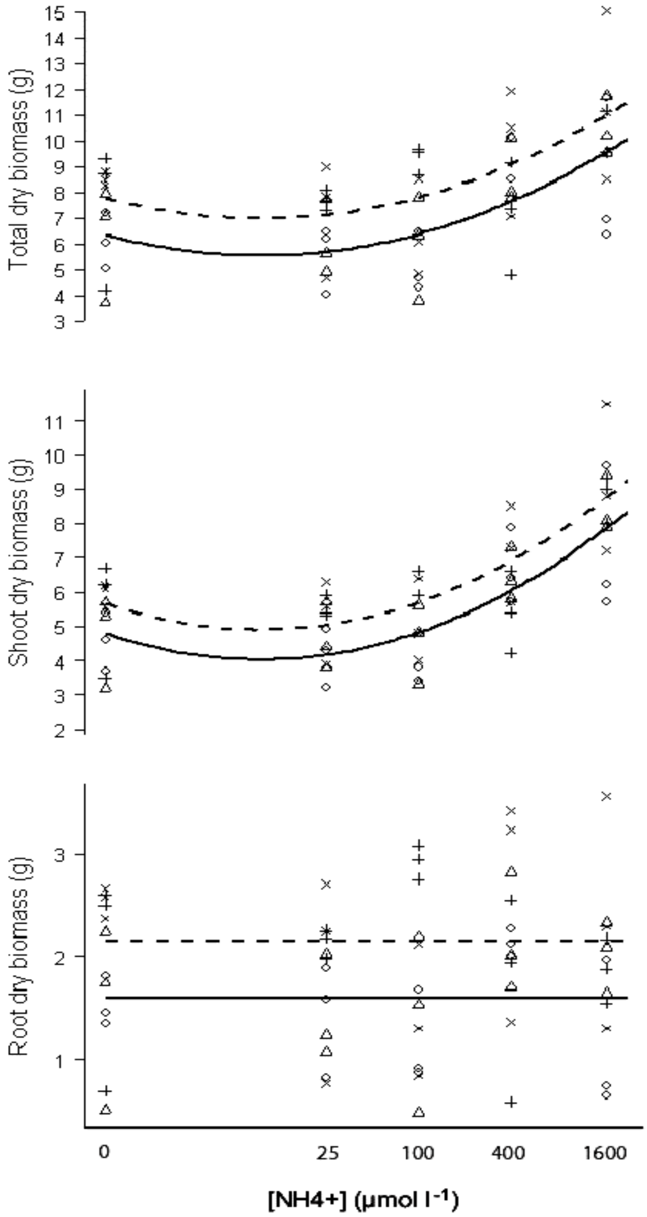


Figure 5


Total dry biomass (g)
15
14
13
12
11
10
9
8
7
6
5
4
3
Shoot dry biomass (g)
11
10
9
8
7
6
5
4
3
2
Root dry biomass (g)
3
2
1
0
25
100
400
1600
[NH4+] (µmol l⁻¹)

+