Does ecosystem diversity affect soil hydraulic properties? Investigation of biotic and abiotic factors on infiltration capacity in a grassland biodiversity experiment

Dissertation

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“We know more about the movement of celestial bodies than about the soil underfoot.”

- Leonardo da Vinci -

Contents

Abbreviations

ANOVA	analysis of variance
B	block
BM	biomass
ρ_d	bulk density
C	carbon
CV	coefficient of variation
d_e	equivalent diameter
+ew	plot with ambient earthworm population
-ew	plots with reduced earthworm population (extraction)
GR	grasses
GLM	general linear models
FG	functional groups
K(h)	unsaturated hydraulic conductivity
K_s	saturated hydraulic conductivity
LEG	legumes
N	nitrogen
Ψ_G	gravitational potential
Ψ_M	matrix potential
Ψ_O	osmotic potential
Ψ_T	total potential
PTFs	pedotransfer functions
PVC	polyvinyl chloride
r	pearson correlation coefficient
SH	small herbs
SOC	soil organic carbon
SR	species richness
Tl	time linear
TH	tall herbs

Abstract

The present thesis aims to evaluate the relationships between soil hydraulic properties and earthworms, plant community, soil structural parameters, soil texture, and soil moisture in the frame of a long-term grassland biodiversity experiment, the so called Jena Experiment. Hydraulic properties such as infiltration capacity play an important role in soil erosion, run-off and water availability to plants for the prediction and management of ecosystems. Global change has led to an increase in flood frequency events caused by heavy rainfalls. For sustainable soil management (reducing soil erosion and run-off) as well as for improving hydrological models, it is important to know which factors influence infiltration. Generally, soil texture considered one of the most important factors for explaining hydraulic properties, but other influences like bulk density or soil fauna have also been recognized. However, because infiltration is a complex process, a multitude of interrelated processes affects infiltration capacity, and therefore investigations yield controversial results regarding specific factors. In this thesis, I distinguish between abiotic soil factors (texture), which are constant in time, and biotic factors (soil fauna, ecosystem structure), which change dynamically depending on environmental factors. The majority of previous experiments has focused on one or two selected factors influencing hydraulic properties, and do not account for interaction. The aim of this thesis was to identify the most important drivers for the infiltration capacity in a grassland experiment (The Jena Experiment), while explicitly taking into account interaction.

The Jena Experiment was established to investigate the effects of biodiversity on ecosystem processes. Its statistical design allowed me to investigate several factors of interest for shaping soil hydraulic properties on independent gradients. This well-replicated and compositionally-balanced design is a powerful background to investigate interrelationships between plant communities, earthworms, soil structural parameters, soil texture and soil moisture. For this I performed field measurements along the relevant gradients at The Jena Experiment field site. Also, I measured infiltration capacity on a depth gradient on 11 monoliths with two diversity levels (4 and 16 plant species), originating from The Jena Experiment site in the CNRS Ecotron, Montpellier.

The first field survey in 2011 (Chapter 4) was focused on the role of earthworms together with the effects of plant community, vegetation factors (above-and belowground biomass), soil texture and matric potential on infiltration capacity along a short diversity gradient (42 plots containing 1, 4 and 16 plant species). The spatial and temporal variations of infiltration capacity were driven by interacting of biotic processes. The results suggest that certain functional groups such as legumes and grasses affect earthworm biomass, which in turn influences infiltration capacity.

The objective of the second field experiment in 2012 (Chapter 5) was to find out whether patterns in biomass productivity and soil organic carbon reflect on soil structure and infiltration capacity. It was carried out in 82 plots containing between 1 to 60 plant species. Plant species diversity was significantly correlated with porosity and bulk density (negative relation), which seemed to be conducive for water flow through soil. Additional analysis identified soil organic carbon as the essential link between soil structure parameters and plant diversity. Surprisingly, earthworm biomass was neither affected by plant community, nor by soil structural parameters, although it correlated weakly with the infiltration capacity independently.

The third batch of experiment was carried out in 2012 on soil monoliths taken from the Jena experiment to the Ecotron facility in Montpellier. The removal of these monoliths allowed investigating the impact of biotic and abiotic factors along a depth gradient, thus circumventing the fact that excavation is normally not possible at the original field site. At the soil surface the variation of infiltration capacity was correlated with biotic factors (earthworm and root biomass), which was in accordance with results from Chapter 3. Based on layer conditions such as color, bulk density, soil organic carbon content and root abundance, we could distinguish between topsoil, plough pan and subsoil layers. At and below the observed dense layer, at approximately 30 cm of soil depth (presumably an old plough pan), infiltration capacity was reduced and varied little. Neither biotic factors nor soil texture explained the variation of the infiltration capacity.

In the next analysis (Chapter 7) we tested the application of several models based on easy to measure input parameters such as soil texture (sand, silt and clay content), soil bulk density and soil organic matter for estimating hydraulic conductivity. Our study showed that, at the soil surface, the Jabro Pedotransfer function, which includes besides soil texture also bulk density, was best able to explain the variation of hydraulic conductivity. However, at and below the plough pan the PTFs were inappropriate for estimating the real hydraulic conductivity.

Overall, the present thesis indicates that infiltration capacity is affected by macropores formed by earthworms, as well as structural heterogeneity expressed as soil bulk density. Soil texture (percent of sand) played a subordinate role for infiltration capacity. These separated effects on infiltration capacity depend probably on whether, which affect the dynamic patterns of biotic processes, for example earthworm activity. Thus, open questions relate to the cause for different drivers in different years (earthworms vs. productivity). Further studies on a similar statistical plot design are needed for observing the single and interaction effects of earthworms and bulk density and accordingly in which environmental condition one or both of these factors play a role for shaping water flow into the soil

Kurzzusammenfassung

Eingebettet in das interdisziplinär ausgerichtete Jena Experiment war es das Ziel dieser Arbeit, die Einflüsse von Regenwürmern, Pflanzenbedeckung, Bodentextur und Lagerungsdichte, Porosität und organischen Kohlenstoff auf bodenhydraulische Eigenschaften zu untersuchen und die daraus resultierenden Konsequenzen für Ökosystemdienstleistungen bzw. Funktionen abzuleiten. Hydraulische Eigenschaften des Bodens, wie die Infiltrationskapazität, spielen bei der Vorhersage und Modellierung von Bodenerosion, Oberflächenabfluss und Wasserverfügbarkeit für Pflanzen eine bedeutende Rolle. Die anthropogen bedingte Zunahme von Starkregenereignissen sowie damit einhergehende Hochwasserereignisse führen zur Verdichtung, Verschlämmung und Verlust biologischer Aktivität. Für ein nachhaltiges Bodenmanagement ist der Erhalt der standorttypischen Infiltrationskapazität von zentraler Bedeutung. In den meisten hydrologischen Modellen wird die Bodentextur als wichtige Faktoren zur Ableitung von hydraulischen Eigenschaften herangezogen. Untersuchungen zeigten jedoch, dass die Infiltration durch eine Vielzahl von Faktoren beeinflusst wird. In dieser Arbeit unterscheide ich zwischen abiotischen (Textur) Eigenschaften, die konstant sind, und biotischen Faktoren (Ökosystemzusammensetzung, Bodenfauna), welche sich dynamisch den Umweltbedingungen anpassen. Das Ziel dieser Arbeit war die Identifikation der bedeutendsten Faktoren, die die Infiltrationskapazität in einem europäischen Grasland beeinflussen, wobei die Interaktion dieser Faktoren explizit beachtet wurde.

Das Design des Jena Experiments bietet die einzigartige Gelegenheit, die Bedeutung physikalischer und biologischer Prozesse entlang unabhängiger Gradienten zu untersuchen. Dadurch ist es möglich einzelne und interagierende Einflüsse auf die Infiltrationskapazität zu analysieren. Um die wichtigsten direkten und indirekten mechanistischen Zusammenhänge zu erforschen, führte ich im Rahmen meiner Promotion Feldversuche entlang eines Pflanzenartengradienten auf dem Jena Experiment in den Jahren 2011 und 2012 durch. Um einen Einblick in die Tiefengradienten zu erhalten, führte ich zusätzlich eine Messkampagne an elf Großlysimetern des Jena Experiments mit zwei Biodiversitätsstufen (4 und 16 Arten) im CNRS Ecotron (Montpellier) durch.

Ziel der ersten Feldstudie in Jahr 2011 (Kapitel 4) war es, vor allem den Einfluss von Regenwürmern gemeinsam mit Pflanzengemeinschaften und Bodentextur auf die Infiltrationskapazität entlang eines Biodiversitätsgradienten (42 Plots mit 1, 4 und 16 Arten) zu untersuchen. Die Ergebnisse zeigen, dass bestimmte funktionelle Gruppen, wie Leguminosen und Gräser, die Regenwurmbiomasse beeinflussen und sich diese wiederum auf die Infiltrationskapazität auswirken. Die räumlichen und zeitlichen Schwankungen der Infiltrationskapazität werden durch ein komplexes Zusammenspiel von biotischen Prozessen zwischen den funktionellen Gruppen und den Regenwurmaktivitäten angetrieben.

Das zweite Feldexperiment im Jahr 2012 (Kapitel 5) untersuchte inwieweit bodenstrukturierende Faktoren, wie Lagerungsdichte, Porosität und organischer Kohlenstoff, entlang eines Artengradienten von 1 bis 60 Arten (82 Plots), den Wasserdurchfluss im Boden beeinflussen. Die Ergebnisse verdeutlichen, dass Pflanzenartenvielfalt die Infiltrationskapazität durch Veränderung von Lagerungsdichte, Porosität und organischer Kohlenstoffgehalt beeinflusst. Unabhängig davon wurde die Infiltrationskapazität auch von der Regenwurmbiomasse beeinflusst, welche aber selbst weder mit der Pflanzenartenvielfalt noch mit der Lagerungsdichte korrelierte.

Ziel des dritten Experiments im Jahr 2012 (Kapitel 6) war es, den Einfluss biotischer und abiotischer Faktoren auf die Infiltrationskapazität in verschiedenen Bodentiefen (0, 25 und 55 cm Tiefe) zu untersuchen. Die Infiltrationskapazität korrelierte mit der Regenwurmbiomasse an der Bodenoberfläche, ähnlich wie im Jahr 2011. Der Oberboden konnte durch Bodenfarbe, erhöhte Lagerungsdichte, niedrigerer Kohlenstoffgehalt und Wurzelbiomasse deutlich vom Unterboden unterschieden werden. In etwa 25 cm Bodentiefe (vermutlich eine alte Pflugsohle), hatten weder Regenwürmer, Pflanzenartenvielfalt, Lagerungsdichte, noch Bodentextur einen Einfluss auf die Infiltrationskapazität.

Getestet wurde anschließend die Anwendung von Pedotransferfunktionen (PTFs) zur Berechnung der gesättigten Leitfähigkeit (Kapitel 7). Als Eingabeparameter wurden die verfügbaren Parameter Bodentextur (Sand, Schluff und Ton), Lagerungsdichte und organischer Bodengehalt verwendet. Im Oberboden war es möglich die gesättigte hydraulische Leitfähigkeit mittels des Models von Jabro abzuschätzen. Jedoch an und unterhalb der beobachteten Pflugsohle waren alle verwendeten PFTs für Berechnung der gesättigten hydraulischen Leitfähigkeit ungeeignet.

Zusammenfassend hat die vorgelegte Arbeit aufgezeigt, dass in Grasländern, die Lagerungsdichte und Regenwurmaktivität einen entscheidenden Beitrag zur Erhöhung der Infiltrationskapazität des Bodens leisten. Regenwürmer wurden nicht von der Pflanzenartenvielfalt, sondern werden vielmehr von bestimmten funktionellen Gruppen, wie Leguminosen und Gräsern beeinflusst. Regenwürmer beeinflussten die Infiltrationskapazität unabhängig von der Lagerungsdichte. Pflanzenartenvielfalt hingegen wirkt sich positiv durch Veränderung der Bodenstruktur auf die Infiltrationskapazität aus. In tieferen Bodenschichten hebt sich der biotische Einfluss, durch anthropogen verursachte Kompaktierung (Pflugsohle), wieder auf. Wie stark dieser Einfluss von Lagerungsdichte und Regenwürmern zusammen oder einzeln auf die Infiltrationskapazität ist, hängt wahrscheinlich von weiteren Umweltbedingungen (Wetter) ab. Die Ergebnisse dieser Untersuchungen belegen die komplexen Wechselwirkungen zwischen Wasserdurchfluss im Boden und Ökosystemvielfalt sowie die hohe raumzeitliche Dynamik. Inwieweit diese biotischen Faktoren einzeln oder miteinander über die Bodenstrukturen auf die Infiltration wirken, sollte Gegenstand weiter Forschungsarbeiten sein.

Chapter
1

General Introduction

1 General introduction

1.1. Background

Infiltration is next to precipitation, run-off and evapotranspiration one of the important physical components in the hydrological cycle. Water from precipitation runs into streams, lakes, rivers, and oceans or infiltrates through the soil profile. Water can also run-off over land, causing erosion, flooding and degradation of water quality. To determine strategies for soil and water conservation and to minimize surface run-off and soil erosion it is important to know which factors affected surface hydraulic properties such as infiltration and hydraulic conductivity (Shukla et al. 2006). Especially for agriculture it is important to quantify the infiltration to determine the availability of water for crop growth and the resulting irrigation amount for optimal plant growth.

Infiltration is the movement of water from the ground surface into the soil profile, via pores or small openings and determined by the factors of gravity, capillary action and soil porosity (Hillel 1998). The maximum rate at which water enters into or is absorbed by the soil is termed infiltration capacity (Ward and Robinson 1990). Hydraulic conductivity, an important soil property, is the movement of water in a porous media under a hydraulic gradient and interrelated with the infiltration capacity. Soil hydraulic conductivity is a critically important soil property for predicting and managing ecosystem patterns.

Most simulations of infiltration and redistribution in unsaturated soils are based on the Richards equation (soil water flow equation). When water infiltrates through the soil, it passes through the plant via transpiration into the atmosphere. Water removal by plants via transpiration is treated as a sink term in the Richards equation (soil water flow equation (Richards 1931)). Modeling water flow and chemical transport hydraulic conductivity is estimated using pedotransfer functions (PTFs) based on easy to measure soil properties such as soil texture (sand, silt and clay content), bulk density and soil organic carbon (Schaap et al. 2001, Wösten et al. 2001). But how and how much of the precipitation infiltrates into the soil surface and reaches the river or is released via transpiration in the atmosphere strongly depends on many factors. Figure 1.1 gives an overview on the amount of factors which could influence the water flow through soil. Apart to this categorization of factors influencing infiltration, generally factors can be attribute to biotic (for example earthworm biomass, vegetation type and cover) and in abiotic (for example texture) factors (Ward and Trimble 2004).

In saturated soils infiltration is mainly determined by the different size, shape and continuity of pores (Beven and Germann 2013). Based on the size or capillary potential, soil pores can be classified into different pore size classes: macro-, meso- and micropores (Beven 1981). According to Luxmoore (1981), pores with diameters >10 mm are referred to macropores which tend to be freely draining and are prevalent in coarse textured or sandy soils.

In clayey soils, macropores occur as cracks and fissures, and in all soil types they are a result of biological activity such as earthworm and root activity (Messing and Jarvis 1990, Zehe and Flühler 2001, Beven and Germann 2013). In addition, much of root growth is initiated in these pores. Mesopores are medium sized pores (0.1 mm - 10 mm) that are common in medium-textured soils or loamy soils and important for the storage of water for plant growth. Pores with a diameter smaller than 0.1 mm are contributed to micropores and occur typically in clayey soils (Hillel 1998). The arrangement of primary soil particles into individual clusters (secondary units), called soil aggregates, are known as soil structure (Hillel 1998). Change in soil structure is mainly attributed to burrows formed by earthworm and roots which determine the soil hydraulic conductivity (Edwards and Bohlen 1996, Six et al. 2004). The pore space between the primary particles or intra-aggregate pore or micropores is defined as textural porosity, whereas the pore space between micro-aggregates or aggregates containing macropores formed by earthworms, roots and cracks is defined as structural porosity (Alaoui et al. 2011). In heterogeneous (structured) soils the infiltration through soils is determined by biopores and continuous mesopores creating preferential flow (macropore flow) (Horn et al. 1994).

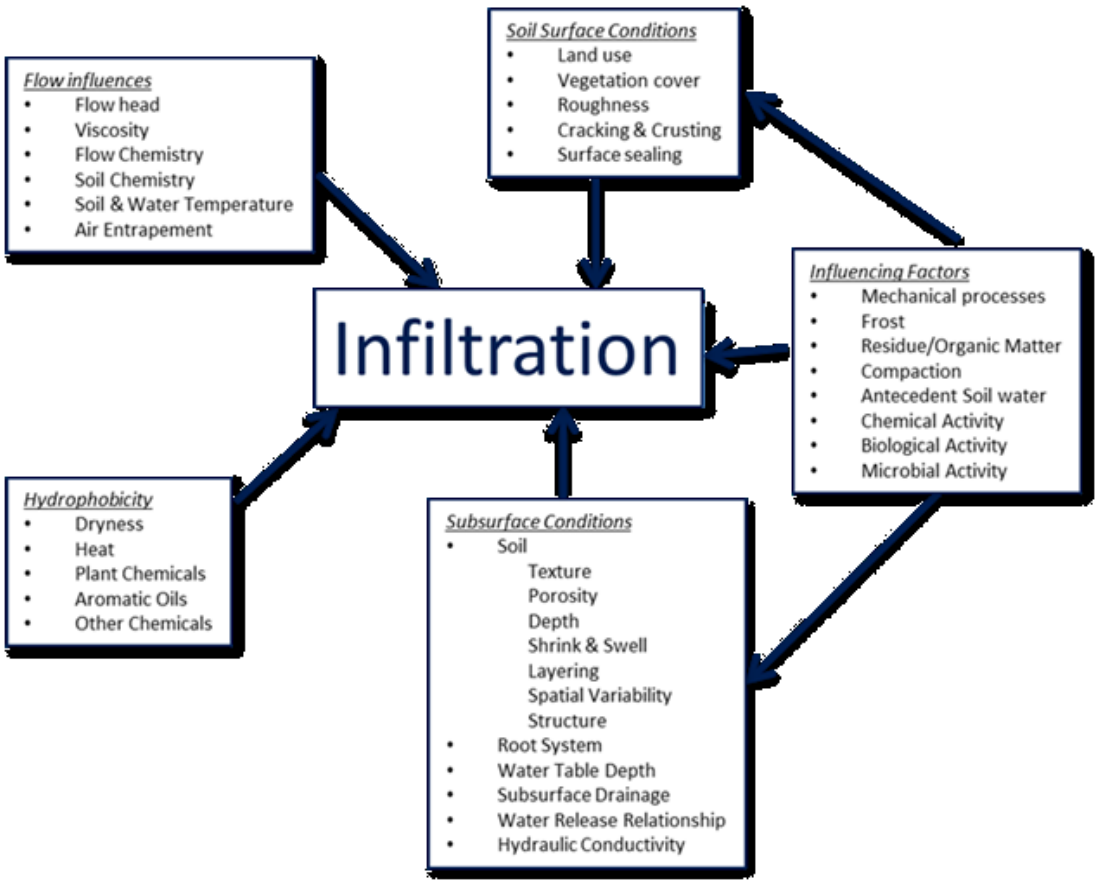

Figure 1.1: Overview of factors affecting water movement through soils (adopted from Ward and Trimble (2004)).

Soil type and soil management which may vary in space and time (Mallants et al. 1997, Kutílek 2004) could shape the soil structure of the soil. Because of this variability of soil structure, the estimation of infiltration and soil hydraulic properties is a very complicated subject. Next to microbes, soil fauna and texture, vegetation factors also influences soil structural parameters such as soil organic carbon, bulk density and porosity (Six et al. 2004). These parameters are good characteristic factors that indicate changes of pore sizes induced to land use, weathering influences, or biological activities. Other studies showed that an increase in soil bulk density decreases hydraulic conductivity due to the reduction of larger pores (Franzluebbers 2002, Zacharias and Wessolek 2007). Additionally, soil bulk density and porosity are good indicators for soil compaction implying a destruction of soil structure impacting infiltration through soil (Logsdon and Karlen 2004). Soils with a good structure are characterized by enhanced water infiltration and decreased run-off and erosion potential. Most of the infiltration measurements on structured soils result in unreliable values because the calculation assumes homogenous soil (Salverda and Dane 1993). For a correct description of the water flow in structured soils, matrix flow as well as macropore flow should be considered in experiments.

Plants which represent the primary components of terrestrial ecosystems play a very important role for ecosystem functioning and composition of soils. Experiments are needed to analyze the consequences of loss in plant species richness by ecosystem processes and functioning long-term observation in biodiversity (Loreau and Hector 2001, Hooper et al. 2005). A number of biodiversity experiments in temperate grasslands have investigated the effects of biodiversity on ecosystem processes and stability, e.g. Ecotron Biodiversity Experiment, Cedar Creek Biodiversity Experiment and the BIODEPTH experiment (Biodiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems: experimental manipulations of plant communities). The results and critique of the previous experiments were considered in the design of The Jena Experiment. In this experiment it is possible to test the effects of plant species richness and plant functional groups separately (Roscher et al. 2004). Additionally, the experimental design allows testing of the effects of biodiversity on ecosystem processes and includes more interactions between plants, soil fauna, invertebrates, physical and chemical soil properties and hydrological conditions and their impact on ecosystem patterns.

For central Europe the IPCC report predicts that in the 21th century, precipitation patterns will change due to climate change: decreasing precipitation in summer and increasing precipitation in autumn/winter. It is therefore likely that flooding events will increase in winter and droughts will increase in the summer (IPCC 2012). Through climate change, biodiversity patterns will mainly be affected which results in a change of hydrological patterns (Weltzin et al. 2003). Inappropriate management can reduce or block infiltration resulting in water ponds on the surface or run offs. Thus plant production decreases because less water is stored in the soil.

An important task in agriculture is to enhance water infiltration potential into soil to prevent, reduce impact, or to avoid the impact of runoff and frequent floods (Mannering and Meyer 1963). Additionally, it is important to look into specific mechanisms in which hydrology impacts biodiversity. In this context, the study of factors affecting infiltration capacity in context with the loss of plant species richness has specific importance, for example in managing agricultural soils. Generally, it is assumed that communities containing less species are less resilient against frequent disturbances and single extreme events such as high precipitation events (Tilman 1996). Knowledge of factors affecting water flow through soil becomes more important for buffering future extreme precipitation events.

1.2 The Jena Experiment

1.2.1 Temperate grasslands

The biome temperate grassland is characterized by a dominance of grasses, absences of trees and shrubs, hot summers, cold winters and moderate rainfall. Precipitation usually occurs in the late spring and early summer. The biome includes the veldts of Africa, the pampas of South America, the steppes of Eurasia, and the prairies of North America. In Europe, temperate grasslands make up an important part of the agricultural area (Isselstein et al. 2005). Because of human use and the transformation of grasslands for agriculture, farming and grazing had an important impact on biodiversity (Smit et al. 2008). Over the last hundred years, many of the natural grasslands have been lost by converting grasslands into agricultural land. Since 1950, the temperate grasslands biome has lost nearly 70% of its native cover (Duraiappah 2005). For food supply, farmlands are important. However, the anthropogenic impact on plants and animals in temperate grasslands have unknown consequences for human well-being.

1.2.2 Experimental set-up

The experiment was performed at the field site of The Jena Experiment which is located in the floodplain of the Saale river near Jena (Thuringia, Germany; 50°55´N, 11°35´E, 130 m above sea level) (Figure 1.2). The mean annual air temperature is 9.3°C and the mean annual precipitation is about 587 mm (Kluge and Müller-Westermeier 2000). The soil of the experimental site is an Eutric Fluvisol (Fao-Unesco 1997), developed from up to 2 m-thick loamy fluvial sediments. Before the establishment of the experiment, the field site was agricultural land for the last 40 years and highly fertilized over the last decades for growing vegetables and wheat (Roscher et al. 2004). After the last harvest in autumn 2000 the field was ploughed and kept fallow throughout 2001. In July 2001 the field was harrowed bimonthly and treated with Glyphosate (N-(Phosphonomethyl)-glycine, Roundup). In spring 2002, the experimental area was harrowed twice before the plots were established. Seeds were sown with

a total density of 1000 seedlings per m², divided equally among the species of each mixture (Roscher et al. 2004). In 2002, with the start of the experiment, organic carbon was determined in the plough horizon in the range of 13 to 33 g C kg^{-1} and C/N ratios were between 8 and 15, while pH ranges from 7.1 to 8.4. Carbonate content varies with distance from the river in a range from 4 and 42 g C g^{-1}. At the beginning of the experiment, all soil properties were homogeneous through the plough horizon (Roscher et al. 2004, Oelmann et al. 2007). Plots were assembled into four blocks following a gradient in soil characteristics from sandy loam near the river to silty clay with increasing distance from the river (see Chapter 1.2.2.2). Each block contains an equal number of plots and plant species and functional group diversity levels.

A pool of 60 native plant species common of Central European mesophilic grasslands (*Molinio-Arrhenatheretea*, Ellenberg and Leuschner (2010)) was used to established a gradient of plant species richness (1, 2, 4, 8, 16 and 60) and functional group richness (1, 2, 3 and 4) on 80 plots of 20 x 20 m (Figure 1.3 A, B). There were 16 replicates for mixtures with 1, 2, 4, 8, species diversity and14 replicates for mixtures with 16 species, and 4 replicates for the mixtures with 60 species. All 60 species had been assigned into four groups: 12 legumes, 16 grasses, 12 small herbs and 20 tall herbs based on a cluster analysis of morphological, phenological and physiological traits. Bare-ground plots (0 plant species) were created as control plots in each experimental block. The additional treatment area contained subplots representing “natural” grassland, managed by mowing located outside of the field site and used as reference plots (r). These two plots were not sown after the establishment of the Jena Experiment and thus have no specific definition of species present. The plots were mown twice a year and weeded regularly by hand. For more details see Roscher et al. (2004).

In January 2003 and again in 2011, unusually high rainfall on frozen ground in the upper catchment of the Saale river caused a flood, flooding approximately 75 % of the field site, affecting Blocks 1 to 3. Additionally, in June 2013, the experiment was flooded again for approximately 2 weeks, affecting again Block 1 and 3.

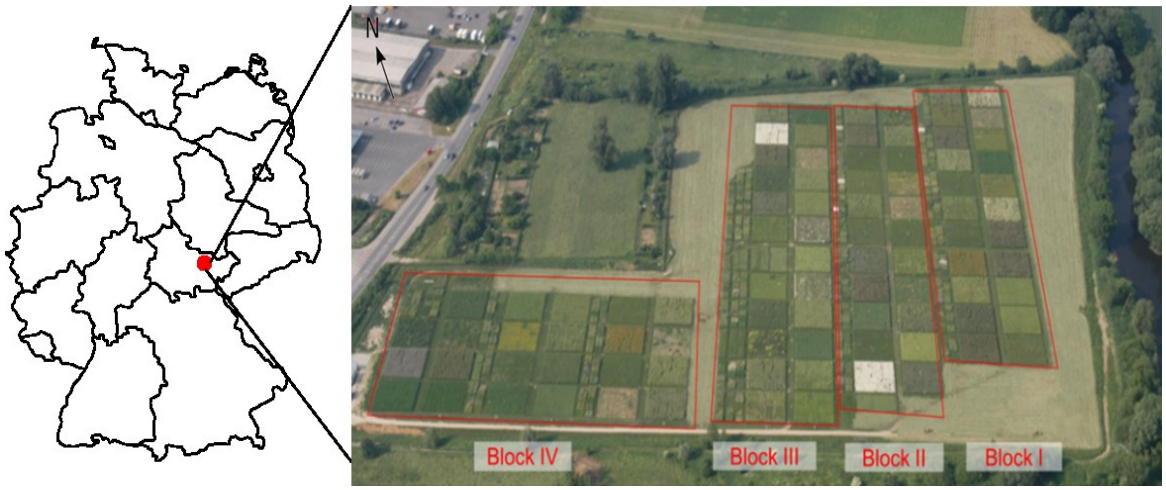

Figure1.2: Location of The Jena Experiment: Photograph of The Jena Experiment, a biodiversity treatment with more than 500 experimental plots with grassland species located in the floodplain of the Saale river, red lines marking the four blocks, (Photo by J. Baade).

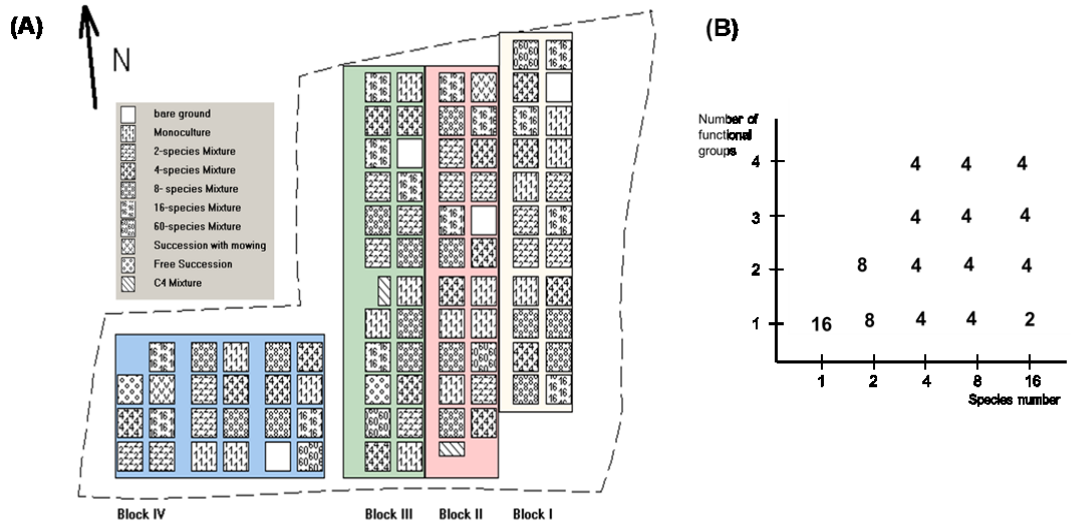

Figure 1.3: (A) Design of The Jena Experiment indicating plant species diversity levels of the large plots and the four blocks. (B) Experimental Design of the "Jena Experiment" with number of species and functional groups in different mixtures per diversity level.

1.2.2.1 Earthworm plots

On plots with one (14 replicates), four (16 replicates) and 16 (14 replicates) plant species richness, two randomly selected subplots with 1x1 m and a distance of 50 cm were enclosed with PVC shields (20 cm aboveground and 15 cm belowground) to reduce the escape of *L. terrestris* and avoid the return of endogeic earthworms (Figure 1.4A and C). The shields were removed two times a year during the mowing period. On one subplot (-ew) the earthworm density was reduced twice a year (spring and autumn) by electroshocking (Figure 1.4C). For this octet method (Thielemann 1986), four devices (DEKA 4000, Deka Gerätebau, Marsberg, Germany) were used powered by two 12 V car batteries. In each –ew subplot the extraction took

35 min. In this time the voltage was increased from 250 V (10 min) to 300 V (5 min), to 400 V (5 min), to 500 V (5 min) and to 600 V (10 min).

In the years 2003, 2004 and 2005 25 adult earthworms of *Lumbricus terrestris* were added to the subplots with non-reduced Earthworm populations (+ew). For more details about the arrangement of the steel rods for the octet devices see (Eisenhauer et al. 2009a). The measurements (one replicate) were conducted with the hood infiltrometer to obtain steady infiltration capacity on each subplot (+ew and –ew) on the weeded site (Figure 1.4 B).

1.2.2.2 Soil texture

Due to the flooding and sedimentation history of the field site, the texture in the plough horizon (0-30 cm) gradually changes from sandy loam close to the river in the east, into a strong silt loam with increasing distance from the river in the west (Figure 1.5). Soil texture was determined from soil cores at 38 locations distributed throughout the experimental site prior to plot establishment (G. Büchel, pers. Comm.). Values for each plot were interpolated by ordinary kriging (for calculated sand, silt and clay content values (%) in 10,20,30,40, 60, 80 and 100 cm soil depth see Appendix Table 1-3). The sand content (average from 10-30 cm depth) varies from 40 % near the river to 11% in the west, in contrast to the silt content which ranges from 44% to 66% respectively. The clay content shows no significant spatial trend (16-23%). Below a depth of 60 cm the gradual changes in soil texture show a rather patchy pattern (Figure 1.5).

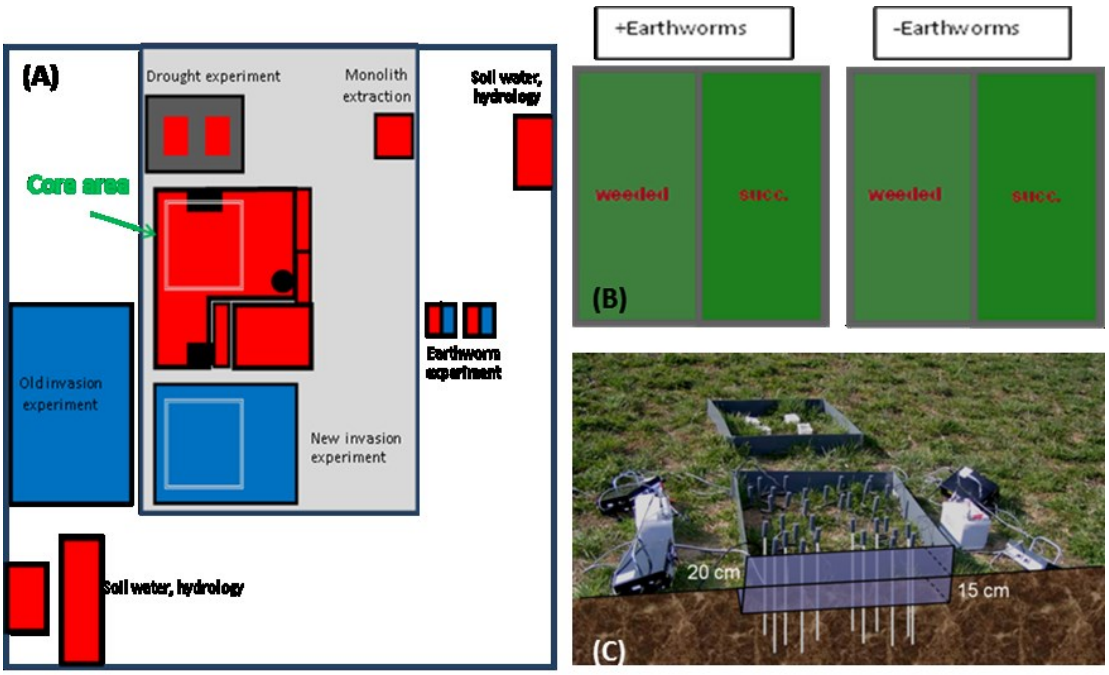

Figure 1.4: Design of the subplots (1 x 1m) for extraction from the subproject 4: (A) Layout of a large plot with overview over subplots of different subprojects (B) Design of the Subplots (1x 1m) of Subproject 4 (succ.-successions plots). (C) Photograph showing the subplots for earthworm density manipulation with the four octet devices used for the earthworm extraction by electro-shocking (picture by N. Eisenhauer).

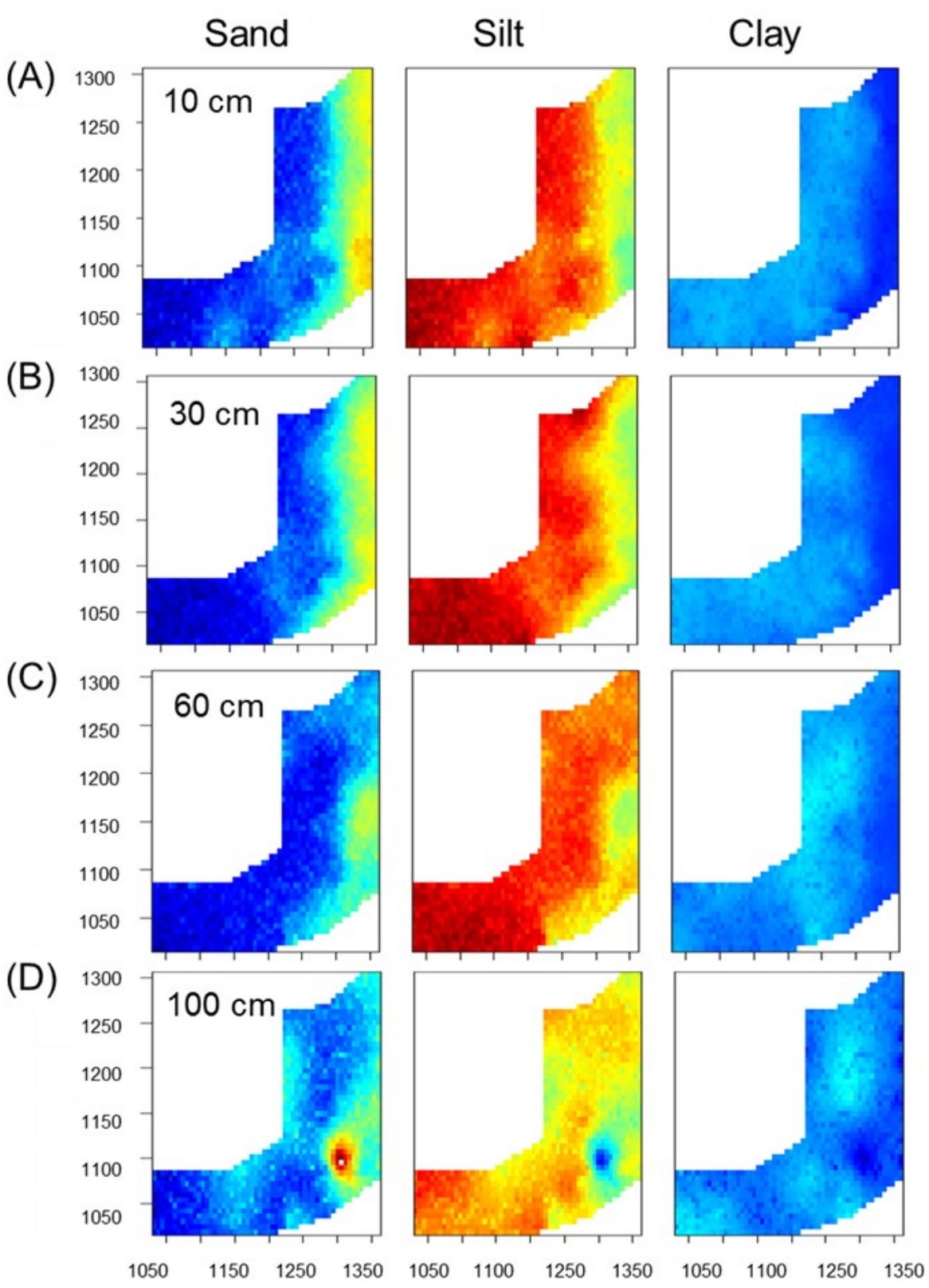

Figure 1.5: Texture gradient on the field site of the Jena Experiment for silt, sand and clay at A) 10 cm, B) 30 cm, C) in 60 cm and D) in 100 cm deep (as indicated).

1.2.3 Ecotron (Montpellier)

The monoliths originate from a temperate grassland site (Jena Experiment) located in the floodplain of the Saale river near Jena (Germany; 50°55´N, 11°35´E, 130 m NN) (Roscher et al. 2004). In December 2011, soil cores were excavated from selected plots (4 and 16 plant species) of the experimental field by UMS GmbH (München, Germany). For the excavation the lysimeters (diameter 1.60 m) with cutting edges were pushed down by a hydraulic press site to a depth of 2 m and were then extracted with a crane. Before the transport to the Ecotron facility at the end of March in 2012, the lysimeters were buried to the surface level near the field site for the winter in 2011, in order to expose the lysimeter to the same environmental conditions as the plots of the field site.

The Montpellier European Ecotron is a new experimental infrastructure developed by the Centre National de la Recherche Scientifique (CNRS, France) and provides the possibility to study ecosystems and organism under controlled environmental conditions. The large Ecotron facility in Montpellier consists of transparent and confined Tefzel domes (highly transparent ethylene-tetrafluoroethylene film for UV radiation, Figure 1.5A, B) for analyzing elementary functions under simplified conditions in order to study complex patterns observed in the field in a simplified way. The lysimeters were randomly assigned to the 12 controlled environmental chambers with controlled atmospheric conditions (air temperature, humidity and CO_2 concentration). Additionally, there are also belowground chamber under each dome that include a weighting system, soil sensors, soil temperature control system and a Marriott´s bottle to maintain a constant below ground water table (Figure 1.5 C). For four months (end of March to end of July) the lysimeters were kept under the average temperature and precipitation regimes from 2007. The spring-summer conditions in 2007 were very close to the average climate conditions in the Jena Experiment since 2002. During the Ecotron Experiment the achieved air temperature was close to the set point (14.0°C compared to 14.9°C in Jena), while the achieved averaged relative air humidity was lower (58.9% compared to 73.4% in Jena). Because the lysimeters were exposed to lower air humidity during the experiment and to slightly higher temperatures during the transport, the precipitation was increased by +23 %, compared to 2007, to reach similar soil moisture conditions. Target plant communities were maintained by regular weeding. As in the Jena Experiment the mowing took place at the end of April and at the end of July. The infiltration measurements were conducted immediately after the July mowing (Fig. 1.5B). Because one of the 12 monoliths was broken during transport, our measurements were conducted on 11 of the 12 monoliths.

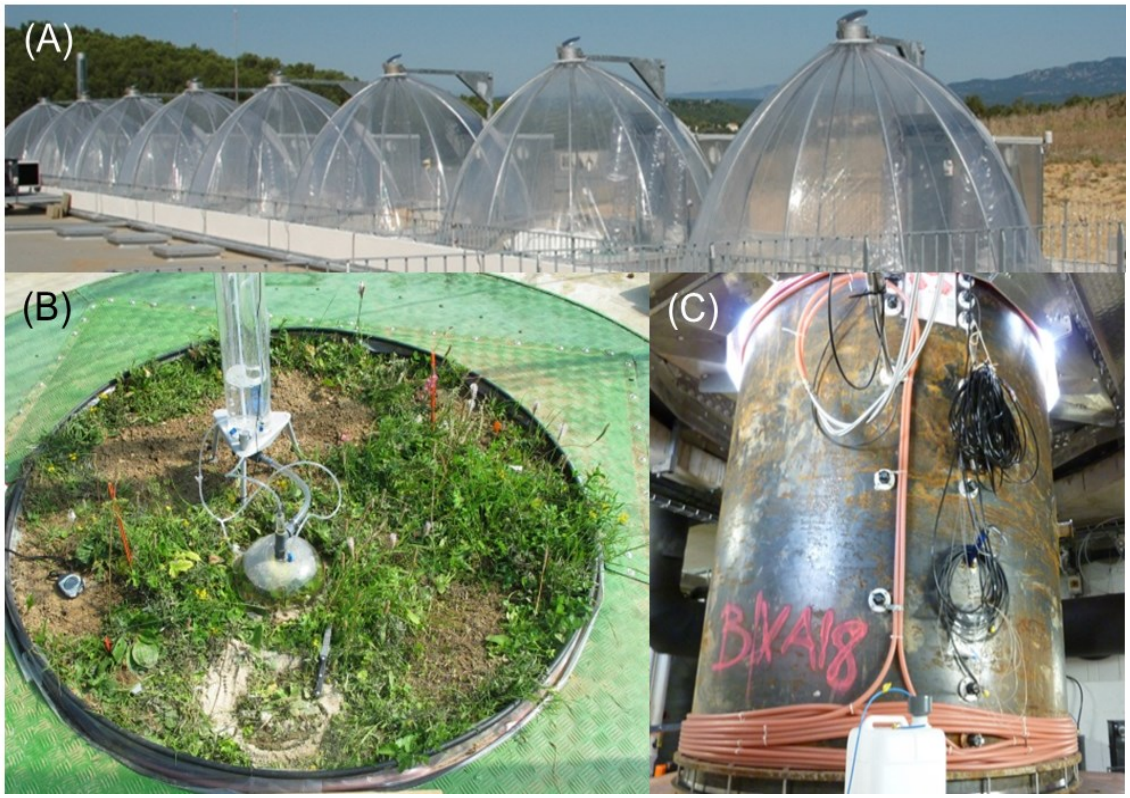

Figure 1.6: Photograph of the experimental Tefzel domes (macrocosm) at the ECOTRON facility (Montpellier European Ecotron, France) (photo by CNRS Ecotron Montpellier), (B) photograph of one macrocosms showing the infiltration procedure using a hood infiltrometer (C) Photograph of one belowground chamber under the dome (photo by CNRS Ecotron Montpellier). For more details see Chapter 1.2.3..

1.3 Objectives

1.3.1 Research Questions

The design of The Jena Experiment, with a controlled manipulation of plant diversity and covering experimental blocks with differences in soil structure and texture, allows for disentangling the relative importance of biotic (plant community, earthworms), soil structural parameter (bulk density, porosity and soil organic carbon) and abiotic (soil texture) factors on soil hydraulic properties such as infiltration capacity. In the first field experiment (Chapter 4), we aimed to explore the relation between soil water fluxes and plant community, earthworms and soil texture. In the second field experiment (Chapter 5), the objective was to quantify the change in infiltration capacity affected by soil structural parameters (bulk density, soil organic carbon, and porosity), plant community, earthworms and soil texture. In the third experiment we measured infiltration capacity on 11 monoliths with two diversity levels (4 and 16 plant species), originating from The Jena Experiment site at several depths in the CNRS Ecotron, Montpellier (chapter 6 and 7).

As a part of the hydrology subproject of The Jena Experiment the overall aim of this thesis was to investigate the several factors that improve biological activity, and therefore

counteract the compaction and loss of mechanical stability that decreases infiltration capacity and increases the intensity of flooding events. Based on several studies (Ward and Trimble 2004, Van Eekeren et al. 2010, Deb and Shukla 2012) indicating many direct influencing factors on hydraulic properties leading to contradictory results, I focused on direct and indirect mechanisms to disentangle the interrelated factors shaping infiltration capacity. This leads us to ask the overall questions:

(1) Which factors shape soil hydraulic properties such as infiltration capacity? – Are abiotic factors (soil texture) more important compared to biotic factors (earthworms, plant and functional diversity, root biomass) for the infiltration through soil?

Generally it is believed that earthworms have a positive effect on infiltration capacity (Stockdill 1966, Zachmann and Linden 1989, Edwards and Bohlen 1996). However, these positive effects are known for agriculture systems and knowledge about effects in natural communities is rare. The mechanisms behind the impact of earthworms and the plant community are not fully understood. In order to evaluate the effects of earthworms, plant species richness, plant functional group richness and texture on soil hydraulic properties in a plant diversity experiment, we try to answer the following questions:

(2) Does earthworm activity increase infiltration capacity?

(3) How does the plant community influence earthworm activity?

Summarizing the present knowledge according to the effects of biodiversity on soil water plant interactions, it has to be stated that it is difficult to derive a clear picture of the interactions between the water cycle and plant biodiversity. An increased soil water infiltration depends on soil aggregation and stability which is impacted by texture, soil fauna and vegetation parameters (Angers and Caron 1998, Six et al. 2004, Pérès et al. 2013). In order to improve the understanding of the relationship between soil structural parameters (soil bulk density, porosity and soil organic carbon) and water infiltration with respect to plant diversity, plant functional group richness and texture gradient the following questions were investigated:

(4) Do patterns in soil organic carbon content, induced by biodiversity gradients, relate to structural parameters bulk density and porosity?

(5) Do those parameters affect infiltration capacity?

Next to spatial variability of hydraulic properties across the field site, knowledge of spatial variability along a soil profile is also important for the development of optimal agricultural and land management strategies. For irrigation and soil management, it is also important to consider the role of the several factors on infiltration also through several depths. We therefore measured, in addition to field experiments, the infiltration capacity on Lysimeter taken from the field site in Montpellier (France) at several depths. The main questions of this field study were:

(6) Do the observed factors influencing soil hydraulic properties at the soil surface also affect infiltration into deeper soil strata? What factors are important drivers for the infiltration at several depths?

Infiltration measurements using the hood infiltrometer directly estimated the hydraulic conductivity via Wooding´s equation (Wooding 1968). Because these direct measurements are costly and time consuming, indirect methods were developed to estimate hydraulic conductivity based on easy to measure soil properties (Schaap et al. 1998, Schaap et al. 2001). In order to test the application of the most common pedotransfer functions (PTFs) at several depths, we ask the following questions:

(7) Can we predict observed saturated hydraulic conductivity using the pedotransfer functions (PTFs) at several depths?

1.3.2 Layout of thesis

This thesis is divided into the following chapters (Figure 1.7):

- Chapter 1 deals with the general introduction and objectives of the study. In this chapter the overall design of the Experiment is also outlined.
- Chapter 2 reviews the literature covering soil physics and structure, infiltration theory and measurement techniques of tension infiltrometer, and major factors that influence surface soil hydraulic properties.
- Chapter 3 gives a short overview of the effect of spatial variability of infiltration capacity
- The three research objectives are described in chapter 4, 5 and 6: The format of the chapters is in the form of intact papers for submission to journals. As a result this format leads to some duplication of introductory material in each chapter.
- Chapter 4 analyzes the variation of infiltration along texture, plant species and earthworm gradient
- Chapter 5 links the infiltration patterns to soil structural parameters and identifies the most important structural parameters influencing soil hydraulic properties

- Chapter 6 characterizes infiltration patterns along several soil depths (soil surface, within rooting zone, below rooting zone) and quantifies the relationship with soil structural parameters, biotic factors, soil texture, and soil moisture. In this chapter we examine if flow patterns at the soil surface continue to deeper soil layers and which factors influence this.
- Chapter 7 tests the application of several Pedotransfer functions (PTFs) for the measured hydraulic conductivities on Lysimeter in several depths.
- Chapter 8 summarizes and discusses the findings by addressing the research questions

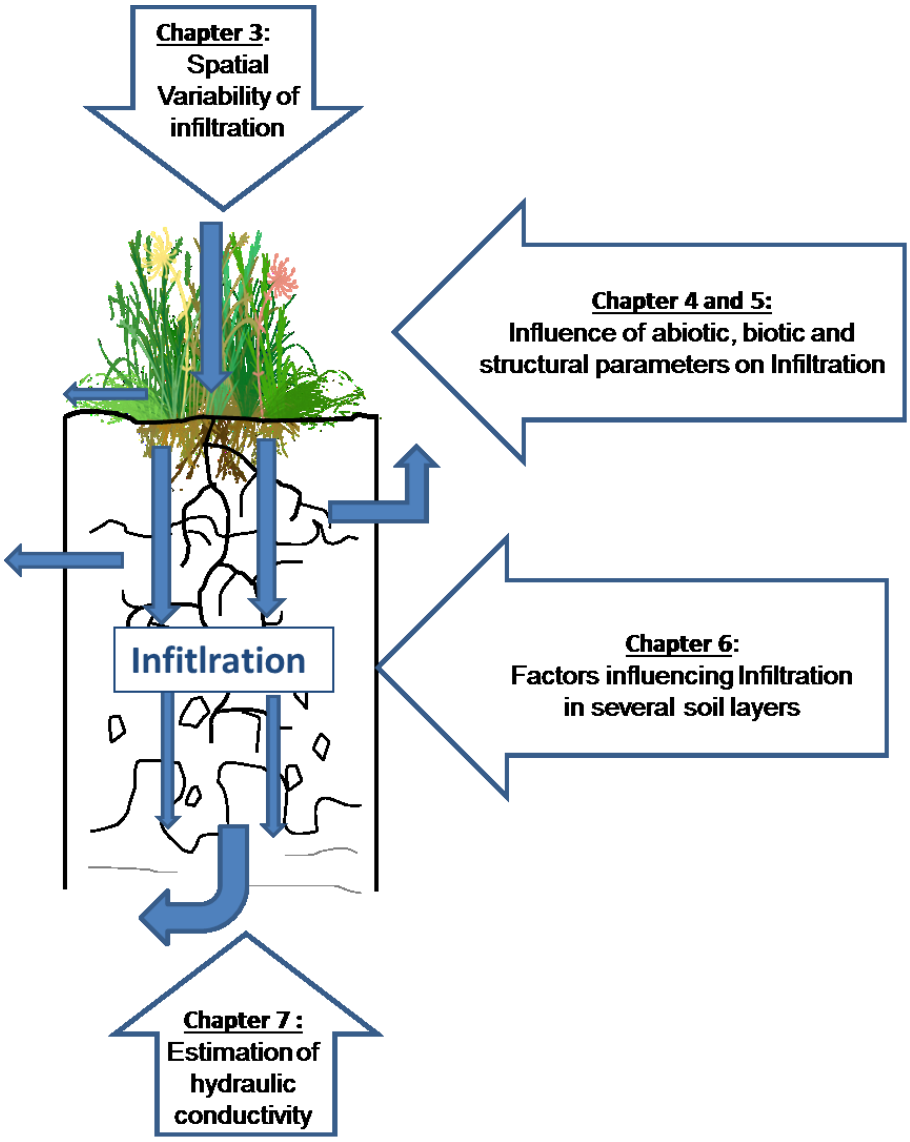

Figure 1.7: Overview of chapters of the present thesis. Further explanations can be found in the respective chapter.

Chapter
2

Background: Applied concepts

2 Background: Applied concepts

2.1 Water flow through soil

2.1.1 Components of soil

A soil mass can be described as a three phase systems: soil solid (solid particles or soil matrix), soil solution (water with dissolved substances) and gaseous (soil atmosphere) (Figure 2.1 (A).The solid matrix also contains amorphous substances, particularly soil organic matter (SOM). Generally, soils consist of approximately 45 % mineral material, 5% organic matter, and 50% void space filled with a part of water, and a part of air. In saturated soil, the voids are completely filled with water and a dry soil with air. Sandy soils normally have 35-50% pore space, while medium to fine-textured soils have 40-60% pore space. The soil mass consists of these three components forming a complex material, varying depending on weather, vegetation and management strategies. In Fig. 2.1 (B) the hypothetical composition of these components for a medium-textured soil are presented.

The relative percentage of these components, arrangement as well as the size, shape, and chemical and mineralogical composition of the particles characterizes soil structure. Thus, Dexter (1988) defined soil structure as "*the spatial heterogeneity of the different components or properties of soil*" at various scales. The determination of soil structure is mostly indirectly performed by measuring soil properties that influences the soil structure. Three categories can be classified ranging from "structureless" to a good structure: single grained, massive, and aggregated.

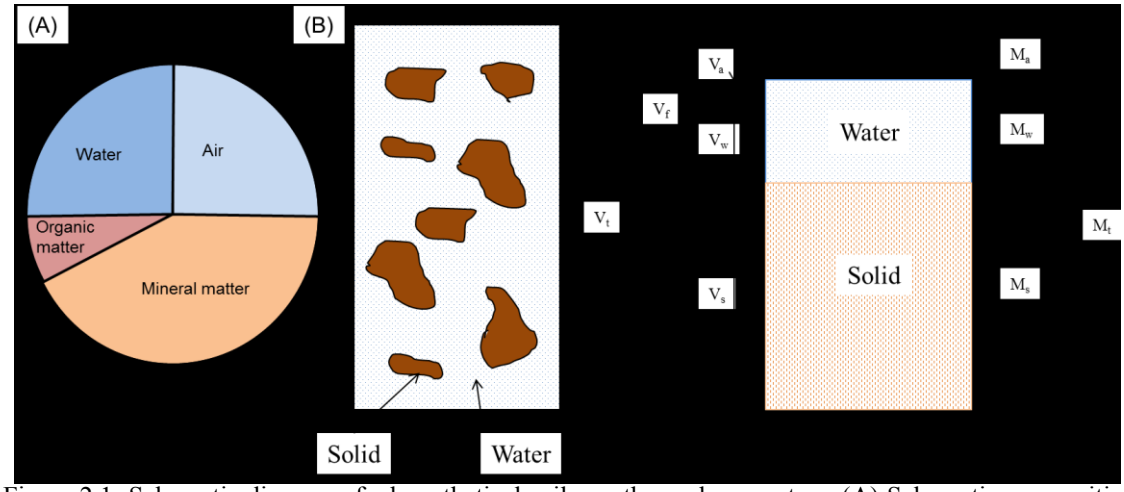

Figure 2.1: Schematic diagram of a hypothetical soil as a three-phase system. (A) Schematic composition (by volume) of the soil components for a medium-textured soil. Mineral matter and organic matter make up the soil fraction. Air and Water comprise the pore space fraction. A medium-textured soil consists of around 50% solid particles and 50% pores. (B) The three phases have been separated, showing their relative volumes and masses. The masses of the phases are indicated with: M_a = mass of air, M_w = mass of water and M_s = mass of solids and M_t = total mass. The volumes are represent with V_a = volume of air, V_w = volume of water, V_s=volume of solid, volume of pores $V_f = V_a + V_w$, V_s = volume of solids and V_t = total volume.

2.1.2 The physics of water flow

The retention and movement of water in soil, uptake and translocation in plants and loss via evapotranspiration in the atmosphere, are mainly controlled by energy relationships. Kinetic and potential energy are the two principle forms. Kinetic energy in soil is quite low and therefore negligible. In 1907 E. Buckingham introduced the term "*potential*" according to soil water flow and used an equivalent equation of Darcy´s law to quantify unsaturated flow in soils. The total potential of soil water, according to the International Soil Science Society, is "the amount of work that must be done per unit quantify of pure water in order to transport reversibly and isothermally an infinitesimal quantity of water from a pool of pure water at a specific elevation at atmospheric pressure to the soil water (at a specific point)" (Aslyng 1963).

Water flow through soil is driven by three major forces. This includes soil water potentials of gravitational (Ψ_G), matric (Ψ_M) and osmotic (Ψ_O) potential. The sum of these potentials ($\Psi_= \Psi_{G+} \Psi_M + \Psi_O$) resulted in the total soil water potential (Miller 1989). Total water potential describes the energy state in the soil-plant-atmosphere continuum. The energy status of standing water is zero. Differences in total potential between two points in the soil drive the water flux in the direction of the lower potential. The gravity potential is equal to the work which is needed to lift a body against the earth´s gravitational from a reference level to its present position. Thus the gravity potential is higher the greater the height of water above a given reference point. The gravity potential is taken as positive or zero, when the reference level is the soil surface then the gravity potential is negative. The gravitational potential near the soil surface is always higher compared to Ψ_G of the subsoil. Under saturated conditions, difference in Ψ_G drives the water flow, whereas under unsaturated conditions matric potential determines the water flow. Matric potential is the measurement for the influence of the matric or how much water is held in the soil by adhesion and cohesion (Figure 2.2). This potential is always the opposite of the gravity potential. Therefore it receives a negative sign. The osmotic potential is determined by the amount of dissolved salts and therefore plays an important role in arid areas. However, for the water flow into plant root osmotic potential is important. Normally, plant root potential is lower than the soil water potential, water moves from the soil to the root. The less the water content of a soil, the greater the forces you need to exclude water from the soil. The required energy to move water differs between the soil moisture states: saturation, filed rate and permanent wilting point (Figure 2.2).

When all soil pores are filled with water during a heavy rain event or irrigation, the soil becomes saturated. After the drainage has stopped water in the larger pores is replaced by air.At field capacity, smaller pores (micro - and mesopores) retain water and larger pores are filled with both air and water. The direction of potential energy is downward through the soil forced by gravity and mainly through larger pores.

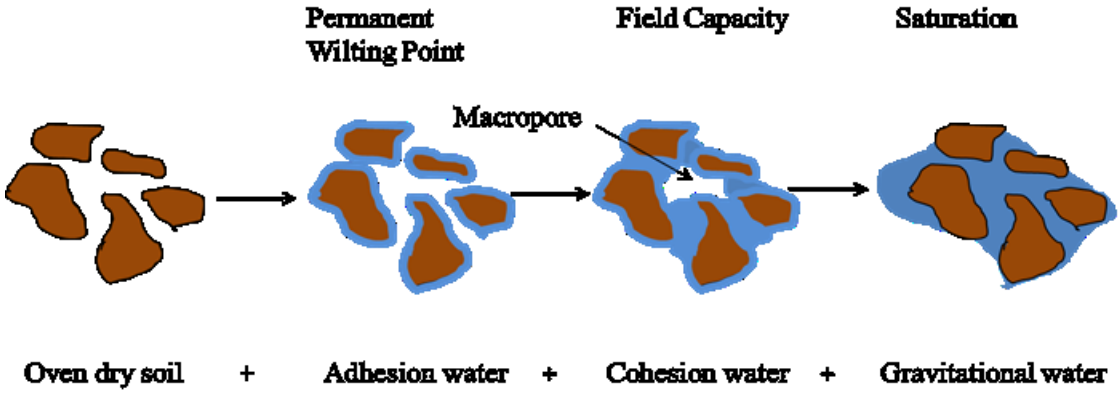

Figure 2.2: Schematic overview of air-water interface during wetting processes in porous media.

If the water content decreases again and the soil matric potential becomes more negative, water is held to mineral surfaces (capillary forces). At this soil moisture level (permanent wilting point), plants can no longer adsorb water from the soil. Soil texture, particularly clay content, has a strong influence on the field rate and the permanent wilting point (Rowell 1994).

2.1.3 Preferential flow (macropore flow)

The generic term "*preferential flow*" is also known as non-uniform flow, which describes the process of water movement through a porous medium by pores bypassing the soil matrix pore space (Luxmoore 1991). During infiltration, preferential flow is a function of the initial matrix water content, rainfall intensity, rainfall amount, matrix hydraulic conductivity, and the soil surface contributing area (Trojan and Linden 1992). Based on the differences in flow processes, preferential flow can be subdivided into three different types, such as macropore flow (Figure 2.3), fingered and funneled flow (Germann and Beven 1981, Bundt et al. 2001). Macropore flow is the water flow through pores formed by plant roots (Meek et al. 1992), earthworms (Lavelle et al. 1992, Lavelle 1997, Angers and Caron 1998) or cracks and fissures (Germann and Beven 1981, Messing and Jarvis 1990, Zehe and Flühler 2001) and is much larger than flow through soil matrix pores. Water flow from macropores into the surrounding soil matrix can be week or with no interaction (Figure 2.3). Fingered flow (flow instability) can be caused by profile heterogeneity, water repellence and/or air entrapment. The presence of sloping layers or large impeding structures such as clay lenses can cause "*funnelling*" by redirecting the downward water flow. Preferential flow is often attributed to macropore flow (Luxmoore 1991, Bundt et al. 2001) because macropore flow is the dominant flow process in many soils and has a strong influence on the total infiltration through soil (Beven and Germann 1982).

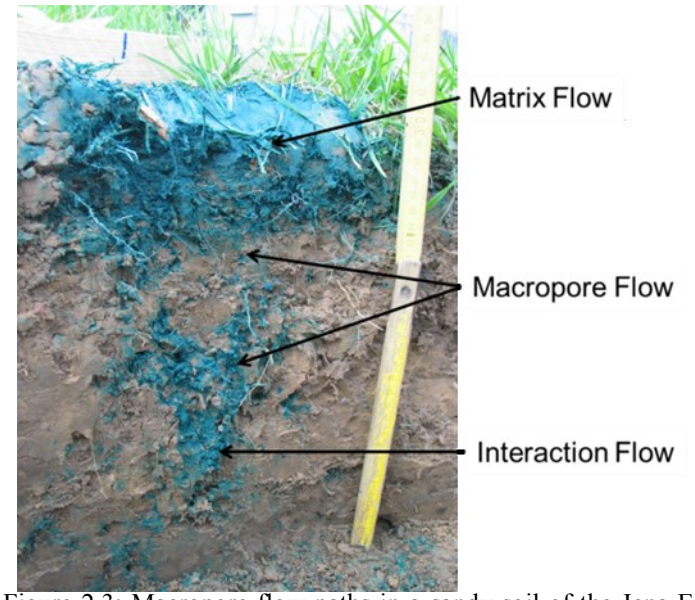

Figure 2.3: Macropore flow paths in a sandy soil of the Jena Experiment, indicated by blue dye. At the soil surface more uniform flow (Matrix Flow) occur, followed by differentiation into macropores in the subsoil (Macropore Flow). Water transfer from the macropores into the surrounding soil matrix is called interaction flow.

The process of macropore flow is shown in Figure 2.4: When the overall water input from precipitation or irrigation (1) exceeds infiltration capacity of the soil, the generated overland flow (3) results in water flux into macropores (2). This causes a water content increase inside the macropore (4). A portion of the infiltrated water is absorbed by the soil matrix at the soil surface (matrix flow) (5) and through the macropores walls (interaction flow) (6). The other portion will percolate downwards into the macropore (4). Factors affecting the flow of macro- and micropore are presented in chapter 2.3.

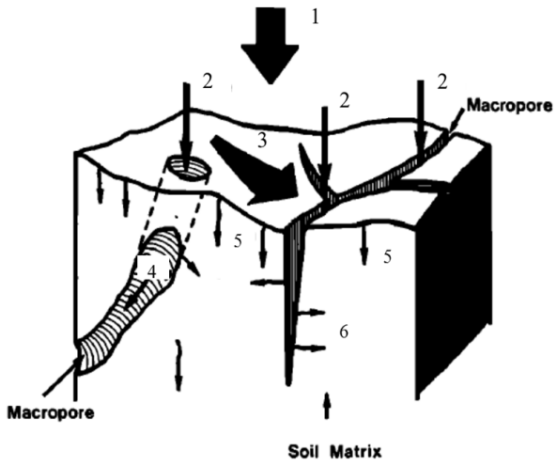

Fig. 2.4: Schematic presentation of fluxes occurring during infiltration into a macroporous soil. 1. represents overall water input (precipitation, irrigation), 2. represents volume flux density into soil macropores (macropore flow), 3. represents overland flow, 4. represents volume flux density and volumetric soil moisture 5. represents infiltration into the top soil matrix (matrix flow), 6. represents water absorbance from macropores into the soil matrix (interaction flow). Modified afterBeven and Germann (1982).

2.2 Infiltration measurements

Because hydraulic conductivity is a complex variable it is difficult to obtain quantitative measurements of this soil property. Direct and indirect methods exist to estimate soil hydraulic conductivity. To determine the saturated hydraulic conductivity (K_s), a good approach is to measure infiltration of the soil. Mohanty et al. (1994) mentioned some field methods for measuring the hydraulic conductivity: the Guelph permeameter method, the constant head permeameter method, the disk permeameter method, the double tube method and the velocity permeameter method. In our field experiment we used a new type of tension infiltrometer called a hood infiltrometer (more details in Chapter 2.2.1, Figure 2.5).

2.2.1 Hood infiltrometer

This *in situ* technique using a hood infiltrometer (Schwärzel and Punzel 2007) is a good method for the determination of infiltration capacity. Therfore, a small hood with a diameter of 17.6 cm (for Ecotron experiment 24.8 cm) is placed with the open site to the soil surface filled with water. Through a "Mariotte" bubble tower with a rate of 5 liters different water pressures can be applied (Figure 2.5A) (Schwärzel and Punzel 2007). We conducted measurements at pressure supply heads to the bubble point of the soil. For hood infiltration measurements no contact layer and therefore no preparation of the soil surface is needed. The source of infiltration takes place by the circular shaped soil surface covered by the hood. The pressure in the hood is regulated by the "*Mariotte*" bubble tower. The effective pressure head (H) can be calculated between the difference value in the U-pipe manometer (U_s) and the pressure value in the standpipe of the hood (H_S):

$$H = U_s - H_s \qquad \text{(Equation 1.1)}$$

In this study negative pressure is matric potential. With increasing matric potential (pressure head becomes more negative), the water flow decreases through pores. For a specific matric potential (Ψ_M) the equivalent diameter (d_e) of the largest soil pore conducting water can be estimated after Jarvis et al. (1987). At Ψ_M = 0 m the soil is saturated and the entire pore spectrum is potentially active. At Ψ_M = -0.02 m, the largest active pores correspond to d_e =1.5 mm, at Ψ_M = -0.04 m to d_e = 0.75 mm and at Ψ_M = -0.06 m to d_e = 0.5 mm (Table 2.1).

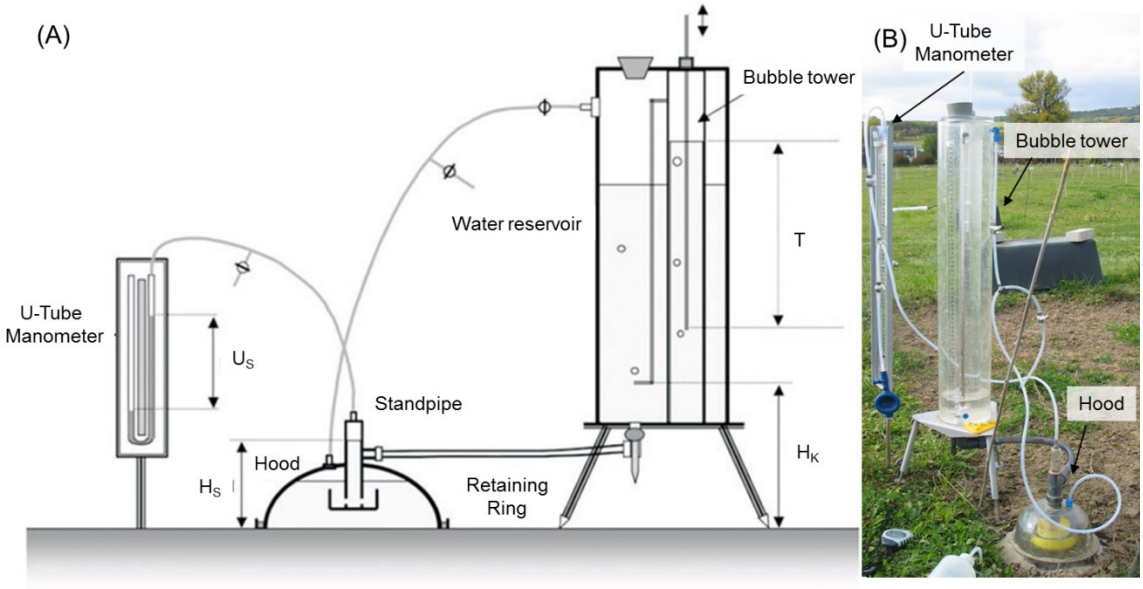

Figure 2.5: A) Schematic of the hood infiltrometer (not to scale) from UGT. From the difference of the height of the water level in the standpipe and the negative pressure head at the U-tube manometer, the effective pressure head on the soil surface can be determined. The zero point of the scale of the standpipe is at the soil surface. U_s = negative pressure at the U-tube manometer, H_s = height of the water table in the standpipe, H_k = infiltration chamber height, T = submergence depth of the air pipe (modified after Schwärzel and Punzel (2007)). B) Infiltration measurement using a Hood infiltrometer at the field site of The Jena Experiment.

Table 2.1: Overview of the equivalent diameter (d_e) corresponding to the specific matric potential (Ψ_M) estimated after Jarvis et al. (1987).

Matric potential Ψ_M (m)	equivalent diameter d_e (mm)
0	> 1.5
-0.02	1.5
-0.04	0.75
-0.06	0.5

2.2.2 Analysis/Calculation

In 1865, Henry Darcy, a French hydraulic engineer, described a series of experiments showing that the flow rate of water through sand filters was proportional to the hydraulic gradient, by using following equation, also called Darcy´s Law (Darcy 1856):

$$q = \frac{Q}{A} = -K(\theta)\frac{d\Psi_p}{dz} - 1 \qquad \text{(Equation 1.2)}$$

where q is the specific discharge Q/A, respectively the volume water flow in units of volume per time/area (m^3/ms).

K is a factor of proportionality, or the saturated hydraulic conductivity (LT^{-1}) for a given grade of sand. The gradient of the water pressure is expressed as $d\Psi p/dz$. Hydraulic conductivity was lower for fine sand in comparison to coarse sand. In general, K depends on the moisture content and pressure head (Ward and Trimble 2004). In saturated soils, K is defined as the saturated hydraulic conductivity (K_{sat}).

Typically, most of the models for the calculation of unsaturated water flow within the soil are based on a numerical solution combining Darcy´s equation with the continuity equation referred to as Richards or diffusions equation (Richards 1931):

$$\frac{d(\theta)}{d(t)} = \frac{d}{dz} * K(\Psi)\frac{d(\Psi+z)}{dz} - q(z) \qquad \text{(Equation 1.3)}$$

where θ is the soil water content [L^3L^{-3}], t is time [T], z is a spatial coordinate [L], Ψ is the matric potential expressed as a pressure head [L], K(h) is the unsaturated hydraulic conductivity [LT^{-1}] as a function of the matric potential, and q(z) is the sink/source term [T^{-1}] that corresponds to the water uptake by roots or the water release from roots due to hydraulic redistribution. The validity of the equations is based on the assumption that the soil is saturated, homogenous and isotrop, while the flow laminar and isothermal. Consequently, the Richards equation does not account for all active processes and therefore does not represent the real water flow in natural systems. Based on Gardner ´s exponential model of the saturated hydraulic conductivity:

$$K(h) = K_s * \exp(\alpha * h_0) \qquad \text{(Equation 1.4)}$$

where K_s [LT^{-1}] is the saturated hydraulic conductivity and α [L^{-1}] is the exponential slope under a given supply potential h_0. Analysis of infiltration measurements are based on Wooding's (1968) solution for infiltration to describe a three dimensional steady state infiltration into soil from a shallow circular source of radius r with a constant pressure head by

$$Q(h_0) = \pi * r^2 * K_s * \exp(\alpha * h_0) * \left(1 + \frac{4}{\pi * r * \alpha}\right) \qquad \text{(Equation 1.5)}$$

where r is the disk radius and $Q(h_0)$ is the steady state flow rate (L^3/T) under a given supply potential h_0 (L). For a given disk radius the unknown parameters K_s and α can be solved by measuring with the hood infiltrometer at multiple supply potentials (Ankeny et al. 1990, Messing and Jarvis 1990, Reynolds et al. 2000). Then α is a constant in the interval between the two applied pressure heads $h_{0(i)}$ and $h_{0(i+1)}$ when Equation 1.4 and 1.5 are applied piecewise:

$$\propto_{i+1/2}=\frac{ln(\frac{Qi}{Qi+1})}{h_{0(i)}-h_{0(i+1)}} \qquad i = 1,\ldots, n\text{-}1 \qquad \text{(Equation 1.6)}$$

where n is the number of supply pressure heads. Rearranging Equation (3) gives

$$K[h_{0_{(i+1/2)}}] = \frac{Q_{i+1/2}}{\left(\pi r^2+\frac{4r}{\propto_{i+1/2}}\right)} \qquad i = 1,\ldots, n\text{-}1 \qquad \text{(Equation 1.7)}$$

The steady infiltration capacity between supply pressure heads $h_{0(i+1/2)}$ are calculated by

$$Q_{(i+1/2)} = \exp\left[\frac{\ln(Q_i)+\ln(Q_{i+1})}{2}\right] \; i = 1,\ldots, n\text{-}1 \qquad \text{(Equation 1.8)}$$

Using the known values $h_{0(i+1/2)}$, $K_{i+1/2}$, and $\alpha_{i+1/2}$ you can calculate the saturated hydraulic conductivity K_s by

$$K_s = \frac{K_{h_{0(1+1/2)}}}{\exp\left[\propto_{i+\frac{1}{2}}*h_{0(i+1/2)}\right]} \qquad i = 1,\ldots, n\text{-}1 \qquad \text{(Equation 1.9)}$$

2.3 Factors affecting surface soil hydraulic properties

Water flow through soil is highly variable in space and time (Messing and Jarvis 1990, Cerdà 1996) due to soil heterogeneity and factors related to soil surface conditions impact the soil pore system. Parameters that are known to be important for spatial and temporal changes in hydraulic parameters and influence soil matric forces and pore space are mentioned in the following chapters. These factors were investigated in more detail in this study. In this thesis, I distinguish between abiotic soil factors (texture), which are constant in time, and biotic factors (soil fauna, plant community and soil structural parameters), which change dynamically depending on environmental factors.

2.3.1 Biotic factors

2.3.1.1 Earthworms (Lumbricidae)

Important components of many terrestrial ecosystems are earthworms that act as soil ecosystem engineers. They have an influence on soil organic matter dynamics, hydraulic properties, pedogenetic processes, and plant performances by altering soil structure, water movement, nutrient dynamics, and plant growth (Lavelle 1988, Edwards and Bohlen 1996, Scheu 2003, Six et al. 2004). Aristotle was probably one of the first to recognize the importance of earthworms. He referred to them as the "intestines of the soil“. In the middle of the 18th century, Linnaeus gave the first description of *Lumbricus terrestris* taxonomy. Darwin (1882)

was one of the first scientists who showed the biological importance of earthworms to soil fertility and development for the agriculture.

Bouché (1977) defined the zone 2mm around earthworm burrows as the term drilosphere. Later in 1988 Lavelle also included the earthworm itself and all the soil volume that is directly and indirectly modified by earthworms to the drilosphere. Earthworms can be defined into three major ecological types based on their different localization in soil, burrowing behavior and food resources: endogeic, epigeic and anecic earthworms (Bouché 1977) (Figure 2.6). Depending on the ecological type, earthworms create burrows ranging from 2-11mm in diameter (Ehlers 1975, Syers and Springett 1983). They have different influences on the drilosphere components because they differ in depth and orientation of the burrows, casting manner, morphology, size, pigmentation and relationship to the soil microflora (Lavelle, 1988). Epigeic species (surface soil and litter species) live within the surface plant litter. Endogeic species (upper soil species) build only temporary horizontal channels and refill their burrows (Lavelle et al. 1995). These small worms with a diameter ranging between 2-5 mm are adapted to highly variable moisture, temperature and high organic matter content of soil (Pérès et al. 1998). An intermediate type of earthworm between the litter-dwelling epigeic and the soil-dwelling endogeics are anecic species (deep-burrowing species). A typical representative of the anecic species is *Lumbricus terrestris*. These species burrow long vertical casts in the soil and feed mainly on surface litter. Most of the burrows have a diameter larger than 5 mm (Edwards and Bohlen 1996) and can exist for a long time up to a depth of 2 m (Edwards et al. 1992), even after the death of the worm. Because of the different mixing and crawling strategies, endogeic and epigeic earthworms mainly increase the infiltration in the topsoil, as opposed to anecic species which enhance water flow to deeper soil strata (Shuster et al. 2002) (Figure 2.6). The burrowing activity is different not only between the ecological types, but also between the different species from one ecological group (Bastardie et al. 2003).

Through their burrowing activity, earthworms affect infiltration (Shipitalo and Butt, 1999), water movement (Shipitalo et al. 2004), plant performance (Wurst and Jones 2003), soil physical properties (Lavelle 1988), microbial communities (Brown 1995, Scheu 2003) nutrient cycling (Edwards and Bohlen 1996), soil aggregation (Shipitalo and Protz 1988, Six et al. 2004) and vegetation development (Milcu et al. 2006). Some studies have documented that earthworms enhance plant productivity (Hopp and Slater 1948, Stockdill 1966, Schmidt and Curry 1999). Eisenhauer et al. (2009b) showed that earthworms also increase belowground competition by increasing plant diversity, and that legumes benefit from earthworm abundance. Earthworm performance is negatively affected mainly by the presence of grasses and benefits by the presence of legumes (Eisenhauer et al. 2009a). It has been suggested that legumes and earthworms are mutualistic related (Eisenhauer et al. 2009b).

Figure 2.6: Three major ecological types of earthworm defined by Bouché (1977). A) Pictorial representation of the three ecological functional groups of earthworms as proposed by Bouché (1977; (modified after http://www.regenwurm.ch/files/mediapics/LEBENSRAUM/full/Illustration_retouchiert.jpg).

Several studies found that the infiltration capacity is two to ten times higher in soils with earthworms (Slater and Hopp 1947, Stockdill 1966, Zachmann et al. 1987). Also soil properties, management practices (Lachnicht et al. 1997), soil types (Visa 1992) and vegetation cover (Zartman et al. 2012) affect earthworm abundance. It should be mentioned that earthworms can also have an opposite effect on soil structure by increasing bulk density due to "compacting species" (Blanchart et al. 2004, Six et al. 2004). The impact of earthworms on soil structure and aggregation can vary considerably between the different ecological groups (Six et al. 2004). Epigeic species have no or little effect on soil structure and stability, whereas anecic and endogeic species play an important role for soil formation and aggregation (Shipitalo and Protz 1988).

2.3.1.2 Plant biodiversity

The term "*Biodiversity*" is "*the variation of life at all levels of biological organization*" (Gaston and Spicer 2004). It can be described by the number of entities, evenness of their distribution, and the differences in their functional traits (Hooper et al. 2005). Because it is

difficult to measure biodiversity, species richness has become an often used approach in ecological studies (Gotelli and Colwell 2001).

The effect of how plant biodiversity might influence hydraulic pathways in soil is not clearly understood. However, there is an increasing number of ecological studies that highlight the influence of plant species numbers and/or composition on ecosystem processes and properties such as plant productivity and nutrient cycling (Hector et al. 1999, Loreau and Hector 2001, Spehn et al. 2004). Higher Biomass production is associated with larger and longer macropores (Grevers and Jong 1990). As well, earthworm abundance and root biomass are positively related to plant species richness, which changes the number of macropores and have an influence on water relations and movement in the soil (Bardgett et al. 2001).

Other soil properties, like aggregate stability, are influenced by plant species richness (Angers and Caron 1998, Pohl et al. 2009), due to their differences in root functional traits (root biomass, diameter of coarse and fine roots, root orientation and distribution) (Gyssels and Poesen 2003). Next to aggregate stability the root system affects the infiltration capacity, bulk density, organic and chemical content and shear strength (Six et al. 2004, Bronick and Lal 2005). Therefore, first growing plant roots can clog pore, thus resulting in a reduced infiltration capacity. However, if the roots decompose, the created channels increased the infiltration capacity (Barley 1954, Gish and Jury 1983, Mitchell et al. 1995).

2.3.2 Soil structural properties (bulk density, porosity and soil organic carbon)

Bulk density and porosity are good soil structural indicators for characterization changing soil structure and aggregation (Six et al. 2000). High bulk density indicates a low porosity and implies that root growth is reduced, which results in poor air and water flow through the soil (Stirzaker et al. 1996). Management and vegetation cover affect organic matter content, soil structure and porosity. Soils with high organic matter content and porous structure are contributed to lower bulk density and higher porosity (Franzluebbers 2002). Additionally, Berglund et al. (1980) have shown that organic matter correlates positively with infiltration capacity, reflecting the importance of organic matter for enhancing soil structure and macroporosity by improving humus and clay complexes in the soil.

The change of bulk density is used as an indicator of soil compaction (Alaoui et al. 2011). Compacted soils have a bulk density higher than 1.6 g/cm³, while porous soil with high organic matter have bulk densities around 1.0 g/cm³. The greater the bulk density the lower the total pore space for water flow and root growth. But bulk density cannot account for changes of the shape and size of the pores in the soil. In contrast to silt and clayey soils, sandy soils have a higher bulk density caused by a low volume of pores. Generally, most rocks have a bulk density

of 2.65 g/cm³, while medium textured soils with 50 percent pore space have a bulk density around 1.33 g/ cm³.

Soil porosity refers to that part of a soil volume that is not occupied by soil particles or organic matter, it is the fraction of the total volume occupied by pores or voids. This value can range from 30 to 60% (Hillel 1998). Pore spaces are filled with air, other gases, or water. Large pores (macropores) allow the movement of air and the drainage of water. Also within these pores, root growth and soil fauna activity is promoted. Sandy soils are often less porous compared to silt or clayey soils, because they consist of a lower amounts of small pores and are dominated by larger, fewer pores. Because of the shrinking and swelling characteristic of clayey soils, the porosity here is very variable. With increasing organic matter, the porosity also increases, which leads to a higher infiltration (Franzluebbers 2002).

Besides the primary matrix porosity (solid phase of soil), pores created by root, soil fauna and cracks form a secondary porosity. Therefore water flow in soils can occur between the primary and secondary porosity systems. Generally, porosity is mainly divided into textural porosity (matrix), as the pore space between the primary particles (intra-aggregate), and structural porosity (inter-aggregate), as the pore space between micro-aggregates containing macropores such as biopores, cracks and fissures (Hillel 1998). Macroporosity (structural porosity) is the most dynamic part of total porosity due to tillage, climate and biological activities. These large pores are important for plant growth and improved infiltration. Compaction of the soil by agriculture management results in an increase in bulk density, a decrease in porosity, which leads to a decrease in infiltration, and an increase in run-off and soil erosion (Berglund et al. 1980, Franzluebbers 2002).

Calculations

Soil bulk density (ρ_b) is calculated as the dry weight of soil divided by its total soil volume (volume of soil particles and pores):

$$\rho_d = \frac{oven\ dry\ weight\ soil}{volume\ of\ soil} = \frac{M_s}{Vs} \qquad \text{(Equation 1.10)}$$

where M_s is the weight of oven dry soil (g) and V_s the volume of the container (cm³).
Soil porosity is the ratio of the volume of soil pores to the total soil volume:

$$Porosity = \frac{volume\ of\ pores}{volume\ of\ the\ soil\ sample} = \frac{V_v}{V_t} \qquad \text{(Equation 1.11)}$$

where V_v is the volume of pores (cm³) and V_t the volume of soil sample (cm³).

2.3.3 Soil texture

A very important abiotic factor, which is controlled the rate of infiltration, is the type of soil. Soil can be classified into four soil texture classes: sands, silts, loams and clays depending on the proportion of small, medium and large particles (clay, silt, and sand). Sand particles range in size from 63–2000 μm, silt particles ranges from 2–63 μm and clay is made up of particles less than 2 μm in diameter (Ad-hoc-AG Boden, 2005). Generally, water moves faster through coarse (sandy) soil because of the large pores as opposed to through fine grained (clayey) soil with smaller pores. Traditionally, prediction of hydraulic conductivity is based on soil texture, bulk density or organic matter content, implying a decrease of hydraulic conductivity with an increase of a fraction of fine grains (Blackburn 1975, Wösten and Van Genuchten 1988, Archer et al. 2002). This relationship can be reversed due to soil structuring processes leading to interconnected macropores (Jarvis and Messing 1995, Lin et al. 1999). Several studies showed that soil texture in dry regions plays an important role for water availability in soil, thus affecting the vegetation structure (Barnes and Harrison 1982, Knoop and Walker 1985, Parker 1991).

Chapter

3

Spatial variability of infiltration capacity

3 Spatial variability of infiltration capacity at field scale

3.1 Introduction

Hydraulic conductivity is an important parameter for soil-water-plant interactions and therefore a critically important input parameter in hydrological models for modeling water and solute transport through the soil profile (Schaap et al. 2001). Among soil properties hydraulic conductivity has the greatest statistical variability (Deb and Shukla 2012), which leads to a high error term in the output of hydrological models. The variability of soil hydraulic conductivity depends on the method of measurement, as well as on several factors such as soil type, soil management and biotic factors (Hillel, 1998; Ward, 2004). The objective of this study was to determine the spatial variability of the soil surface hydraulic properties such as infiltration capacity depending on plant species richness (2.4 and 8 plant species) by using a hood infiltrometer. The results serve as a basis to get an idea about the results from the statistical analysis in the next measurement experiments.

3.2 Material and methods:

3.2.1 Experimental set-up

At the Jena Experiment field site (chapter 1.2) we measured infiltration capacity on three plots in Block 3 under nearly same texture content for 2, 4 and 8 plant species. To explore spatial variation we replicated our measurements 9 times on one monolith (Figure 3.1) in May and June using a hood infiltrometer (Chapter 2.2.1).

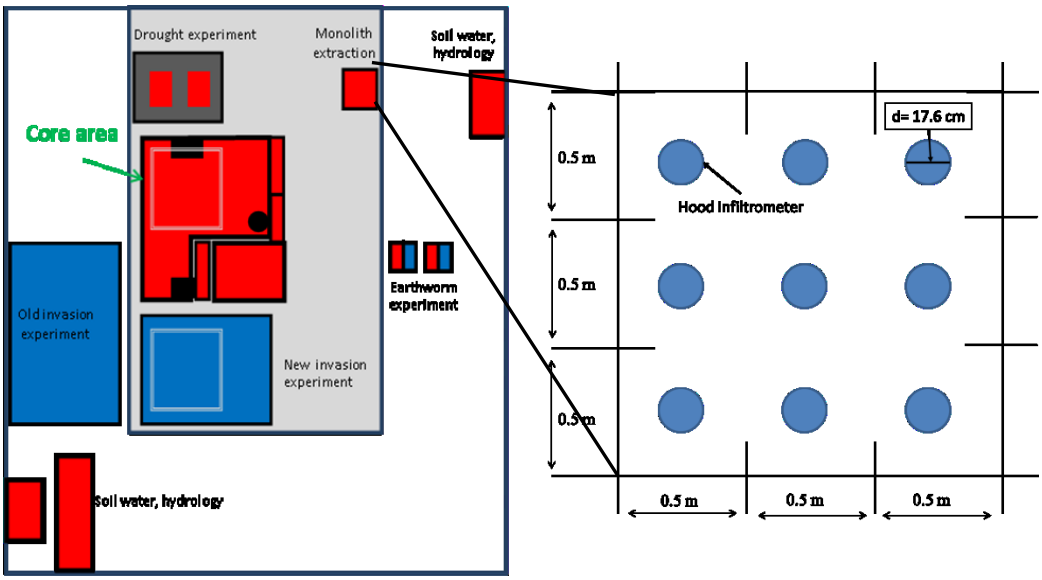

Figure 3.1: Repeated measurement (n=9) points on monoliths taken in 2011 in spring and autumn. Measurements were conducted with a hood infiltrometer with a diameter of 17.6 cm.

3.2.2 Analysis

For the characterization of the spatial variability of the infiltration capacity within plant species richness and month, we used the Coefficient of Variation (CV), standard deviation and mean. A CV≤10% contributes to a weak variability, a CV between 10 and 100% to a moderate variability, and CV ≥ 100% to a strong variability. We also check our data for outliers. After Zuur et al. (2010) an outlier is defined as an observation with a large or small value compared to the majority of data points. There is no mathematical definition to determine when an outlier is an outlier. In the past there has been much discussion regarding the handling of extreme data points and their removing from the dataset. According to Wainer (1976) we define an outlier or so called "*fringeliers*" as an outlier, when the observed value lies three standard deviations from the mean.

3.3 Results

The CVs for the infiltration capacity decreased for 2 plant species (CV=111%) to 4 plants species (CV=44%) and then increased slightly for 8 plant species (CV=57%) at saturation in May. CVs decreased for 2 plant species (CV=105%) to 4 plant species (CV=26%), and then also increased for 8 plant species (CV=63%) in June 2011 (Table 3.1). In May two data points and in June one data point all on plots containing 2 plant species were detected as outliers because the value was three times higher than the standard deviation of the overall mean (Figure 3.2). By removing the outliers in May, the CV increased continuously from 2 species (CV=33 %) to 8 species (CV=57 %). For two plant species the variation changed from strong to moderate by removing outliers. But in June, the removed outliers did not change the overall pattern and only reduced the CV for 2 plant species richness from 105% to 102% (Table 3.1). For all data points, removing the two outliers in May strongly reduced the mean, SD and CV. In June, removing one outlier, the mean, SD and CV was only slightly reduced. In May infiltration capacity did not correlate with plant species richness (r= -0.192, p=0.328), but after removing the outliers a trend was observed (r=0.288, p=0.154). Also in June infiltration capacity did not correlate with plant species richness (r=0.034, p=0.867), even after removing outliers (r=0.203, p=0.321).

Table 3.1: The statistical variability of infiltration capacity (*10^{-6} m/s) at saturation for 2,4 and 8 plant species in Block 3 for spring (first number) and summer (second number).

	May	**July**
SR 2		
Mean (*10^{-6} m/s)	215.82/95.67*	96.27/71.01*
SD	241.47/31.10*	101.66/72.46*
CV (%)	111.88/32.50*	105.59/102.04*
SR 4		
Mean (*10^{-6} m/s)	74.49	91.23
SD	32.99	23.79
CV (%)	44.29	26.08
SR 8		
Mean (*10^{-6} m/s)	121.30	100.29
SD	69.56	62.93
CV (%)	57.34	62.74
All Plots		
Mean (*10^{-6} m/s)	134.96/96.40*	95.93/88.14*
SD	150.56/50.87*	67.73/55.40*
CV (%)	111.56/ 52.77*	70.60/62.85*

* indicates results after removing outliers

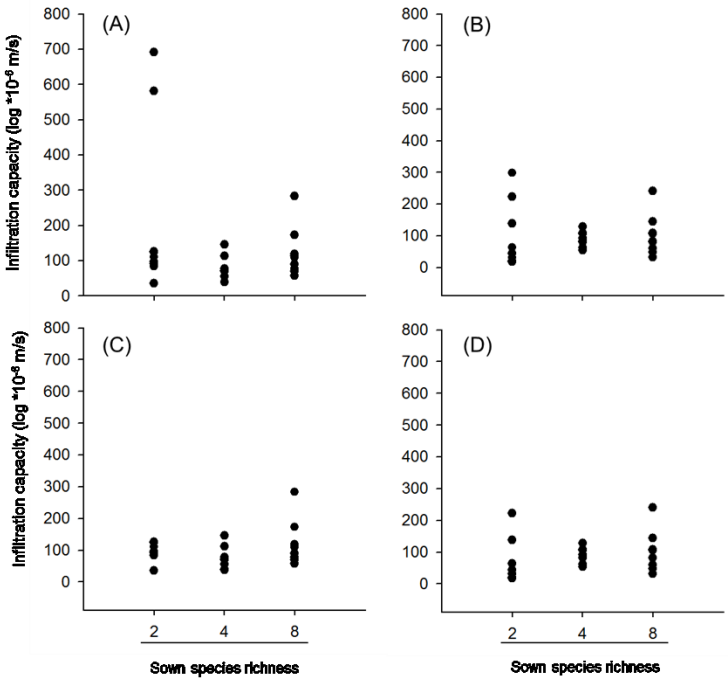

Figure 3.2: Relationship between species richness and infiltration capacity (log*10^{-6} m/s) for A) and C) in May and B) and D) in June as mean value per plot against sown species richness. Left panel includes all data points, right panel includes data points after removing outliers.

3.4 Conclusion

Generally, it is assumed that samples collected close to each other are more similar than those collected at a greater distance (Deb and Shukla 2012). Surprisingly, the data shows that there is a high variation between samples taken next to each other, up to very high variation in plots containing two plant species. By not removing these outliers, a possible effect on infiltration capacity is probably masked by these variations. The spatial pattern varied within plant species richness and the dates highlighting the fact that one set of measurements is not sufficient for describing the spatial variability of water flow through soil. The results showed that infiltration varies for plant species richness and measurement date. To achieve proper estimates it is necessary to take many samples covering the whole field site. By increasing the number of measurement points, it is possible to deal with the "noise", by reducing the impact of outliers (Wen et al. 2013). The high variation of hydraulic conductivity has dramatic effects on the output. In spring, when outliers were removed from our dataset, the correlation between plant species richness changed from no significant negative correlation to a positive trend. Therefore, we have to be aware that no effect may be overwhelmed by spatial variation, and that trends could also give a hint of possible effects on water flow through soil. Additionally, the variability of infiltration capacity within plant species richness was larger than the variability between the measurement dates. In our next field campaigns we aimed to increase our data points to reduce the impact of the high variation of infiltration on our results.

Chapter

4

How do earthworms, soil texture and plant composition affect infiltration along an experimental plant diversity gradient in grassland?

4 How do earthworms, soil texture and plant composition affect infiltration along an experimental plant diversity gradient in grassland?

4.1 Abstract

Infiltration is a key process in determining the water balance, but so far effects of earthworms, soil texture and plant diversity their interactions have not been studied in detail. We measured infiltration capacity in subplots with ambient and reduced earthworm density nested in plots of different plant species richness (1, 4 and 16), plant functional group richness and composition (1 to 4; legumes, grasses, small herbs, tall herbs). In summer, earthworm presence significantly increased infiltration, whereas in fall effects of grasses and legumes on the infiltration were mediated by suppressing or enhancing earthworm biomass. Both grasses and legumes modified infiltration and may even reverse effects of texture. We propose two pathways: (i) direct, probably by modifying the pore spectrum and (ii) indirect, by enhancing or suppressing earthworm biomass, which in turn influenced infiltration capacity due to burrowing activity. Overall, the results suggest that substantial spatial and temporal variation of soil hydraulic properties can be explained by biotic processes, especially by the presence of certain plant functional groups affecting earthworm biomass due to shaping soil structure, while soil texture had no significant effect. Therefore biotic parameters should be taken into account in hydrological applications.

4.2 Introduction

The water balance of the soil is determined by the interaction of water supply and water removal due to processes such as precipitation, infiltration, run-off, percolation and evapotranspiration. For efficient soil and water management, knowledge of soil hydraulic properties, including soil hydraulic conductivity and infiltration characteristics, is necessary to understand how rainwater moves from the soil surface to groundwater. Hydraulic conductivity describes the rate of a porous medium to transmit water. It depends on total pore space, pore size distribution and tortuosity (Kutílek 2004). Soil pores are of various origin. The smallest ones (micropores) are related to the grain size distribution and constitute the largest fraction of the total pore volume (Dexter 1988, Lin et al. 1999, Ward and Trimble 2004). Larger pores (often referred to as meso- and macropores) make up a characteristic property of the soil structure (Angers and Caron 1998, Lipiec et al. 2006). Soil structure is determined by aggregates of different sizes, divided into intra-aggregate and inter-aggregate pore structures (Alaoui et al. 2011). According to the pore size classification intra-aggregate pores include micro- and mesopores, whereas inter-aggregate pores include meso- and mainly macropores (Hillel 1998).

Traditional predictions of hydraulic conductivity are based on soil texture, bulk density or organic matter content (mainly intra-aggregate pores) (Rawls et al. 1982, Wösten and Van Genuchten 1988, Vereecken 1995), implying a decrease of hydraulic conductivity with increasing fraction of fine grains. However, this relationship can be weakened by soil structuring processes forming larger inter-aggregate pores such as interpedal voids and biopores (Jarvis and Messing 1995, Lin et al. 1999). Macropores constitute a comparatively small fraction of the total pore space, but can contribute substantially to total flow through the porous medium, mainly during high intensity rainfall events (Watson and Luxmoore 1986, Beven and Germann 2013). Thus, they provide channels for bypass flow or deep macropore infiltration.

Macropores created by both earthworms and plant roots also play a major role for preferential flow (Edwards et al. 1990, Angers and Caron 1998, Beven and Germann 2013). For example, Weiler and Naef (Weiler and Naef 2003) observed in grassland that the flow rate through vertically oriented macropores formed by earthworms or plant roots was higher than through the soil matrix. On the other hand, root growth can have opposite effects by clogging of pore space and thus decrease hydraulic conductivity (Bodner et al. 2008).

Macropores formed by earthworms range between 2 to 11 mm in diameter (Ehlers 1975) depending on the ecological group of earthworms, i.e. endogeic, epigeic and anecic (Bouché 1977). Endogeic and epigeic earthworms that live in upper mineral soil or at the soil surface mainly form small and tortuous pores ranging between 2 and 5 mm in diameter (Pérès et al. 1998). In contrast, anecic species form pores larger than 5 mm in diameter, which may reach as deep as 2 m into the soil (Edwards and Bohlen 1996) and thus enhance infiltration into deep soil layers (Shuster et al. 2002). As a consequence of the different specific burrowing behaviors the impact on water flow through soil varies among the different ecological groups (Edwards et al. 1990). Further, roots form voids of substantial size, but the majority of pores stemming from root growth are smaller (0.1-0.6 mm) than those from earthworms (Tippkötter 1983). However, root induced pores differ with plant species and can be much larger. For example, most of the root channels formed by the legume alfalfa were between 0.5 and 2.5 mm in diameter (Meek et al. 1989). Besides the formation of macropores mentioned above, biotic processes are also involved in creating and stabilizing of soil structure (Six et al. 2004, Pérès et al. 2013). Soil aggregates are more stable in biologically active soil with high carbon content, which is therefore associated with low soil bulk density and high porosity (Zacharias and Wessolek 2007).

The processes contributing to structuring of the soil and shaping its hydraulic properties are intensively interlinked. For example, earthworm activity depends on a number of factors which influence soil structure and hydraulic properties themselves, such as soil type (Visa 1992) and texture (Edwards and Bohlen 1996), management practices (Lachnicht et al. 1997) and vegetation cover (Zartman et al. 2012). Earthworms also alter above- and belowground plant

productivity by creating additional macropores and their effect varies with plant diversity and plant functional groups (Eisenhauer et al. 2009a, Eisenhauer et al. 2009b). Several experimental studies have shown that above- and belowground biomass production change with increasing plant diversity (Tilman et al. 2001, Spehn et al. 2004, Bessler et al. 2009). Furthermore, larger and longer macropores were associated with increased plant biomass production and earthworm abundance (Grevers and Jong 1990). Plant species richness not only affects rooting density, but also improves soil stability, accumulation of organic matter and promotes the activity for soil biota (Angers and Caron 1998, Thompson et al. 2010). Relatedly, the presence of certain plant functional groups, such as legumes and grasses, has been shown to affect the abundance and activity of soil organisms (Milcu et al. 2008, Eisenhauer et al. 2011). Understanding how plant diversity, functional group composition and earthworms influence soil water fluxes and resulting soil moisture distribution is important to improve predictions on how water fluxes will change in taxonomically simplified ecosystems.

Our measurements were conducted in the frame of the Jena Experiment (Roscher et al. 2004), a long-term grassland biodiversity experiments with a manipulation of plant diversity and covering experimental blocks with differences in soil structure and texture. This orthogonal experiment presents the opportunity to study Infiltration capacity in the field and allows for disentangling the relative importance of soil-physical and biological processes for soil hydraulic conductivity. The main questions of the field study were:

(i) Does earthworm activity increase infiltration capacity?

(ii) How does the plant community influence earthworm activity?

4.3 Material and methods

4.3.1 Study area and experimental design

4.3.1.1 The Jena Experiment

The study was performed on the field site of The Jena Experiment which is located in the floodplain of the Saale river near Jena (Thuringia, Germany; 50°55´N, 11°35´E, 130 m above sea level). Mean annual air temperature is 9.3°C and mean annual precipitation is 587 mm (Kluge and Müller-Westermeier 2000). Before the establishment in 2002 the experimental field site was an arable land and highly fertilized over the last decades. After the last harvest in autumn 2000 the field was ploughed and kept fallow throughout 2001, and the experimental plant communities were established in spring 2002 for investigating the interactions between plant diversity and ecosystem processes, focusing on element cycling and trophic interactions (Roscher et al. 2004). The soil of the experimental site is an Eutric Fluvisol (FAO-Unesco 1997) developed from up to 2 m thick loamy fluvial sediments (Roscher et al. 2004). The soil texture on the field site in the upper 10 cm of the soil profile changes with increasing distance from the

river, gradually from sandy loam to silt clay. The sand content decreases from 40% near the river to 11% at distance, while the silt content increases proportionally from 44% to 66%. The clay content (16-23%) shows no significant spatial trend. Plots were assembled in a10 ha area into four blocks, arranged parallel to the river, thus accounting for changes in soil properties and water conditions.

A pool of 60 native plant species common of Central European mesophilic grasslands was used to established a gradient of plant species richness (1, 2, 4, 8, 16 and 60) and functional group richness (1, 2, 3 and 4) on 82 plots of 20 x 20 m. To account for differences in morphology and physiology, species were assigned to four functional groups: grasses (16 species), small herbs (12 species), tall herbs (20 species) and legumes (12 species). In addition to test on effects of plant species richness and functional group richness, the experimental design allows for tests caused by the presence and absence of certain functional groups and texture. The plots were mown twice a year and the mown material was removed from the plots shortly after cutting. All plots were weeded regularly to maintain the target species composition. More details on the experiment and management are given in (Roscher et al. 2004).

4.3.1.2 Earthworm subplots

Earthworm abundance was observed and manipulated on subplots of the main experimental plots with species-richness levels of 1 (12 plots), 4 (16 plots) and 16 (14 plots) since September 2003 (Table 4.1). Two subplots (size 1 x 1 m) are located in close vicinity to each other (50 cm distance). Two treatments were established: ambient earthworm (+ew) and earthworm reduction (-ew). Subplots were enclosed with PVC shields (20 cm aboveground and 15 cm belowground) to decrease the re-colonization of earthworm reduction subplots (Eisenhauer et al. 2009a). Aboveground shields were removed two times a year during the mowing period. Earthworms were extracted from reduction subplots twice a year in spring (beginning of April) and autumn (end of September) by electro-shocking. A voltage was applied to the soil for 35 min. *via* four octet devices (Thielemann 1986) (DEKA 4000, Deka Gerätebau, Marsberg, Germany) powered by two 12 V batteries. During the application time the voltage was increased sequentially from 250 V (10 min) to 300 V (5 min), 400 V (5 min), 500 V (5 min) and 600 V (10 min). For more details on the arrangement of the steel rods of the octet devices and management of the earthworm subplots see (Eisenhauer et al. 2009a). Notably, steel rods were installed in both earthworm subplots controlling for potential side effects on infiltration. Two sampling campaigns on the –ew and additional extraction on control subplots in 2006 (Eisenhauer, unpupl. data) confirmed that earthworm data from –ew subplots is an adequate measure of earthworm data in the +ew subplots. Extracted earthworms were identified, counted and weighted (with gut content) in the laboratory. Earthworms at the field site of the

Jena Experiment mainly belong to two ecological groups (Bouché 1977): anecic (*Lumbricus terrestris*) and endogeic (*Aporrectodea caliginosa, Octolasion tyrtaeum, Allolobophora chlorotica, and Aporrectodea rosea*) species. Only a small number of epigeic earthworms (*Lumbricus castaneus*) was extracted and therefore contributed to the total number and biomass of earthworms.

4.3.2 Infiltration measurement

For *in situ* infiltration measurements we used a hood infiltrometer (UGT, Müncheberg, Germany; (Schwärzel and Punzel 2007)). Conduction of the experiment does not require preparation of the soil and therefore can be applied on an undisturbed, vegetated soil surface. In 2011, we conducted three infiltration measurement campaigns (June, September and October) on plots containing 1, 4 and 16 plant species (Table 4.1). The first measurement campaign was conducted at end of June, the second at the beginning of September and the third at the end of October. Per plot we carried out paired measurements: one on the reduced and one on the ambient earthworm subplot. The first and second measurement campaign were conducted about 65 and 160 days after the first earthworm extraction and the third measurement campaign 30 days after the second earthworm extraction. The extracted earthworm biomass in spring was related to the infiltration capacity in June and September. And the earthworm biomass from the second extraction campaign, which was conducted after the second infiltration campaign, was related to the infiltration of October.

Table 4.1: Combinations of plant species richness and plant functional group richness levels and the number of plots per diversity level for the earthworm subplots with 1, 4 and 16 plant species (n = 42, 84 subplots).

	Plant species richness			**Plots**
Plant functional group richness	**1**	**4**	**16**	
1	12	4	2	18
2	-	4	4	8
3	-	4	4	8
4	-	4	4	8
Plots	**12**	**16**	**14**	**42**

A hood with a diameter of 16 cm was placed with the open side on the undisturbed soil surface. The contact between the soil and hood was sealed with wet sand. We conducted measurements at increasingly negative matric potentials (Ψ_M) beginning with ψ_M = 0 m and reducing it stepwise by -0.02 m until the bubble point of the soil was reached. The bubble point refers to the matric potentials, upon which a pore channel allows for penetration of air into the hood and therefore the maximum applicable matric potential at this location. For a specific matric potential (Ψ_M) the equivalent diameter (d_e) of the largest soil pore conducting water can be estimated after (Jarvis et al. 1987). At Ψ_M = 0 m the soil is saturated and the entire pore spectrum is potentially active. At smaller matrix potential larger pores are no longer active and infiltration capacity deceases. This allows evaluating infiltration capacity through different parts of the pore spectrum. At Ψ_M = -0.02 m the largest active pores correspond to d_e = 1.5 mm, at Ψ_M = -0.04 m to d_e = 0.75 mm and at Ψ_M = -0.06 m to d_e = 0.50 mm. At each pressure level we recorded infiltration capacity until they were constant in time. This steady infiltration capacity was used for further analysis. Infiltration capacity at a given matric potential are directly linked to hydraulic conductivity (Wooding 1968). The flow conditions in natural soils, however, are far from ideal with anisotropic behaviour, heterogeneous initial soil water contents and flow dynamics that do not correspond to the Richards equation near soil saturation (Beven and Germann 2013). Therefore, we refrained from deriving hydraulic conductivity from our infiltration capacity, for example via Wooding´s formula (Wooding 1968). Instead, we worked with the observed infiltration capacity, considering those as a surrogate for the rate of the soil to conduct water at the applied matric potential.

4.3.3 Soil texture and moisture

Soil texture was determined from soil cores at 38 locations (average of 0-100 cm depth) distributed throughout the experimental site before plot establishment (G. Büchel, pers. comm.) and values for each plot were interpolated by ordinary kriging. The fraction of sand and silt are negatively correlated (clay showing no spatial trend). Thus, in the following statistical analysis for simplicity we used the sand fraction as factor representing soil texture.

The volumetric soil water content (m^3 m^{-3}) was determined with a FDR probe (ML2x Theta Probe, Delta-T Devices, Cambridge, United Kingdom). The device was inserted from the top 6 cm deep (length of the prongs) into the soil surrounding the hood before the infiltration experiment. The average of three measurements was used for further analysis.

4.3.4 Statistical analyses

Statistical analyses were performed using the statistical software R 2.6.2 (R Development Core Team, http.//www.R-project.org). The data were checked for heteroscedasticity and log-

transformed if required. Analyses were performed with mixed effect models using the *lme* function implemented in the *nmle* package (Pinheiro and Bates 2000). Starting from a constant null model with random effects only, we stepwise added the fixed effects and estimated their significance using the maximum likelihood method and likelihood ratio tests. To remove spatial variability in all analysis we fitted block first and then tested the effects of plant community. First, we analysed the variation of the infiltration capacity for each month separately by using plot identity as a random factor and a sequence of the following fixed effects according to the experimental design: block (as a factor, BL; 1, 2, 3, 4), plant species richness (log-linear term; SR; 1, 4, 16), plant functional group richness (linear-term; FG; 1, 2, 3, 4), ambient and reduced density (E; 0, 1) and their interactions (E x SR, E x FG). The design also allowed testing for the effects of the presence (or absence) of certain plant functional groups on the response variable. In alternative models the presence of grasses (GR; 0, 1), legumes (LEG; 0, 1), small herbs (SH; 0, 1) and tall herbs (TH; 0, 1) and their interactions with the previously mentioned factors were tested. Second, we analysed the variation of the infiltration capacity between sampling dates with plot identity as random factor and the fixed effects BL, SR, FG, E and time (as factor; TI; June, September and October) and two-way interactions between the earthworm treatments, plant diversity and time (E x SR, E x FG, TI x SR, TI x FG, TI x E). Most plots had a bubble point at Ψ_M < -0.06 m. Therefore, for data analysis of individual months, we only considered infiltration capacity for Ψ_M up to -0.04 m. For the integral dataset (all plots, all months) the experimental factors were tested up to the Ψ_M = -0.06 m. We used simple linear regressions to analyse the influence of texture (sand fraction in 0-10 cm depth), and soil water content before the measurement on the infiltration capacity.

Based on the mixed effect model approach revealing a strong grass and legumes effect on infiltration in October, we used path analysis to investigate how the total earthworm biomass extracted from the earthworm reduction subplot in September, texture and the presence/absence of legumes and grasses directly and indirectly affected the infiltration capacity on plots with reduced earthworm (-ew) and ambient densities (+ew) in October. The impact on nfiltration capacity in reduced and ambient plots was calculated in separate analysis. Path analysis allows testing direct and indirect relationships between variables in a multivariate approach (Grace 2006). Hence, by using path analysis we were able to test if certain plant functional groups such as legumes and grasses directly influence infiltration capacity on +ew and –ew plots or if infiltration is indirectly influenced by earthworm biomass. In the path analysis arrow represent causal relationships, while rectangles represent manipulated (grasses and legumes) or measured variables (sand, earthworm biomass and infiltration capacity). The adequacy of the model was determined via Chi²-tests, AIC and RMSEA. Non-signifcant Chi²-test ($p>0.05$), low AIC and low RMSEA indicating an adequate model fit (Grace 2006). Beginning with the full model (including all possible pathways) the models were improved by stepwise removing of

unimportant relationships based on AIC values (Shipley 2000). Standardized path coefficients were derived based on the correlation matrix of standardized variables. Path analysis was performed using AMOS 5 (http://amosdeveleopment.com).

4.4 Results

4.4.1 Soil texture and moisture and infiltration

The infiltration capacity in June and October did not differ between the four blocks (Table 4.2) encompassing the texture gradient. In September infiltration capacity increased significantly for Ψ_M= 0 and -0.02 m from block 1 (71.34 ± 11.50 and 49.23 ± 8.55 µm/s) to block 4 (143.65 ±21.73 and 100.10 ± 14.50 µm/s). When replacing the variable 'block' with 'sand fraction in 0-10 cm depth' as a covariate in our analysis, texture became significant in September (Table 4.2), but not in June and October. Surprisingly, the infiltration capacity at saturated conditions decreased with increasing sand content (Figure 4.1). However, tested only plots without legumes, we did not find a significant correlation between sand content and infiltration capacity (data not shown). Additionally, there was an interaction effect between sand and legumes (Table 4.2), highlighting the differential effect of legumes with varying soil texture. In our experiment the initial soil moisture measurements did not correlate significantly with the infiltration capacity (log $*10^{-6}$ m/s) at matric potential zero in June (R^2=<0.01, p=0.806), September (R^2=0.193, p=0.078) and October (R^2<0.01, p=0.993).

Table 4.2: Results of mixed effects models for the infiltration capacity as affected by Sand in 10 cm depth (Sand_10 cm), Plant species richness (SR), Plant functional group richness (FG), Grasses (GR), Legumes (LEG), Small herbs (SH), Tall herbs (TH), Earthworm (E), Plot (PL) for measurements in September.

	September		
Source	0 m		
	L-ratio	p	
Sand	**8.41**	**0.004**	↓
SR (log-linear)	<0.01	0.969	
FG (linear)	0.10	0.750	
GR	2.73	0.098	
LEG	**6.96**	**0.008**	↑
SH	1.34	0.247	
TH	0.06	0.802	
Sand×LEG	**12.67**	**0.002**	
E	0.24	0.628	
E×SR(log-linear)	0.21	0.646	
E×FG (linear)	0.25	0.615	
E×GR	0.62	0.430	
E×LEG	0.02	0.876	
E×SH	0.07	0.796	
E×TH	0.46	0.498	

Models were fitted by stepwise inclusion of fixed effects. Likelihood ratio tests were applied to assess model improvement (L ratio) and the statistical significance of the explanatory terms (p values). Significant effects are marked in bold. Arrows indicate increase (↑) or decrease.

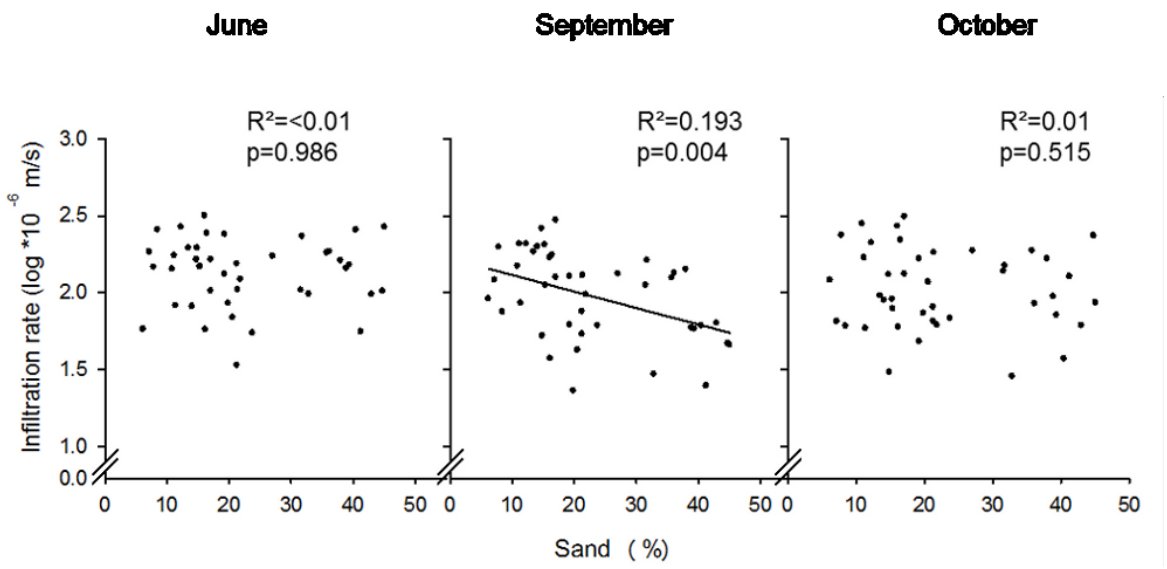

Figure 4.1: Regressions between infiltration capacity at matric potential zero and texture (sand fraction in 0-10 cm depth in %) for different months (as indicated). The line indicates significant relationships.

4.4.2 Plant species richness and infiltration

Plant species richness (1, 4 and 16) did not affect the infiltration capacity at any sampling date (Tables 4.3, 4.4). However, we observed a significant E x SR interaction effect in October (Table 4.3), which was mainly caused by 16 species subplots (Figure 4.2C). Additionally, the infiltration capacity was negatively correlated with plant species richness on plots with reduced earthworm densities (R^2 = 0.11, p = 0.036). For infiltration on ambient earthworm plots a weak trend with plant species richness (R^2=0.047, p= 0.166) was observed.

4.4.3 Plant functional groups and infiltration

Infiltration capacity was significantly affected by the presence of certain plant functional groups, such as grasses and legumes in September and October. In the presence of grasses infiltration capacity decreased in comparison to plots without grasses at Ψ_M = 0 m (-21 % in September, -23 % in October) and slightly at Ψ_M = -0.02 m (-23 % in September, -27 % in October). In contrast, in the presence of legumes infiltration capacity increased at Ψ_M = 0 m (+39 % in September, +36 % in October) and Ψ_M = -0.02 m (+40 % in September, +38 % in October) (Figure 4.3B, C, Table 4.3). Additionally, also for Ψ_M = -0.04 and -0.06 m the infiltration capacity decreased significant in the presence of grasses and increased in presence of legumes (Table 4.4). No significant effects of plant functional groups were detected in June.

the infiltration capacity as affected by Block (BL), Plant species richness (SR), plant functional group
Small herbs (SH), Earthworms (E), Plot (PL) for measurements in June, September and
= 0 m and ψ_M = -0.02 m.

Source	June				September				October			
	0 m		-0.02m		0 m		-0.02 m		0 m		-0.02 m	
	L-ratio	p	L-ratio	p	L-ratio	p	L-ratio	p	L-ratio	p	L-ratio	p
BL	4.05	0.256	4.02	0.259	**10.77**	**0.013**	**11.76**	**0.008**	2.89	0.409	2.92	0.403
SR (log-linear)	0.28	0.596	0.12	0.724	0.14	0.834	0.06	0.800	0.76	0.385	0.50	0.480
FG	0.70	0.403	2.43	0.119	0.33	0.853	<0.01	0.991	0.05	0.825	0.03	0.870
GR	0.31	0.578	0.65	0.419	**4.27**	**0.038** ↓	**4.62**	**0.032** ↓	**6.39**	**0.015** ↓	**7.59**	**0.006** ↓
LEG	0.72	0.398	0.76	0.384	**7.60**	**0.006** ↑	**8.96**	**0.003** ↑	**10.95**	**<0.001** ↑	**10.53**	**0.001** ↑
SH	1.98	0.160	0.70	0.403	1.46	0.227	1.36	0.244	2.01	0.157	1.70	0.193
TH	1.02	0.311	0.72	0.395	0.44	0.508	0.10	0.758	0.33	0.563	0.58	0.446
E	**4.14**	**0.042** ↑	1.89	0.169	0.23	0.630	0.46	0.498	0.88	0.349	0.34	0.557
E×SR(log-linear)	1.33	0.248	0.19	0.664	0.11	0.745	0.14	0.706	**4.69**	**0.030**	**5.50**	**0.019**
E×FG	0.60	0.437	1.80	0.406	0.26	0.614	0.49	0.484	1.24	0.264	**12.95**	**0.002**
E×GR	0.24	0.624	0.54	0.463	0.22	0.638	2.01	0.156	0.07	0787	0.16	0.692
E×LEG	1.06	0.304	0.49	0.485	0.22	0.876	0.09	0.770	0.01	0.906	0.09	0.758
E×SH	2.50	0.114	2.95	0.086	0.07	0.795	0.12	0.894	0.60	0.438	0.67	0.413
E×TH	<0.01	0.969	0.28	0.598	0.26	0.610	0.95	0.330	0.31	0.575	0.68	0.409

itted by stepwise inclusion of fixed effects. Likelihood ratio tests were applied to assess model improvement (L-ratio) and the statistical signifi
nificant effects are marked in bold. Arrows indicate increase (↑) or decrease (↓).

Table 4.4: Results of mixed effects models for coefficients of variation for infiltration capacity as affected by Block (BL), Plant species richness (SR), Plant functional group richness (FG), Grasses (GR), Legumes (LEG), Small herbs (SH), Tall herbs (TH), Earthworms (E), Plot (PL) and Time linear (TI) at matric potentials ψ_M= 0, -0.02 and -0.04 and -0.06 m combined for all months (June, September and October).

Ψ_M	0 m			-0.02 m			-0.04 m			-0.06 m		
	L ratio	p		L ratio	p		L ratio	p		L ratio	p	
Block	5.21	0.157		5.23	0.155		2.62	0.454		2.83	0.419	
SR (log-linear)	0.02	0.893		0.01	0.915		<0.01	0.946		0.66	0.417	
FG	4.16	0.245		3.79	0.286		5.13	0.163		3.60	0.308	
LEG	**10.53**	**0.001**	↑	**11.00**	**<0.001**	↑	**7.49**	**0.006**	↑	**8.24**	**0.004**	↑
GR	**5.66**	**0.017**	↓	**6.69**	**0.010**	↓	**7.75**	**0.005**	↓	**10.11**	**0.002**	↓
SH	3.21	0.073		2.40	0.121		1.71	0.191		1.46	0.226	
TH	0.78	0.378		0.64	0.424		1.59	0.207		1.49	0.222	
E	3.56	*0.059*		2.16	0.142		0.15	0.701		0.35	0.556	
ExSR	**5.27**	**0.022**		**4.44**	**0.035**		2.02	0.155		1.19	0.276	
ExFG	0.83	0.843		1.19	0.756		1.39	0.707		0.68	0.878	
ExLEG	0.35	0.552		1.11	0.291		1.47	0.225		0.88	0.348	
ExGR	0.11	0.734		1.27	0.260		**5.54**	**0.019**		**5.06**	**0.024**	
ExSH	1.08	0.299		0.97	0.325		0.27	0.604		1.36	0.243	
ExTH	0.48	0.485		0.97	0.324		2.01	0.156		*3.78*	*0.052*	
TI	**15.13**	**<0.001**		**9.97**	**0.007**		4.17	0.124		4.52	0.105	
TIxSR	1.60	0.449		1.04	0.594		0.83	0.662		1.30	0.522	
TIxFG	6.63	0.356		8.40	0.211		10.48	0.106		9.11	0.168	
TIxLEG	**7.10**	**0.029**		**7.53**	**0.023**		**6.82**	**0.033**		3.57	0.168	
TIxGR	2.50	0.287		2.94	0.230		3.66	0.160		0.74	0.690	
TIxSH	0.02	0.990		0.03	0.983		1.41	0.495		1.02	0.600	
TIxTH	2.12	0.347		1.90	0.387		1.95	0.376		1.41	0.492	
TIxE	0.84	0.656		0.27	0.919		1.40	0.497		0.22	0.804	

Models were fitted by stepwise inclusion of fixed effects. Likelihood ratio tests were applied to assess model improvement (L-ratio) and the statistical significance of the explanatory terms (p-values). Significant effects are marked in bold. Arrows indicate increase (↑) or decrease (↓).

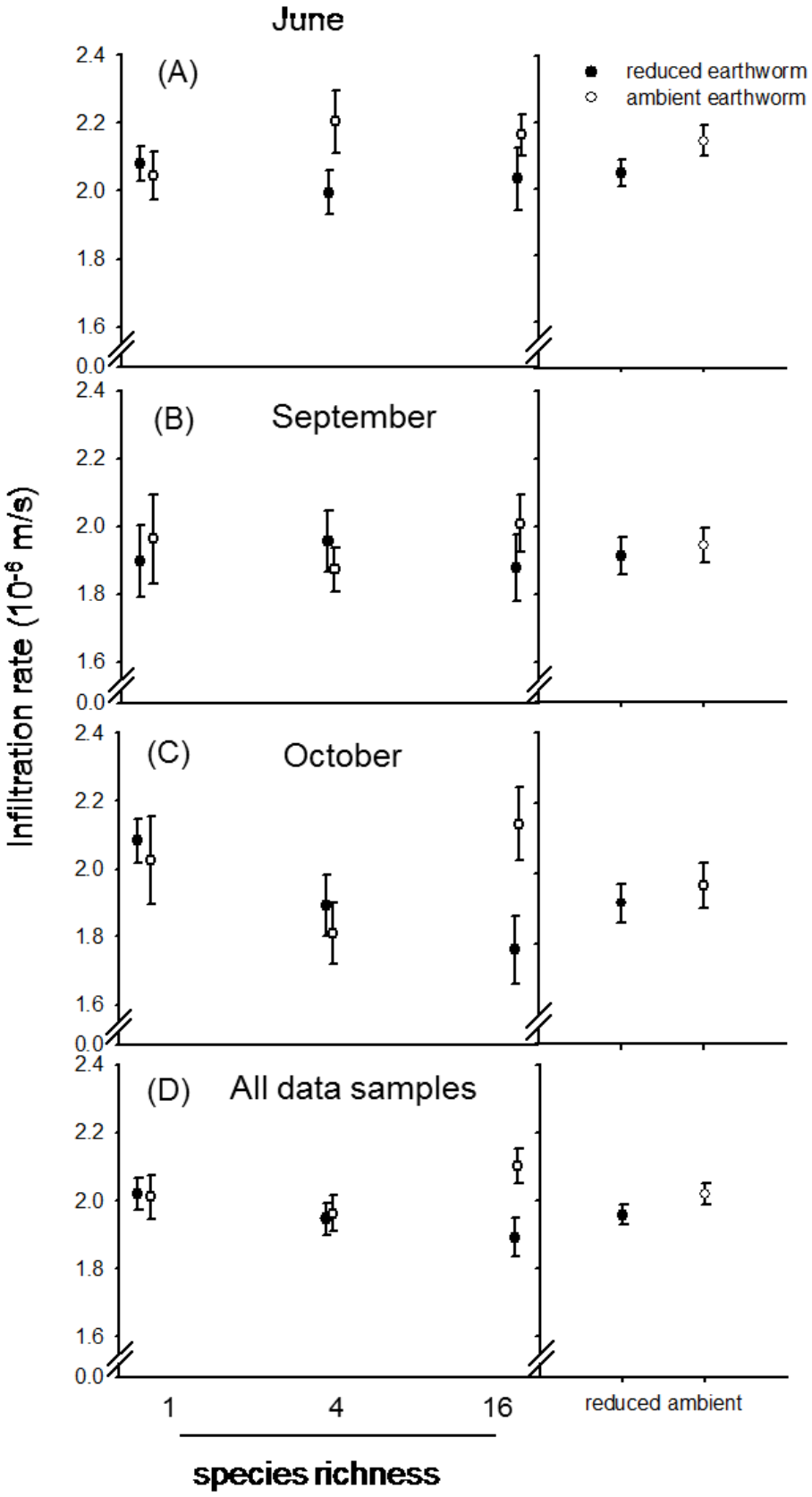

Figure 4.2: Variation in infiltration capacity at matric potential zero as affected by plant species richness (1, 4, 16 species) in earthworm subplots (ambient earthworm density) and earthworm reduction subplots (reduced earthworm density) in (A) June, (B) September, (C) October, and (D) in total for all plant species and sampling dates (right panel). Means with standard errors.

4.4.4 Earthworms, functional groups and infiltration

The biomass of endogeic earthworms accounted for 59 % and 49 % of total abundance in spring and autumn respectively, whereas the biomass of anecic species (*L. terrestris*) accounted for 36 % and 49 % of total biomass in spring and autumn respectively. The total number and biomass of earthworms increased significantly from spring (26.88 ± 2.29 individuals m^{-2} and 13.86 ± 2.03 g m^{-2}) to autumn (40.55 ± 4.02 individuals m^{-2} and 25.78 ± 2.35 g m^{-2}, Table 4.5). Total earthworm biomass increased slightly, but not significantly in presence of legumes in spring, but significantly in autumn (t-test, p=0.001). In presence of grasses, total earthworm biomass decreased not significantly in spring and slightly, but not significantly in autumn (data not shown). For both extraction dates earthworm biomass did not correlate with plant species richness (data not shown).

In June 2011 infiltration capacity were elevated in subplots with ambient earthworm densities (Table 4.3), which was mainly true for the 4 and 16 plant species richness treatment (Figure 4.2). With decreasing matric potential (Ψ_M = -0.02 m, exclusion of pores >1.5 mm) the effect of earthworms disappeared (Figure 4.3A, Table 4.3, 4.4). For all other sampling dates and matric potentials, the earthworm treatment did not significantly affect infiltration capacity (Figure 4.3, Table 4.3), while the earthworm biomass affected the infiltration capacity (see Path analysis).

Table 4.5: Variations in the number (ind. m^{-2}) and biomass (g m^{-2}) of earthworms of the Jena Experiment field site. Earthworm data are the means (± standard error) across plots of the year 2011 for the extraction dates in spring (March) and autumn (September) (as indicated).

Earthworms	March	September
Number of anecics	3.14 ± 0.53	5.47 ± 0.63
Biomass of anecics	4.98 ± 1.03	12.74 ± 1.37
Number of endogeics	21.51 ± 2.25	34.05 ± 3.67
Biomass of endogeics	8.13 ± 1.01	12.62 ± 1.51
Number total earthworms	26.88 ± 2.92	40.55 ± 4.02
Biomass total earthworms	13.86 ± 2.03	25.78 ± 2.35

Total number and biomass of earthworms included also unidentifiable earthworms and the invasive earthworm *Lumbricus castaneus*.

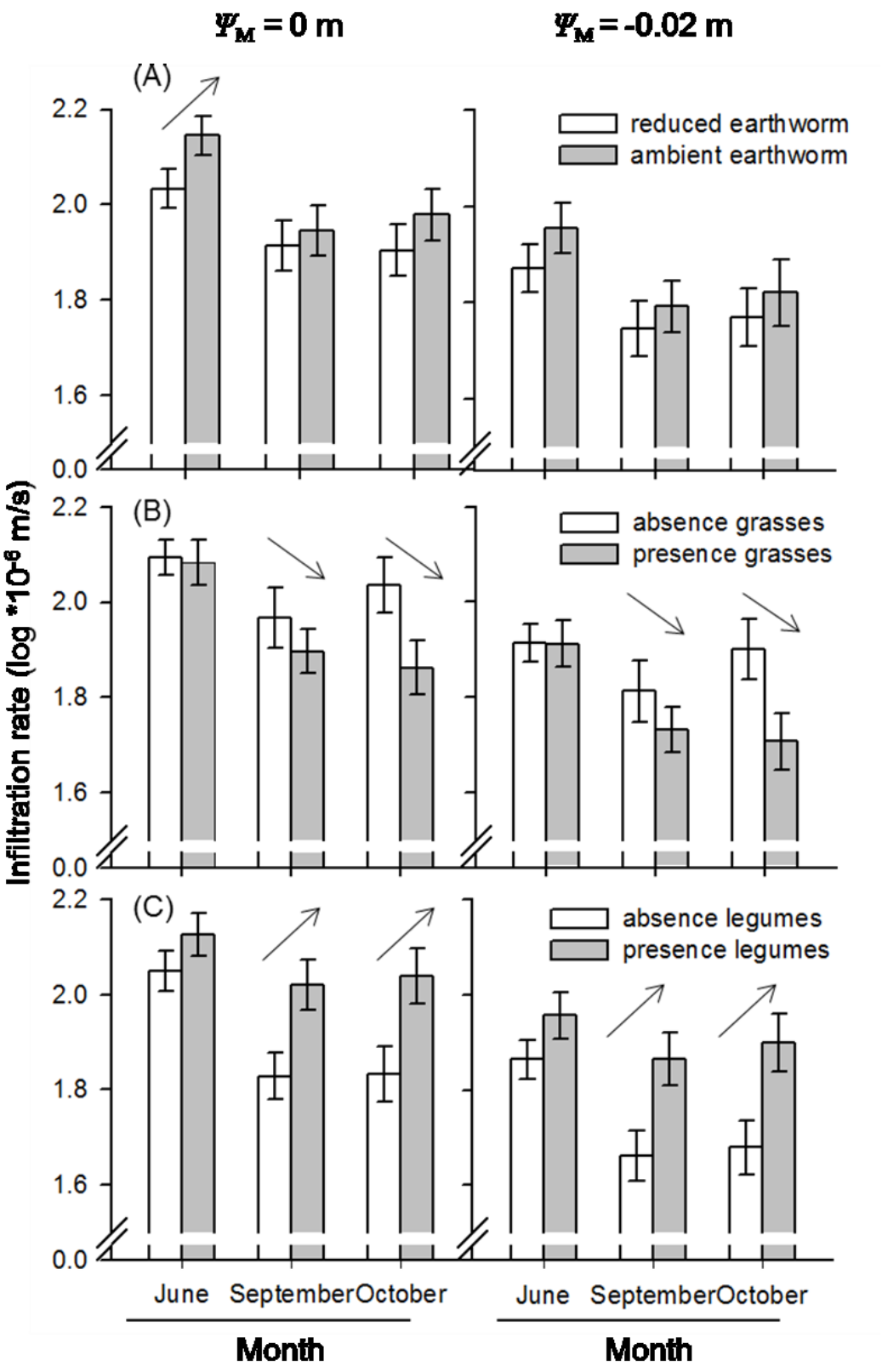

Figure 4.3: Variation in infiltration capacity in June, September and October as affected by (A) earthworms (ambient and reduced earthworm density), (B) presence of grasses, and (C) presence of legumes for applied matric potential Ψ_M = 0 m (left panel) and tension Ψ_M = -0.02 m (right panel). Means with standard errors.

4.4.5 Seasonal variability of infiltration

In 2011 time significantly affected the infiltration capacity at saturated matric potential $\Psi_M = 0$ m and $\Psi_M = -0.02$ m (Table 4.3). The average infiltration capacity decreased from June to September (-24 and -22 % for $\Psi_M = 0$ m and $\psi_M = -0.02$ m) and increased slightly from September to October (+8 and: +14 % for $\Psi_M = 0$ m and $\Psi_M = -0.02$ m, respectively). In particular, the effect of legumes depended strongly on time. The interaction between legumes and time on infiltration capacity was significant for matric potentials $\Psi_M = 0$ m, -0.02 m, and -0.04 m but not for -0.06 m (Table 4.3, 4.4). At lower matric potentials, infiltration capacity did not change between months (Table 4.3, Figure 4.4) suggesting that seasonal processes act mainly on large pores.

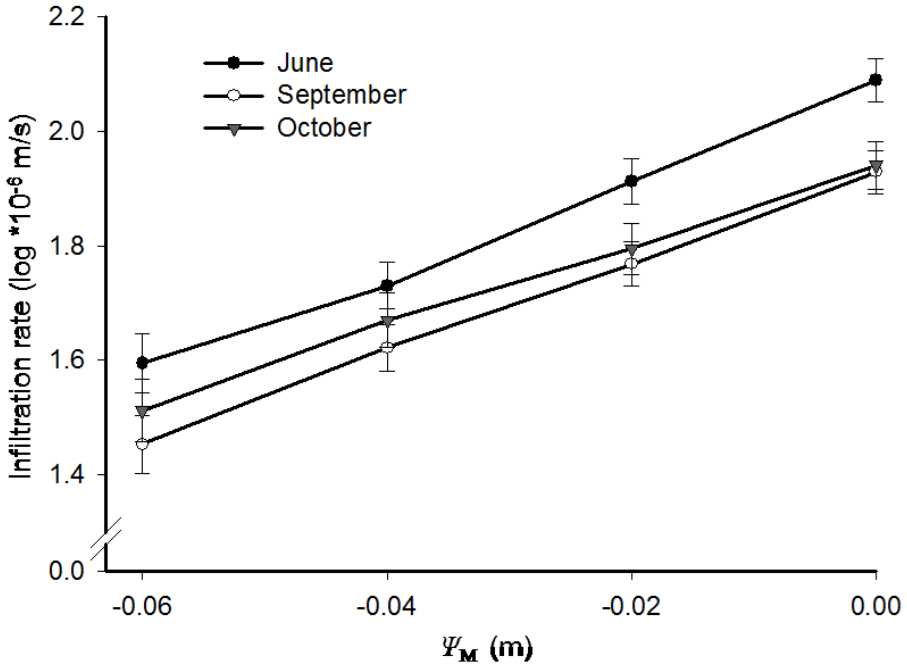

Figure 4.4: Variation in infiltration capacity separated for the different months (June, filled circles; September, open circles; and October, grey triangle) for the matric potential $\psi_M = 0$, -0.02, -0.04 and -0.06 m.

4.4.6 Path analysis

The path analysis supports the results of the mixed linear model approaches, but, in addition, helps to identify possible mechanisms. The initial model for October (AIC = 49.10, Figure 4.5) was improved as described in the method section. In October the improved model explained 13% of the infiltration capacity on plots with ambient earthworm density (Figure 4.6A; $\chi^2 = 1.80$, p = 0.937, AIC = 29.80) and 29% of the infiltration capacity on subplots with reduced earthworm density (Figure 4.7B; $\chi^2 = 1.10$ p = 0.954, AIC = 31.10). The total

earthworm biomass increased in the presence of legumes and decreased in the presence of grasses. Earthworm biomass decreased with increasing sand content, but compared to the effects of grasses and legumes on the infiltration capacity this effect was less important. Increasing total earthworm biomass increases the infiltration capacity on ambient earthworm plots directly (Figure 4.6A).

Grasses decreased and legumes increased infiltration capacity on subplots with reduced earthworm biomass (Figure 4.6B). In summary, grasses had a stronger direct effect on the infiltration capacity on subplots with reduced earthworm density, whereas legumes had a stronger indirect effect on infiltration capacity on subplots with ambient earthworm density (Figure 4.6B). For the improved model where we found a positive impact of the total earthworm biomass on infiltration capacity, we also included different ecological earthworm groups (anecic and endogeic) instead of the total earthworm biomass in separate models. It was therefore possible to separate the different effects of the ecological earthworms groups on the infiltration capacity and also tested the different effects of sand and the presence/absence of legumes and grasses on them. Including only the biomass of anecic earthworms instead of total earthworm biomass in additional models, the effect of grasses and sand content disappeared, but the effect of legumes on the biomass of anecic earthworms increased (Figure 4.7A). In contrast, including the biomass of endogeic species instead of the total biomass, we observed similar results as for the total earthworm biomass model (Figure 4.7B).

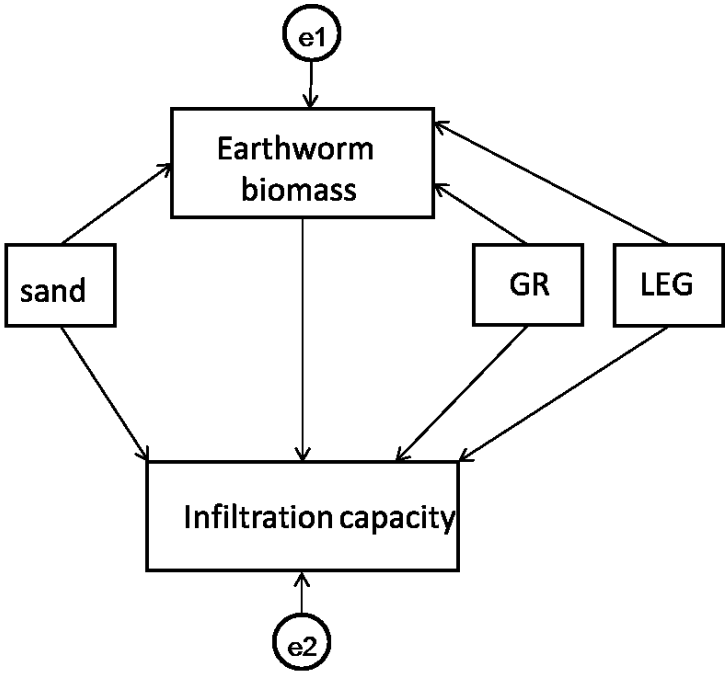

Figure 4.5: Full model path analysis showing the relationships between earthworm biomass (total, anecic or endogeic as indicated), texture (sand in 10 cm depth) and functional groups (GR, Grasses; LEG, Legumes) and infiltration capacity at saturation for ambient (+ew) or reduced (-ew) earthworm plot (as indicated). Unexplained variation is denoted with e1-e3.

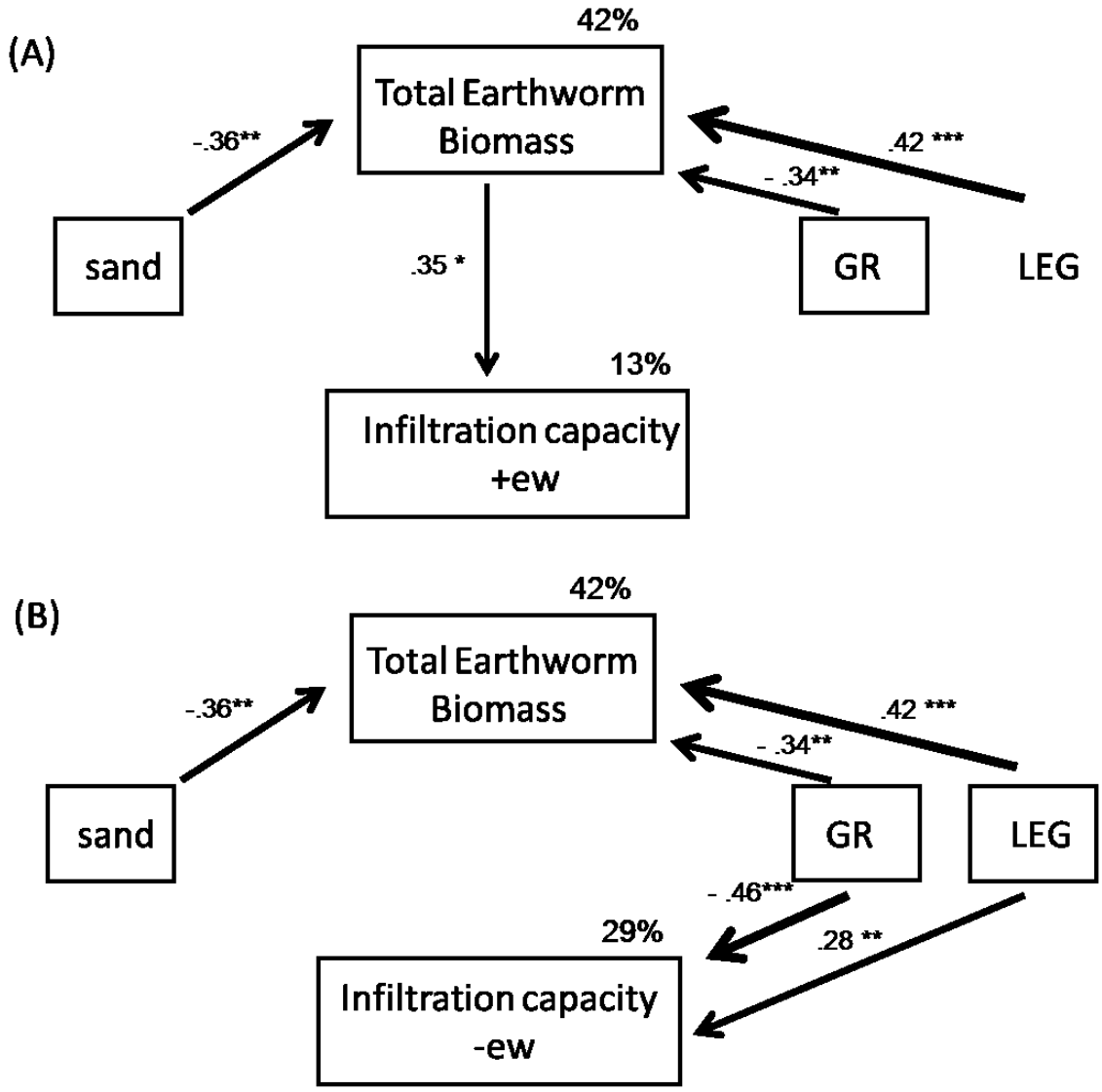

Figure 4.6: Path analysis showing the relationships between total biomass of earthworms (earthworm biomass), texture (sand in 10 cm depth) and plant functional groups (GR, Grasses; LEG, legumes) for (A) infiltration capacity on subplots with ambient (infiltration capacity +ew) and (B) reduced earthworm densities (infiltration capacity –ew) in October. The total earthworm biomass was extracted in September. Standardized path coefficients are given next to path arrows. * $p \leq 0.05$, ** < 0.01, *** $p = 0.001$. For details see text.

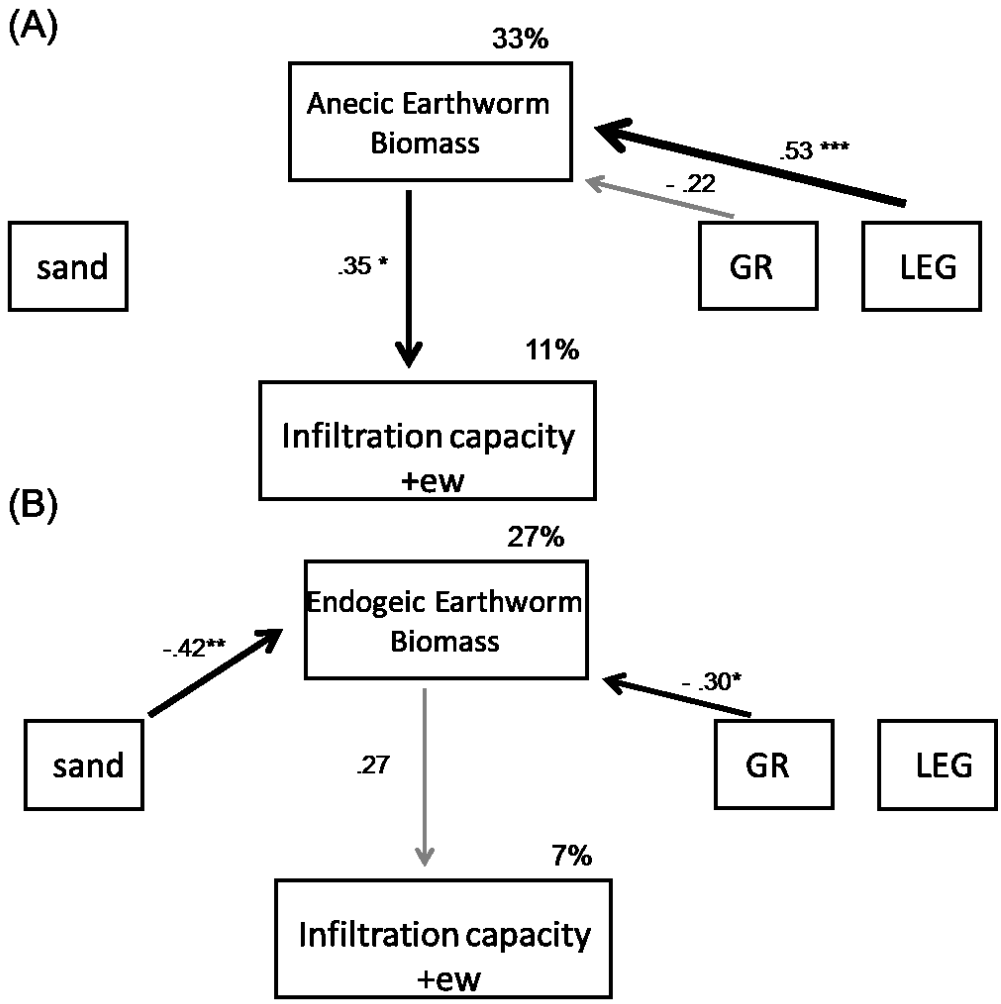

Figure 4.7: Path analysis showing the relationships between (A) anecic and (B) endogeic earthworm with texture (sand in 10 cm depth) and plant functional groups (GR, Grasses; LEG, legumes) for infiltration capacity on subplots with ambient (+ew) earthworm densities in October. Standardized path coefficients are given next to path arrows; * p≤ 0.05, ** < 0.01, *** p = 0.001. Grey arrows indicated p< 0.10. For details see text.

4.5 Discussion

4.5.1 Influence of Earthworms on infiltration

Our results indicate that biotic factors play a decisive role for soil hydraulic soil properties near saturation. In June infiltration capacity slightly increased on subplots with ambient earthworm densities compared to subplots with reduced earthworm densities. Remarkably, this effect was mainly caused by plots in block 1 and block 4 (data not shown) suggesting local changes of earthworm activity and considerable spatial variation due to texture and plant type that interact with infiltration (Kohler-Milleret et al. 2013). In general, burrows of anecic species such as *L. terrestris* but also those of adult endogeic species such as *A. caliginosa* are larger than 2 mm in diameter and this may explain why only water flow through larger pores (> 1.5 mm, at matric potential Ψ_M = 0 m close to saturation), but not through smaller pores was directly affected by the presence of earthworms. This is also in line with the non-capillary

nature of earthworm casts. Earthworm presence, particularly that of anecic species forming vertical burrows, facilitates larger pores conducting water (macropore flow) and contributes to infiltration when water is supplied in large quantities (tension free conditions) (Chan 2004).

We measured infiltration capacity at elevated soil saturation, and it could be argued that saturation will never be reached in most natural soil environments. However, irrigation experiments with dye indicate that macropores, such as those formed by anecic earthworms, are activated at realistic rain intensities (Flury et al. 1994, Kulli et al. 2003, Weiler and Naef 2003, Van Schaik et al. 2013). Beven and Germann (Beven and Germann 1982) reported that rainfall intensities of 1-10 mm/h can initiate macropore flow. Applying an arbitrary threshold of 5 mm/h (Simmonds and Nortcliff 1998) to the high resolution (10 min) rainfall record of our field site (2003 to 2011) indicates that about 30 % of the total rainfall could deliver macropore flow. One of the pressing questions for future work will be on how this macropore flow potential relates to actual water flow at greater depth. Furthermore, it is expected that precipitation patterns change due to climate change with decreasing precipitation in summer and increasing precipitation in autumn/winter. It is therefore likely that higher frequency of extreme precipitation events increases the proportion of heavy rainfall (IPCC 2012). Macropores formed by earthworms and roots, and their interactions, thus likely to become more important for buffering strong precipitation events in future.

4.5.2 Influence of plant functional group on infiltration

At the end of the growing season infiltration capacity was strongly affected by the presence of certain plant functional groups, such as grasses and legumes. Legumes increased and grasses decreased infiltration capacity (Figure 4.3, Table 4.3). This is consistent with results of Archer et al. (Archer et al. 2002), who reported that the legumes increased and grasses decreased hydraulic conductivity. Further, the significant effect of grasses was more pronounced at smaller matric potential, while the effect of legumes was prevalent over the entire sampled pore spectrum (Table 4.4). It has been shown that decaying tap-roots of legumes form stable macropores and hence increase infiltration (Meek et al. 1989, Mitchell et al. 1995). This observation was supported by Mytton et al. (1993), who showed that water infiltration was higher under clover compared to grass due to a higher fraction of soil pores greater than 60 µm with porosity being equal. Additionally, several studies showed that water flow through soil is enhanced by legumes or legumes-grass mixture compared to pure grass stands due to root proliferation, which increased soil organic matter content and favored soil fauna such as earthworms (Gijsman and Thomas 1996, Obi 1999). The fibrous and rhizomatous roots of grass species tend to reduce infiltration by clogging soil pore space and blocking water flow (Archer et al. 2002).

4.5.3 Path analysis

Path analysis helped to address underlying mechanism: the effect of legumes on infiltration capacity in ambient (control) earthworm density plots may be indirect by enhancing earthworm biomass (Figure 4.6A), suggesting that earthworm performance benefits from the presence of legumes (Eisenhauer et al. 2009a, Eisenhauer et al. 2009b). Additionally, the path analysis suggests that grasses directly influenced the infiltration capacity on plots with reduced earthworm densities, while indirect effects of grasses via decreasing earthworm biomass were less important (Figure 4.6). For the Jena Experiment it was shown by Pérès et al. (2013) that root biomass is strongly increases in presence of grasses while, as mentioned above, legumes signifcantly increase earthworm biomass (Figure 4.6A). This suggests that the observed enhanced infiltration in plots with legumes was probably associated with a larger number of macropores caused by earthworms (Hillel 1998, Logsdon and Cambardella 2000) and warrants further investigations. These results are in agreement with the findings of Abbott and Parker (Abbott and Parker 1981), who reported an increased infiltration of water due the activity of the geophagous earthworm species *Microscolex dubuis* in the presence of clover mulch. By contrast, decreased in infiltration in grass plots was probably due to fine roots clogging soil pores. Thus, our results suggest that the presence of grasses and legumes affected hydraulic conductivity via different mechanisms, directly presumably via root activity and indirectly via altering earthworm biomass. The observed effects increased during the vegetation period (Table 4.3), probably due to the progressive increase of earthworm (Eisenhauer et al. 2008c) (Table 4.5) and root biomass (Pucheta et al. 2004).

The different ecological earthworm groups differ in forming of macro- and microaggregates by changing soil structure features (aggregate size, stability and soil organic content) and porosity (pore size distribution) (Shipitalo and Protz 1988, Six et al. 2004). Interestingly, in October anecic earthworms were positively affected by the presence of legumes, whereas endogeic earthworms were negatively affected by sand content and by the presence of grasses. Additionally, both endogeic and anecic earthworm had a significant effect on the infiltration capacity, with a more pronounced effect of anecic earthworms (Figure 4.7). This is in line with other studies, which showed that the deep dwelling anecic earthworm enhance water infiltration rates (Shipitalo et al. 1994, Edwards and Bohlen 1996), while horizontal pores formed by endogeic earthworms limits the effectiveness in water flow through soil (Ela et al. 1992). Generally, endogeic earthworms are considered as the major group improving soil aggregation, while anecic or compacting species destabilizes the soil due to their casting activity (Six et al. 2004). As shown by Lee and Foster (1991) a mix of endogeic and anecic earthworms supports soil structural health.

In part our results are in contrast to other studies (Stockdill 1966, Zachmann et al. 1987, Wuest 2001), which found a direct impact of earthworm treatment on infiltration. Studies on the influence of earthworms on infiltration capacity usually ignore gradients of texture and plant functional groups. This gradient increased the variance in our data and affected the earthworm populations in the plots. However, our observation area was also rather small (240 cm^2) and the setup prevented from conducting additional measurements. Also, we compared plots with ambient to plots with reduced earthworm density contrasting earlier studies which compared ambient (by earthworm addition) with control plots (no earthworms) (Zachmann and Linden 1989, Joschko et al. 1992). While our setup has the advantage to better reflect 'natural' conditions, it may have caused a comparatively smaller contrast between treatments. Since the used octet extraction method cannot remove earthworms completely (extraction reduced the surface activity of earthworms by about 38 % five weeks after the last manipulation (Eisenhauer et al. 2008b)), the differences between the treatments might not have been as strong as in other experiments, and re-colonization of earthworm reduction subplots may have weakened the contrast further. Unfortunately we cannot exclude completely that extraction efficiency varies dependent on plant community properties, because there exists no detailed studies that evaluated the extraction efficiency of the octet method as a function of plant community structure. Effects of earthworms on plant performance and the resulting impact on soil hydraulic properties depend also on other soil factors, such as soil texture and bulk density, leading to substantial spatial variation and interaction which probably masked earthworm effects. More observations on the pore structure in the different treatments are necessary to validate the proposed complex interactions in soil processes leading to the observed infiltration patterns. In general, we could relate earthworms to infiltration based on earthworm biomass, while the effect of the earthworm treatment was not very strong.

4.5.4 Influence of plant species richness on infiltration capacity

In contrast to the pronounced effects of certain plant functional groups, such as legumes and grasses, plant diversity measures (plant species and functional group richness) had only small effects on the infiltration capacity and earthworm performance. In October, we found that plant diversity had only a marginally significant effect on the infiltration capacity on subplots with ambient earthworm density, but plant species diversity affected infiltration capacity significantly on subplots with reduced earthworm density, presumably due to plant roots clogging macropores (Barley 1954, Gish and Jury 1983). This is supported by data on the relationship between plant diversity and standing root mass in the Jena Experiment, showing that root biomass also increased with diversity level (Bessler et al. 2009, Ravenek et al., in prep.). Additionally, infiltration capacity decreased over the year presumably by the growing

roots clogging macropores, which is in accordance with observations by Gish and Jury (Gish and Jury 1983). Additionally, Angulo-Jaramillo et al. (2000) observed a decrease of hydraulic conductivity caused by sealing of interconnected pores at the soil surface. However, on subplots with ambient earthworm densities this clogging may have been counteracted by the activity of earthworms. These results suggest that water flow through soil is more strongly affected by earthworm biomass which is regulated by the presence of certain functional groups then by loss of single plant species along the observed gradient.

4.5.5 Influence of soil texture and soil moisture on infiltration

Grain size distribution strongly influences hydraulic properties of porous media, and therefore texture has often been related to hydraulic conductivity (Rawls et al. 1982, Saxton et al. 1986). However, in our experiment saturated and near-saturated infiltration capacity in June and October were not affected by soil texture (Figure 4.1). Surprisingly, in September infiltration capacity varied with soil texture, but unexpectedly it was lowest in coarse textured soils. However, the results are in agreement with Jarvis and Messing (1995) and Lin et al. (1999), who found higher hydraulic conductivity in finer as compared to coarser textured soils due to well-developed soil structure (earthworm burrows, root channels) and a high degree of macroporosity. As detailed above, legumes increased infiltration capacity, and interestingly the negative correlation between sand and infiltration capacity disappeared when removing plots containing legumes. This is probably a result of the positive relationship between legumes and earthworms and resulting effects on infiltration. An alternative explanation for increased infiltration in presence of legumes could be that especially finer textured soils roots affect the formation of aggregates and structure (Angers and Caron 1998, Six et al. 2004). Kördel et al. (2008) suggested that the formed macropores are less stable over time in sandy soil. However, investigations on soil stability in the Jena Experiment itself (Pérès et al. 2013) suggest the opposite effect, with legumes decreasing soil aggregate stability (indirectly, by increasing earthworm biomass and decreasing plant root biomass). At the same time, we found a lower number of earthworms in more sandy soils in 2011 (data not shown). This is in line with previous studies (Paoletti 1999, Bens et al. 2007) showing that sandy soils support smaller earthworm populations than clayey soils resulting to lower hydraulic conductivity in sandy soils. Thus, our results may be a result of both legumes and finer soil texture promoting earthworm abundance, but dedicated research is necessary to support these findings. Our results underline the importance of soil structure as influenced by biotic processes. This also corroborates the findings of Bonsu (1992) who suggested that the texture based calculation underestimates the hydraulic conductivity, in particular in fine textured soils.

One important source of error that can dominate or suppress other factors is the initial soil moisture content. Several studies have shown that the infiltration through soil is correlated with the initial soil moisture content (Slater 1957, Azooz and Arshad 1996). This relation was not expected in our setup, since the soil moisture is controlled by fixing the infiltration pressure head. At the beginning of an infiltration experiment low initial soil moisture content enhanced the water flow through the soil because of larger gradients in matric potential and filling up of the soil storage. The influence of initial moisture content decreased during the experiment, when the pores are filled and infiltration reaches a steady state (Blackburn 1975). A potential error source is finishing the experiment before steady infiltration capacity is reached in dry soils and hence overestimating infiltration capacity. Thus, we checked whether infiltration capacity was biased by initial soil moisture and this was not the case. Thus our infiltration measurements were performed correctly. Another factor potentially affecting infiltration capacity is soil hydrophobicity. Hydrophobic exudates are produced by plant roots and soil microbes. Soto et al. (1994) observed that the soil showed a tendency to be water repellent if the volumetric water content fell below $\theta_c = 22$ % for medium textured soils, the so called 'critical soil water content' (Dekker and Ritsema 1994). The majority of the measured volumetric water contents exceeded this threshold (data not shown). Since most of our observed effects enhanced during the growing season, while the chance for hydrophobicity decreased, we conclude that water repellency did not affect our results.

4.6 Conclusions

Despite large spatial variability of soil hydraulic properties, biotic factors emerged as significant agents for infiltration. The presence of legumes increased and the presence of grasses decreased infiltration capacity with the effects increasing over the course of the growing season. The path analysis suggests that modifications in hydraulic conductivity are probably due to (i) roots directly, modifying the pore spectrum and (ii) indirectly, suppressing or enhancing earthworm activity. The results suggest that earthworm biomass is synchronized with other soil processes such as plant root growth, such that the observed effects of plant functional groups include earthworm and root activity.

Most predictions of near surface soil hydraulic properties are based on easily accessible soil properties such as soil texture. Our results suggest that biotic effects, especially the presence of certain plant functional groups affecting earthworm biomass, shape hydraulic conductivity and may even reverse effects of texture. Therefore, for explaining variations in hydrological processes, such as infiltration capacity, the structure of soil fauna and plant communities need to be considered.

Chapter

5

Soil and plant community characteristics governing soil hydraulic properties in a grassland plant diversity experiment

5 Soil and plant community characteristics governing soil hydraulic properties in a grassland plant diversity experiment

5.1. Abstract

Soil hydraulic properties such as infiltration capacity play an important role for soil erosion, run-off and water availability to plants for the prediction and management of ecosystem patterns. There have been only a few studies about the mechanisms and characteristics of how plant diversity might influences vertical soil water fluxes by modifying soil infiltration capacity. In this study we quantify the change in infiltration capacity affected by soil structural variables (bulk density, porosity and soil organic carbon content) in a grassland plant diversity experiment (Jena Experiment). We conducted two infiltration measurement campaigns (in May and October 2012) along a plant species richness gradient from 1 to 60. Although the spatial variation of the infiltration capacity and the interactions among soil- and vegetation characteristics are very complex, our research showed that plant diversity systematically increased infiltration capacity in the studied grassland. Soil structure variables played a major role in mediating this relation. Texture (percent of sand) did not correlate with the infiltration capacity at any time. In May earthworm biomass marginally affected water infiltration but did not influence soil structural parameters. In the present study plant species richness, bulk density (or inversely porosity) and soil organic carbon are important parameters for studying changes of water flow through soil. Our observations identified important ecological drivers of infiltration capacity, suggesting complex interactions between plant species richness, earthworms and soil structural variables, while showing little impact of soil texture.

5.2 Introduction

Studies linking plant diversity and water fluxes have so far focused on the role of water as a resource. Besides providing a resource for plants and soil organisms, soil water also acts as a transport agent for dissolved matter and as a medium for microbial activity. Understanding how diversity influences soil water fluxes and resulting soil moisture distribution is an important step for understanding other biological processes. To determine strategies for soil and water conservation and to minimize surface run-off and soil erosion, especially in agriculture when predicting and managing ecosystem patterns, it is important to know which factors influence surface hydraulic properties such as hydraulic conductivity and infiltration capacity (Shukla et al. 2006).

The measurement and monitoring of the soil hydraulic properties are quite difficult and expensive (Wösten and Van Genuchten 1988). Hydraulic conductivity is often estimated indirectly from pedotransfer functions (PTFs) based on soil texture and structure (Rawls et al. 1982; Vereecken 1995; Wösten et al. 1998).

The reliability of these models are limited in their application due to regional dependence of the resulting functions used for the pedotransferfunction (PTFs) derivation (Tietje and Hennings 1996, Wösten et al. 1998). To better understand the hydrologic behavior of grassland sites, field measurements for defining factors shaping soil hydraulic properties, such as infiltration capacity, are therefore important for the characterization of water flow processes through soil.

Based on the size, shape and continuity, soil pores can be classified into macro-, meso and micropores (Beven 1981, Beven and Germann 2013). In grassland, infiltration capacity is enhanced by water flow through macropores. These can be biological macropores caused by soil fauna or plant roots development (Meek et al. 1992, Lavelle 1997, Angers and Caron 1998), or structural macropores due to cracks and fissures (Germann and Beven 1981; Messing and Jarvis 1990; Zehe and Flühler 2001). Soil organic matter may have an indirect influence on both formation and the stabilization of pores (Six et al. 2004), and a strong relation has been observed between soil organic content and bulk density or porosity (Franzluebbers 2002; Lipiec et al. 2006).

Increasing plant species richness is associated with higher plant and root biomass production (Spehn et al. 2000, Tilman et al. 2001, Marquard et al. 2009) implying a higher input of above- and belowground organic matter (Steinbeiss et al. 2008). Besides water removal by plants via transpiration through root water uptake, soil hydraulic properties are also shaped by plant species richness directly via roots (Angers and Caron 1998) and indirectly by shaping soil structure (Oades 1993). Water flow through vertically oriented macropores formed by plant roots can enhance infiltration (Mitchell et al. 1995), whereas root growth clogging of soil pores can result in a decrease of water flow (Bodner et al. 2008). The most commonly known soil structural parameters are soil bulk density, porosity and soil organic carbon which are influenced by the type of vegetation cover and partly by plant species richness, microbes, fauna or other soil properties such as texture (Six et al. 2004). Generally, it is known that biological activity is greater on higher plant species richness plots leading to higher carbon content, decreased bulk density and increased porosity (Zacharias and Wessolek 2007, Périé and Ouimet 2008). Other studies have shown that an increase in soil organic matter content leads to a higher pore development, which increases soil aggregate stability, water holding rate and water infiltration through soil (Berglund et al. 1980, Haynes and Naidu 1998, Franzluebbers 2002). Also larger soil animals such as earthworms improve the water infiltration by modifying soil structure and aggregate stability through burrowing, casting and mixing of litter and soil by creating burrows as pathways for water flow (Six et al. 2004; Pérès et al. 2013; Edwards and Bohlen 1996). The stability of soil aggregates and the pores between the aggregates improve infiltration, drainage and storage of water, activity of soil fauna, and plant growth (Lee and Foster 1991; Bronick and Lal 2005).

In agriculture an important task is to increase infiltration to prevent and/or reduced run-off and frequent flood events (Mannering and Meyer 1963). Therefore, slow water infiltration is a serious problem that leads to reduced plant water use efficiency, increased run-off and erosion. On bare ground or low plant cover ground rain water drops can compact the soil surface layer by clogging soil pores and thus reduced infiltration through soil. There is little research on the understanding of how plant diversity might influence vertical soil water fluxes by modifying soil hydraulic properties in grasslands. The objective of this field study was to quantify the change in infiltration capacity in a grassland plant diversity experiment covering a gradient in soil texture and plant species diversity. In order to unravel possible mechanisms affecting water infiltration through soil improve, the following questions were investigated:

(i) Do patterns in soil organic carbon content, induced by biodiversity gradients, relate to structural parameters bulk density and porosity?

(ii) Do those parameters affect infiltration capacity?

5.3 Material and methods

5.3.1 Study area and experimental design

5.3.1.1 The Jena Experiment

The study was performed on the field site of The Jena Experiment which is located in the floodplain of the Saale river near Jena (Thuringia, Germany; 50°55´N, 11°35´E, 130 m above sea level). The mean annual air temperature is 9.3°C and the mean annual precipitation is about 587 mm (Kluge and Müller-Westermeier 2000). Before its establishment in 2002 the experimental field site was arable land and had been highly fertilized over the last decades. After its last harvest in autumn of 2000, the field was ploughed and kept fallow throughout 2001, and the diversity treatment was started in spring of 2002. The texture on the field site at the upper soil surface changes gradually with increasing distance from the river from loam into a silt loam. The clay content shows no significant spatial trend. The soil of the experimental site is an Eutric Fluvisol (Fao-Unesco 1997) developed from up to 2 m thick loamy fluvial sediments (Roscher et al. 2004). The species were drawn from a pool of 60 plant species common to the Central European mesophilic grasslands to established a gradient of plant species richness (1, 2, 4, 8, 16 and 60) and functional group richness (1, 2, 3 and 4) on 80 plots of 20 x 20 m.. To account for differences in morphology and physiology, species were assigned to four functional groups: Grasses (16 species), small herbs (12 species), tall herbs (20 species) and legumes (12 species). Plots were assembled into four blocks, arranged parallel to the river, thus accounting for changes in soil properties and water conditions. Independently of the plant species richness, the statistical design allows for the testing of effects caused by the presence and absence of certain functional groups. For more details on the experiment and management,

please refer to Roscher et al. (2004). The plots were mown twice a year and the hay was removed from the plots some days after cutting. All plots were weeded regularly to maintain the target species composition.

5.3.1.2 Earthworm subplots

For infiltration measurements in May 2012, earthworm biomass was determined at the same time, but only on plots with species-richness levels of 1 (12 plots), 4 (16 plots) and 16 (14 plots). The subproject was completed before the next extraction campaign in October. Earthworm performance was performed in May 2012 on one subplot (size 1 x 1 m) by electro-shocking. A voltage was applied to the soil for 35 min. *via* four octet devices (Thielemann 1986) (DEKA 4000, Deka Gerätebau, Marsberg, Germany) powered by two 12 V batteries. During the application time the voltage was increased sequentially from 250 V (10 min) to 300 V (5 min), 400 V (5 min), 500 V (5 min) and 600 V (10 min). For more details on the arrangement of the steel rods of the octet devices and management of the earthworm subplots see Eisenhauer et al. (2009a). Extracted earthworms were identified, counted and weighed (with gut content) in the laboratory. Earthworms at the field site of the Jena Experiment mainly belong to two ecological groups (Bouché 1977): anecic (*Lumbricus terrestris*) and endogeic (*Aporrectodea caliginosa, Octolasion tyrtaeum, Allolobophora chlorotica*, and *Aporrectodea rosea*) species.

5.3.2 Infiltration measurement

For in situ infiltration measurements we used a hood infiltrometer (UGT, Müncheberg, Germany; method described in Schwärzel & Punzel, 2007). With the in situ technique it is possible to determine the water flow through different pore size classes and consequently quantify the role of soil texture, moisture, earthworms or plant roots without destroying the measurement environment. In 2012, we conducted two infiltration measurement campaigns (in May and October) along a species richness gradient on plots containing 1 (n=12), 2 (n=16), 4 (n=16), 8 (n=16), 16 (n=14) and 60 (n=4) plant species.

A small hood with a diameter of 16 cm was placed with the open side on the undisturbed soil surface. The contact between the soil and hood was sealed with wet sand. We conducted measurements at increasingly negative matric potentials (Ψ_M) beginning with Ψ_M = 0 m and reducing it stepwise by -0.02 m until the bubble point of the soil was reached. The bubble point refers to the matric potentials, upon which a pore channel allows for the penetration of air into the hood and therefore the maximum applicable matric potential at this location. For a specific matric potential (Ψ_M) the equivalent diameter (de) of the largest soil pore conducting water can be estimated after Jarvis et al. (1987). At Ψ_M = 0 m the soil is saturated and the entire pore

spectrum is potentially active. At Ψ_M = -0.02 m the largest active pores correspond to de =1.5 mm, at Ψ_M = -0.04 m to de = 0.75 mm. At each pressure level, we recorded infiltration capacity until they were constant in time. This steady infiltration capacity was used for further analysis. Infiltration capacity at a given matric potential is directly linked to hydraulic conductivity (Wooding 1968). The flow conditions in natural soils are however far from ideal, with anisotropic behaviour, heterogeneous initial soil water contents and flow dynamics that do not correspond to the Richards equation near soil saturation. Therefore, we refrained from deriving hydraulic conductivity from our infiltration capacity, for example via Wooding´ s formula (1968). Instead, we worked with the observed infiltration capacity, considering those as a surrogate for the rate of the soil to conduct water at the applied matric potential.

5.3.3 Soil structural parameters

In October 2012, three samples per plot were taken from each plot using soil sample rings with an internal diameter of 57 mm and 40.5 mm height (inner volume of 100 cm³). The samples were dried at 105°C and weighed to calculate the bulk density [g/cm^3] (0-5 cm soil depth). Prior determination of bulk density we measured porosity on a sand plate at saturation.

Soil organic carbon was measured in 2011 (one year before we measured bulk density and soil organic carbon). Three samples per plot were taken using a split tube sampler with an inner diameter of 4.8 cm (Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands) and sieved through a 2 mm sieve. After drying at 40°C the soil samples were segmented to a depth resolution of 5 cm. For our analysis we used the first 5 cm segment (0-5 cm depth). The three samples from one plot were mixed into one sample. Total carbon concentration was analyzed on ball-milled subsamples (time 4 min, frequency 30 s^{-1}) by an elemental analyzer at 1150°C (Elementaranalysator vario Max CN; Elementar Analysensysteme GmbH, Hanau, Germany) before and after incubation. For the calculation of organic carbon, the difference between elemental analyses of the total carbon concentration and soil inorganic carbon concentration was determined (Steinbeiss et al. 2008).

5.3.4 Soil texture, moisture and hydrophobicity

Soil texture was determined from soil cores at 38 locations distributed throughout the experimental site prior to plot establishment (G. Büchel, pers. comm.). Values for each plot were interpolated by ordinary kriging. The fraction of sand and silt are negatively correlated (clay showing no spatial trend). For simplicity, in the following statistical analysis we used the sand fraction as a factor representing soil texture. The volumetric soil water content (in m³ m^{-3}) was determined with a FDR probe (ML2x Theta Probe, Delta-T Devices, Cambridge, United Kingdom). The device was inserted from the top to 6 cm deep (the length of the prongs) into the

soil surrounding the hood before the infiltration experiment. The average of three measurements was used for further analysis. In each season the water repellency of the soils was measured with the water drop penetration time (WDPT) test before measuring infiltration capacity. A further 9 drops of distilled water were placed on the smooth surface of the soil using a pipette. The time for their complete penetration was recorded and classified according to Dekker and Ritsema (1994). Seven classes were observed ranging from time measurements under 5 s (wettable) to over 6 h (extremely repellent).

5.3.5 Vegetation parameters

Community biomass was recorded in each plot in 20 x 50 cm rectangles shortly before the infiltration measurements were started. Two randomly allocated samples were taken. Plant material was cut 3 cm above ground. Species which did not belong to the initial sowing plant community were removed by hand and collected at the beginning of the growing season and after the first and second mowing. Plant and weed biomass were sorted in plant functional groups, dried (70° C, 48 h) and weighed. Species not sown in a particular plot were removed and dried separately.

Plant root biomass was taken with a 35 mm root corer with 3 replicates per plot up to a depth of 40 cm. The samples were divided to a depth solution of 5 cm. For root extraction, samples were washed through a sieve (0.5 mm mesh). Roots were dried at 60-70 °C for 24, and weighed.

5.3.6 Statistical analyses

Statistical analyses were performed using the statistical software R 2.6.2 (R Development Core team, http.//www.R-project.org). The data were checked for normality, and log-transformed if required. Analyses were performed with mixed effect models with the *lme* function implemented in the *nlme* package (Pinheiro and Bates 2000). To compare models and estimate the significance of fixed effects, the maximum likelihood method (Likelihood ratio test) was applied. Block was entered as random effect. We analysed the variation of the infiltration capacity for May and October separately by adding the following fixed effects sequentially: plant species richness (log-linear term; SR; 1, 2, 4, 8, 16 and 60) and plant functional group richness (FG; 1, 2, 3, 4). The design also allowed us to test for the effects of the presence (or absence) of each plant functional groups on the response variable.

Further, we used structural equation modelling AMOS 5 (http://amosdeveleopment.com) to test the direct and indirect effects of plant species richness, soil structural properties (soil organic carbon and porosity), texture (silt content) and vegetation parameters (Plant species richness, shoot biomass, root biomass and bare ground cover) on infiltration capacity in a multivariate approach (Grace 2006). Additionally, we include

earthworm biomass in a separate analysis for spring data. The adequacy of the model was determined via Chi²-tests, AIC and RMSEA. Non-signifcant Chi²-test ($p>0.05$), low AIC and low RMSEA indicating an adequate model fit (Grace 2006). Beginning with the full model (including all possible pathways) the models were improved stepwise by removing unimportant relationships based on AIC values (Shipley 2000). For soil structural properties we used soil organic carbon content and porosity and excluded soil bulk density, because it was highly correlated with porosity ($R^2=0.392$, $p=<0.001$). For both months plant shoot biomass and bare ground cover did not stay in the path analysis as it did not significant influence infiltration capacity (data not shown). Standardized path coefficients were derived based on the correlation matrix of standardized variables.

5.4. Results

5.4.1 Plant community composition (Plant species richness and functional groups)

With increasing plant species richness the infiltration capacity increases for May and October at saturation (Figure 5.1A, B) and lower matric potentials (data not shown). None of the plant functional groups affected the infiltration capacity (Table 5.1). Porosity is positively and bulk density is negatively correlated with plant species richness, plant biomass, and root biomass (Figure 5.1C, D; Table 5.2, 5.3). Organic carbon content also correlates significantly with plant species richness, plant shoot biomass, root biomass (Table 5.2, 5.3) and infiltration capacity for both seasons (positive relationship, data not shown).

5.4.2 Soil structural variables (bulk density, porosity, soil organic carbon)

The soil structural variables of bulk density, porosity and soil organic carbon are highly correlated with each other (Table 5.2, 5.3). Bulk density showed a significant negative linear relationship with the soil organic carbon content ($r = - 0.600^{***}$) and porosity ($r = - 0.728^{***}$). Porosity and soil organic carbon content were significantly positive related to each other ($r = 0.626^{***}$). With increasing porosity the bulk density decreased and organic carbon also increases (Table 5.2, 5.3). Additionally, for both months the infiltration capacity increases with increasing porosity and soil organic carbon, while it decreases with increasing bulk density (data not shown).

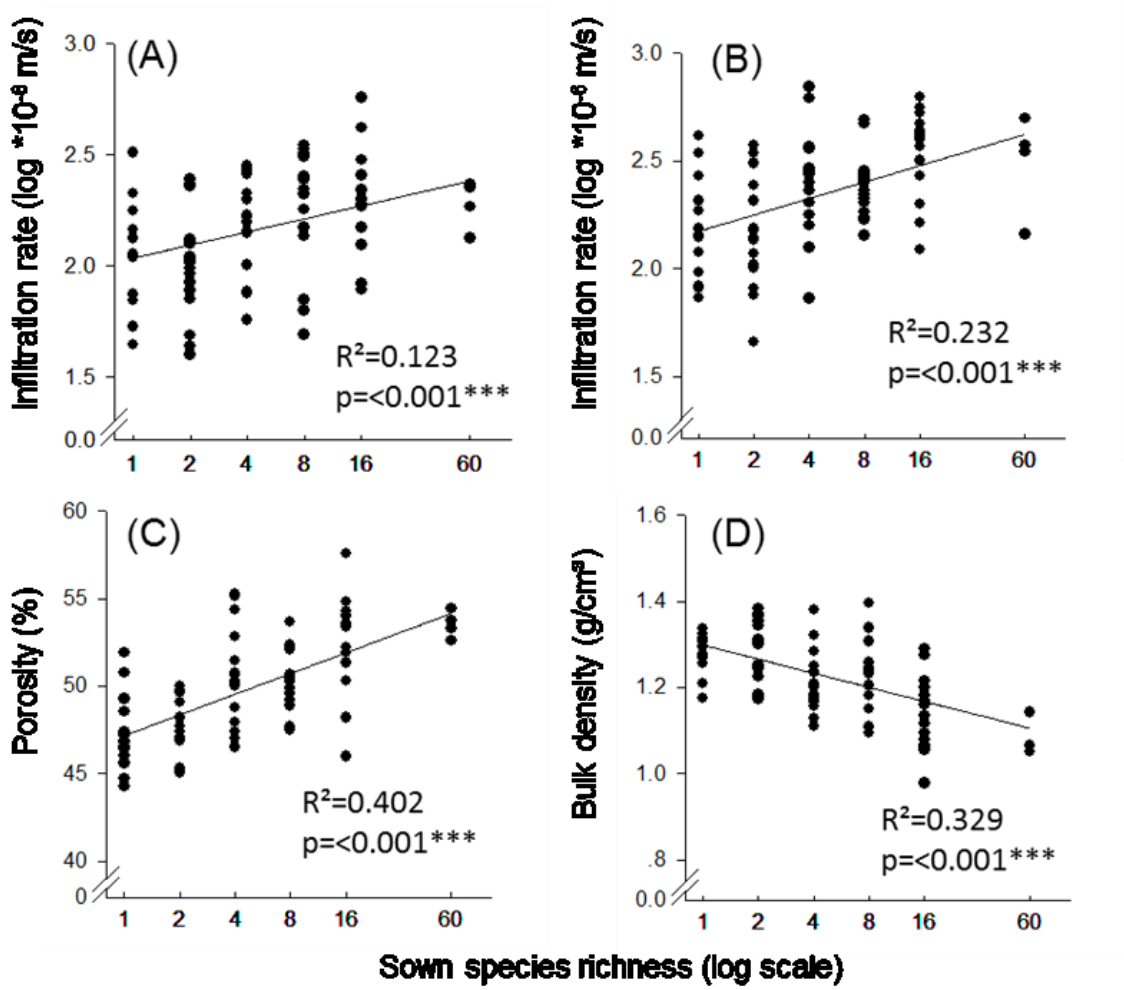

Fig. 5.1: Relationship between species richness and infiltration capacity , porosity and bulk density for A) infiltration capacity in May (log*10^{-6} m/s), B) infiltration capacity in October (log*10^{-6} m/s), C) Porosity (%) and D) Bulk density (g/cm³) as mean value per plot against sown species richness (log scale).

Table 5.1: Summary of mixed-effect model analyses for infiltration capacity (log *10^{-6} m/s) in A) May and B) October for the matric potentials ψ_M = 0, 0.02 and 0.04 m.

	0 m			-0.02 m			-0.04 m		
	L ratio	p		L ratio	p		L ratio	p	
(A) May									
SR (log-linear)	**9.58**	**0.002**	↑	**11.52**	**<0.001**	↑	**12.83**	**<0.001**	↑
FG	4.91	0.178		5.31	0.151		4.01	0.260	
LEG	0.01	0.929		0.01	0.938		0.17	0.683	
GR	2.22	0.137		1.89	0.170		0.84	0.360	
SH	0.12	0.731		<0.01	0.958		0.01	0.911	
TH	1.40	0.236		1.69	0.194		2.07	0.150	
(B) October									
SR (log-linear)	**22.80**	**<0.001**	↑	**29.18**	**<0.001**	↑	**16.67**	**<0.001**	↑
FG	1.70	0.634		2.99	0.393		2.07	0.558	
LEG	0.07	0.799		0.52	0.472		0.02	0.897	
GR	<0.01	0.955		0.65	0.420		0.52	0.472	
SH	0.36	0.550		2.39	0.122		0.28	0.597	
TH	0.65	0.421		2.27	0.132		1.76	0.185	

Models were fitted by stepwise inclusion of fixed effects. Likelihood ratio tests were applied to assess model improvement (L ratio) and the statistical significance of the explanatory terms (p values). Significant effects are marked in bold. Arrows indicate increase (↑) or decrease (↓).Abbreviations: SR = species richness (log-linear), FG = functional group, LEG = legume presence/absence, GR = grasses presence/absence, SH = small herbs presence/absence, TH = tall herbs =presence/absence.

5.4.3 Soil texture, soil moisture and hydrophobicity

In both months (May and October) texture content (percent of clay, sand and silt) did not correlate with the infiltration capacity (data not shown). In May the moisture content weakly correlated with the infiltration capacity at Ψ_M = 0 m (R^2=0.07, p=0.026), -0.02 m (R^2=0.06, p=0.028) and -0.04 m (R^2 =0.09, p=0.009). With increasing moisture content the infiltration capacity increases. In October moisture content did not correlate with the infiltration capacity for any of the applied matric potentials. In both seasons almost all measurements testing the water repellency were below 5s, only single drops of one plot required time between 5s and 1 min (slightly water repellent). On average all plots were wettable and we therefore concluded that wettability did not influence our results.

Table 5.2: Pearson correlation matrix for studied variables in May.

May	Bd (g/cm^3)	BM root (mg/cm^3)	BM shoot (g/m^2)	Sand (%)	Porosity (%)	SR	Moisture (%)
Corg	-0.600***	0.400***	0.219*	-	0.626***	0.437***	-
	Bd	-0.522***	-0.288**	-	-0.728***	-0.574***	-
		BM root	0.378***	-	0.567***	0.590***	-
			BM above	-0.219*	0.347**	0.556***	0.411***
				Sand	-	-	-0.326**
					Porosity	0.634***	0.251*
						SR	-
							Moisture

Abbreviations: SR= species richness (log-linear), Bd=Bulk density, BM root =Biomass root, BM above= plant biomass aboveground, BM weed= Plant biomass weed, LAI= Leaf Area Index, Bare = Bare ground cover; * p≤0.05, ** < 0.01, *** p=0.001

Table 5.3: Pearson correlation matrix for studied variables in October (Oct).

Oct	Bd (g/cm^3)	BM root (mg/cm^3)	BM shoot (g/m^2)	Sand (%)	Porosity (%)	SR	Moisture (%)
Corg	-0.600***	0.400***	-	-	0.626***	0.437***	-
	Bd	- 0.522***	-0.251*	-	-0.728***	-0.574***	-
		BM root	0.266*	-	0.567***	0.590***	-
			BM above	-	0.245**	0.528***	0.349**
				Sand	-	-	-0.269*
					Porosity	0.634***	-
						SR	-
							Moisture

Abbreviations: SR= species richness (log-linear), Bd=Bulk density, BM root =Biomass root, BM above= plant biomass aboveground, BM weed= Plant biomass weed, LAI= Leaf Area Index, Bare= Bare ground cover; * p≤0.05, ** < 0.01, *** p<0.001

5.4.4 Path analysis

Because of a strong effect of the interrelated variables on infiltration, we used path analysis for the visualisation of direct, indirect and interaction effects. Using path analyses, we were able to investigate the effects of plant species richness through changes in root biomass, soil organic carbon content and porosity for both months. The initial model (AIC=51.52; Figure 5.2A) was improved as described in material and methods. In May the path analysis model explained 20 % of the infiltration capacity at saturation (Figure 5.2B). For the improved model (Fig. 5.2 B, $\chi^2 = 7.203$, $p = 0.408$, AIC = 47.203) root biomass, porosity and soil organic carbon increased significantly with increasing plant species richness. Infiltration capacity at saturation was mainly explained by the variation of porosity (positive relationship), while there was

negative trend between root biomass and infiltration. Root biomass affects infiltration capacity indirectly by increasing porosity. In October the path analysis model explained 42% of the infiltration capacity (Figure 5.2C). The initial model (Figure 5.2A) was improved as described above. For the improved model (Figure 5.2 C, $\chi^2 = 8.34$, $p = 0.303$, AIC = 48.34) root biomass, porosity and soil organic carbon increased significantly with increasing plant species richness. Infiltration capacity was positively related to soil organic carbon content and porosity (Figure 5.2 C). In both months soil texture (sand content) did not have a direct significant influence on the infiltration capacity, but affected plant root biomass. When including clay instead of sand in the full model, clay is positively related to the soil organic carbon content (R^2=0.06, p=0.029).

5.4.5 Earthworms

In May the biomass of the deep burrowing earthworm species *Lumbricus terrestris* accounted for 89% of the total biomass (Table 5.4). In an additional path analysis in May, we were able to explain the variation of the infiltration capacity based on a reduced dataset for which earthworm data was available (plots containing 1, 4 and 16 plant species). The improved model in May including earthworm biomass explained 25% of the infiltration capacity at saturation (Figure 5.3). Infiltration was still mainly driven by porosity (positive relationship), while instead of root biomass earthworm biomass marginally correlated (trend) with infiltration capacity (positive relationship). Additionally, soil organic carbon significantly affected the total earthworm biomass (positive relationship). Interestingly, at saturation none of the ecological groups (anecic and endogeic) could better explain the infiltration capacity compared to the total biomass (data not shown).

Table 5.4 Variations in biomass (g m^{-2}) of earthworms of the Jena Experiment field site. Earthworm data are the means (± standard error) across plots of the year 2011 separated into the ecological groups anecic and endogeic.

Earthworms	March
Biomass of anecics	4.47 ± 0.46
Biomass of endogeics	0.46 ± 0.13
Biomass total earthworms	5.04 ± 0.74

Total number and biomass of earthworms included also unidentifiable earthworms and the invasive earthworm *Lumbricus castaneus*

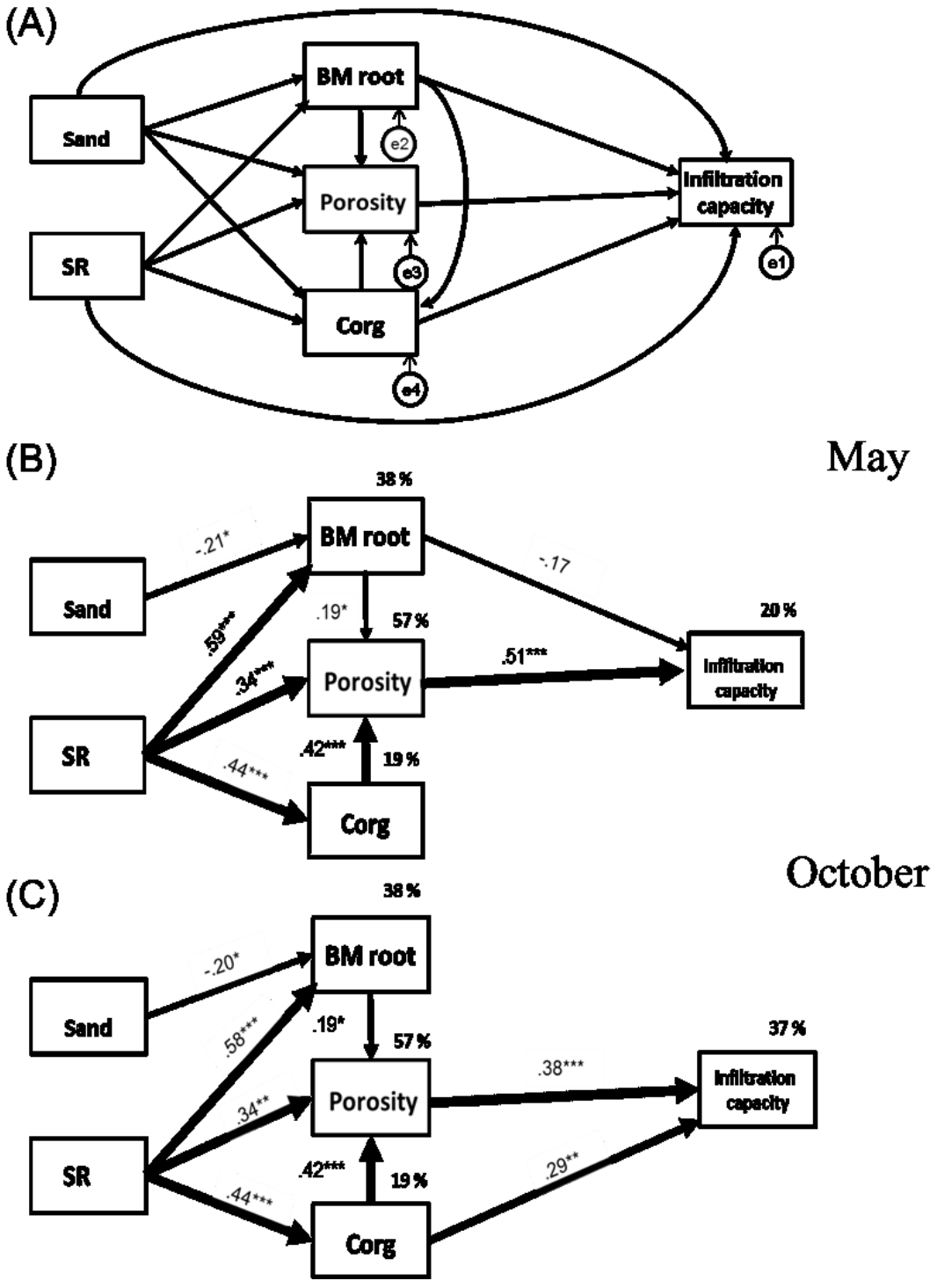

Figure 5.2: Path analysis showing the relationships between plant species richness (SR), texture (silt in 10 cm depth), the soil process parameter soil organic carbon (Corg) and porosity (Porosity) , root biomass (BM root) and bare ground cover (Bare) on the infiltration capacity for (A) the full model, (B) for May and (C) for October at saturation. Standardized path coefficients are given next to path arrows. Unexplained variation is denoted with e1-e3; * $p \leq 0.05$, ** < 0.01, *** p=0.001. For details see text.

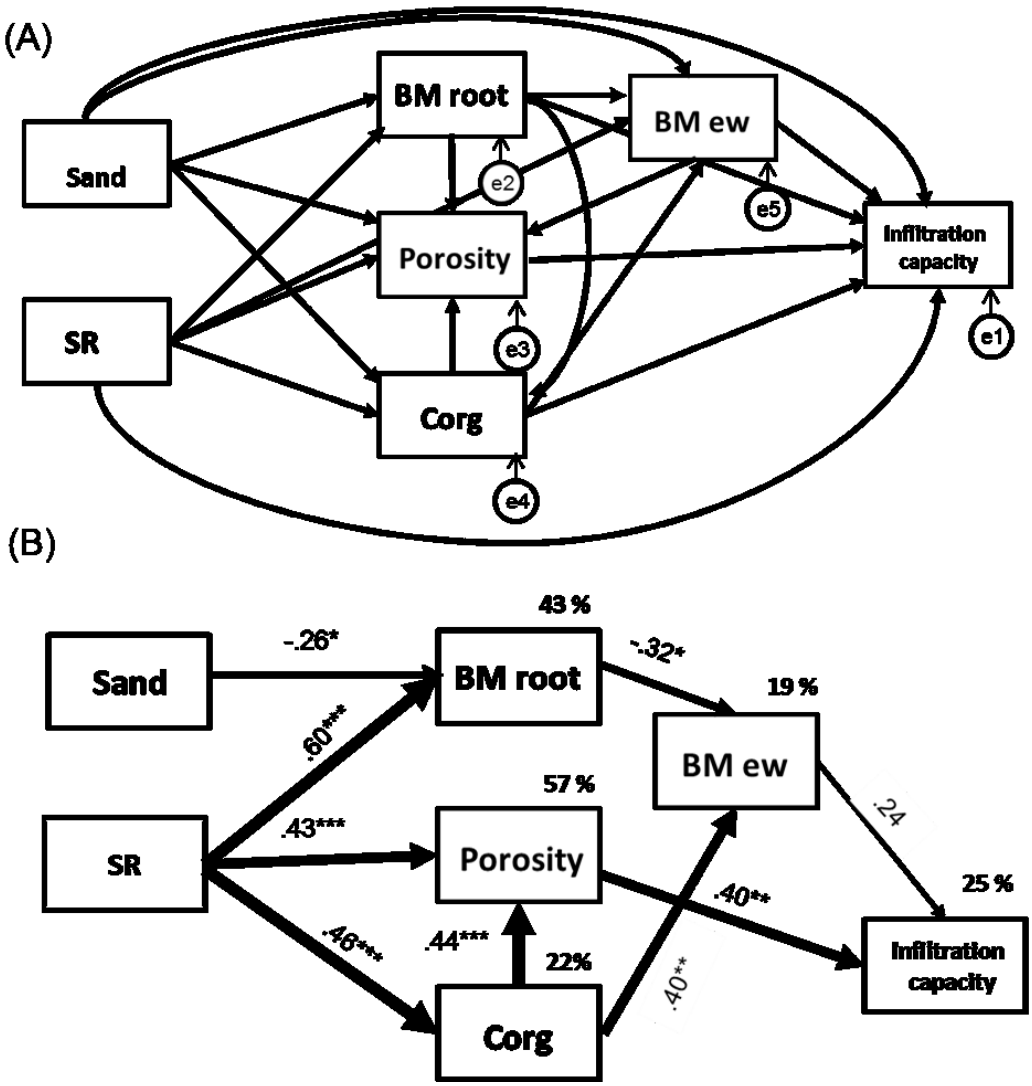

Figure 5.3: Path analysis showing the relationships between Plant species richness (SR), texture (sand in 10 cm depth), the soil process parameter soil organic carbon (Corg), porosity (Porosity) and root biomass (BM root) on the infiltration capacity for saturated conditions (equal to pore size diameter > 1.5 mm) including total earthworm biomass (BM ew) for A) full model and B) the improved model. Standardized path coefficients are given next to path arrows. Unexplained variation is denoted with e1-e3; * p≤0.05, ** < 0.01, *** p=0.001. For details see text.

5.4.6 Temporal variation of infiltration capacity

Time significantly affected the infiltration capacity at matric potentials ψ_M = 0, 0.02 and 0.04 m (Fig. 5.4A). The average infiltration capacity increased significantly from May to October (Ψ_M = 0 m: +62.95 %, Ψ_M = -0.02 m: +63.31 %, Ψ_M = -0.04 m: +62.48 %). For all matric potentials the infiltration capacity changed during the year with a more pronounced effect for larger macropores (Fig. 5.4A). Lower matric potentials (below Ψ_M = -0.04 m) were not included because of a high percentage of missing data in spring. The moisture content decreased significantly from May to October (t-test, p=<0.001, Fig. 5.4B)

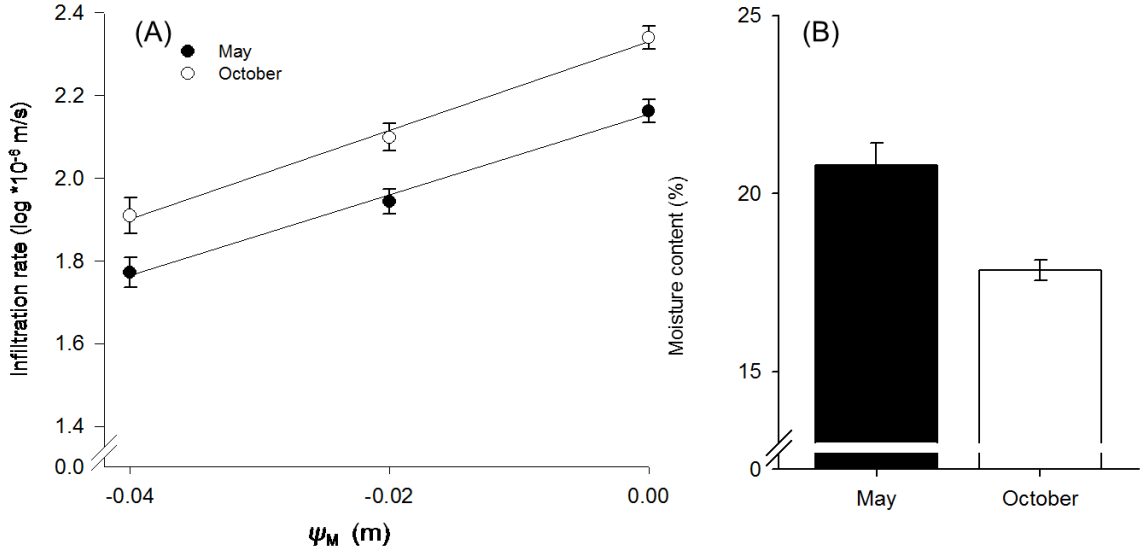

Figure 5.4: Variation in A) infiltration capacity (in log $*10^{-6}$ m/s) separated for the different months May (black dots) and October (white dots) for the matric potential ψ_M = 0, 0.02 and 0.04 m (as indicated); B) variation of initial moisture content for May and October (as indicated). Means with standard error.

5.5 Discussion

5.5.1 Influence of plant species richness and structural parameters on infiltration

In this study plant species richness improved infiltration capacity. Our results suggest that plant species richness enhanced water flow through soil by modifying soil structural variables such as soil porosity (or inversely bulk density) and soil organic carbon. Soil organic carbon and porosity increased, while the bulk density decreased with increasing plant species richness (Table 5.2, 5.3) which in turn enhanced infiltration capacity. These results are consistent with previous research, which found that increasing plant species richness correlated positively with soil organic carbon storage and root biomass (Fornara and Tilman 2008, Steinbeiss et al. 2008). Independently, other studies showed that the increased soil organic carbon, porosity and root biomass can be attributed to an increased soil aggregate stability and macroporosity (Oades 1993, Angers and Caron 1998, Six et al. 2004). It is also well known that an increase in bulk density induces changes in hydraulic properties due to the reduction of large macropores and pore continuity (Fuentes et al. 2004, Dec et al. 2008). Our results connects these different results, showing for the first time that plant species diversity impacts soil hydraulic properties such as infiltration capacity, most likely via changing soil structural variables such as bulk density and soil organic carbon.

In the present study the soil structural parameter porosity (or inversely bulk density), an important factor for soil quality, revealed itself as the most important driver for explaining the infiltration capacity in May and October. Additional analyses revealed that bulk density (0-5 cm

depth) correlated significantly positively with plant species diversity in more than half of the years of the Jena Experiment (Table 5.5). This pattern suggests, that plant species diversity not always, but frequently, contributes to enhancing soil structure and probably also infiltration capacity. It also shows that other factors but biodiversity shape soil structure in other years. Notably in 2011 no effect between species diversity and bulk density was observed, and this was incidentally the year, where we found significant influences of earthworms on infiltration.

Identifying the mechanisms of how plant communities affect water flow through the soil is a significant step forward in understanding the prevention of run-off and soil erosion. Generally, agricultural management practices decrease plant biodiversity and biological activity resulting in a decrease of organic matter content, aggregate stability and decreasing bulk density (Altieri 1999, Lamandé et al. 2003). Several studies have emphasized the positive effect of organic management enhancing water infiltration through channels formed by roots and earthworms, which improve soil water storage and reduce soil erosion and run-off (Schjønning et al. 2002, Bronick and Lal 2005, Papadopoulos et al. 2006, Pfiffner and Luka 2007).

Table 5.5: Relationship between bulk density (ρ_b) and plant species richness for various years (as indicated).

	Plant species richness	
Year	r	p
ρ_b 2004	-0.242	**0.045**
ρ_b 2006	-0.031	0.783
ρ_b 2008	-0.434	**<0.001**
ρ_b 2011	-0.130	0.252
ρ_b 2012	-0.493	**<0.001**

r= Pearson correlation coefficient

5.5.2 Influence of earthworms on infiltration

In 2012, earthworm biomass was only marginally correlated to infiltration capacity in May (Figure 5.3). A positive relation between earthworms and infiltration rate is consistent with other studies (Zachmann et al. 1987, Bouché and Al-Addan 1996) and our previous data taken in 2011 (Chapter 4). However, the earthworm biomass in 2012 was low, very likely due to the much drier soil conditions (Lavelle 1988) compared to 2011 when an effect of earthworms on infiltration capacity was observed. Compared to 2011 earthworm biomass was reduced to one third of the population in spring 2012, and in fall earthworm biomass could not be assessed due to the adverse soil conditions. Some authors associated an increased infiltration with modified soil aggregation and porosity due to the burrowing and casting activity of earthworms (Shipitalo

and Protz 1988, Yeates et al. 1998, Six et al. 2004). But in contrast to these studies, earthworm biomass in 2012 did not correlate with soil structural parameters.

A number of reasons may be responsible for this: First, earthworm biomass was only assessed on a short species richness gradient with fewer plots (only for 1, 4 and 16 plant species), which may have masked possible effects. However, the relation between biodiversity and bulk density with infiltration capacity was significant also on this smaller subset of plots, which suggests, that the effects of bulk density and earthworms on infiltration capacity are probably decoupled. This is supported by the results of the path analysis, which shows separate pathways for these two factors. Second, although in general earthworm activity has a positive effect on soil structure (by increasing porosity and decreasing bulk density) (Lee and Foster 1991, Pérès et al. 1998, Blanchart et al. 2004, Hale et al. 2005), their specific role on soil structure depends next to the ecological group, also on their functional attributes such as compacting (increasing soil bulk density) and decompacting (decreasing soil bulk density) earthworm species (Blanchart et al. 1997, Six et al. 2004). Thus, also negative and no effects on soil structure by earthworms have been reported (Zund et al. 1997, Fonte et al. 2009, Salehi et al. 2013). Furthermore, the positive correlation between bulk density and earthworm mainly in agriculture soils could be attributed to an initially higher bulk density before adding earthworms resulting in a significant decrease of bulk density (Poier and Richter 1992, Hale et al. 2005). Third, since earthworm activity was generally low in 2012, their effect on bulk density would generally be week.

Independent of bulk density, our results show that earthworm biomass increases the infiltration capacity, which could be caused by increasing macropore numbers which not necessarily affect soil structure at the scale of soil sample cylinders (100 cm^3). Also, since earthworm activity changes between years their influence on infiltration likely also depends on population dynamics. This may the reason, why we found a stronger relationship between earthworms and infiltration capacity in 2011 compared to 2012.

5.5.3 Temporal variation of infiltration capacity

Over the year the infiltration capacity increased significantly (Fig. 5.4 A). These results differ from other studies (Archer et al. 2002, Bodner et al. 2008) and data taken in 2011 (Chapter 4), which found that infiltration through soil is decreased over the growing season probably due to plant root growth lead to clogging/sealing of pre-existing pores. The increase of infiltration capacity may be associated with dying roots, in the dryer soil and lower precipitation in 2012 compared to 2011 (Schumm and Lusby 1963, Messing and Jarvis 1993) (Fig. 5.4 B). Root decay, which leaves behind empty macropores (Barley 1954, Gish and Jury 1983, Mitchell et al. 1995), has the rate to increase infiltration capacity. In our study soil porosity was also

positively related to root biomass of the previous year. This finding corroborates with other studies which found that roots increased infiltration indirectly by increasing soil macroporosity (Ela et al. 1992, Beven and Germann 2013).

5.5.4 Conclusion

The reduction of bulk density (or increase of porosity) in diverse species mixtures was the most critical parameter for explaining infiltration capacity. Soil organic carbon and roots are fundamental factors leading to a change in bulk density and porosity. These factors, which improve infiltration through soil, might reduce the impact of rainfall leading to reduced run-off and soil erosion. However, the impact of plant species richness on soil structural parameters does not appear every year, which probably also affects the resulting infiltration pattern. Also earthworms play a role for explaining infiltration capacity, independent of plant species richness and bulk density. After 10 years of the establishment of the biodiversity grassland site, higher plant species richness generally increased infiltration capacity by improving soil structural parameters. For soil management these results highlighted that earthworms and plant species diversity both affecting infiltration capacity, whereby the mechanism are different and probably not related to each other.

Chapter

6

An in situ lysimeter experiment (Ecotron/Montpellier) on abiotic and biotic factors influencing hydrological response through a soil profile

6 An *in situ* lysimeter experiment (Ecotron/Montpellier) on biotic and abiotic factors influencing hydrological response through a soil profile

6.1 Abstract

Water flow through the soil profile is controlled by abiotic and biotic parameters that vary in space and time. Knowledge of the factors affecting soil hydraulic properties through the soil profile is important, for the development of optimal agricultural and land management strategies. We measured Infiltration capacity at two plant diversity levels (4 and 16 species) on monoliths originated from The Jena Biodiversity Experiment in the CNRS Ecotron Experiment (Montpellier, France). We analyzed the infiltration capacity at several depths (soil surface, within the rooting zone, below the main rooting zone). In order to mechanistically understand variations in infiltration we extracted and counted earthworms in the infiltration area after the infiltration experiments, determined soil texture, soil organic carbon, bulk density, initial moisture content and root biomass at each depth, and above shoot biomass. Higher earthworm biomass increases infiltration capacity at the soil surface. The impacts of biotic processes on infiltration at the soil surface have no impact on processes through deeper soil layers (25-55 cm). Infiltration capacity decreased in the subsoil by a visible compacted layer (presumably an old plough pan). This decrease was due to a reduction of larger pores formed by earthworms and plant roots, which can negatively affect water infiltration. Furthermore, in deeper soil layers none of the observed parameters could explain the infiltration capacity. In the present study we show that after 10 years of conversion from arable into grassland, at and below the observed dense layer the biotic impact at the soil surface on infiltration was reversed leading to inappropriate predictions for infiltration in deeper soil layers.

6.2 Introduction

Soil properties are greatly influenced by abiotic and biotic parameters varying in space and time (Deb and Shukla 2012). Saturated hydraulic conductivity is the most important soil property for water-plant-soil interactions and water flow through the soil profile. Field studies have shown that saturated hydraulic conductivity in the topsoil can vary greatly because it is influenced by many factors on different spatial scales (Seyfried and Wilcox 1995, Deb and Shukla 2012). Additionally, soil hydraulic properties are often critical input parameters to irrigation and water management models at scales ranging from plot to catchment. Spatial variability of soil hydraulic properties through a soil profile determines surface run-off, plant water storage and water flow through groundwater. Therefore, this is important for the development of optimal agricultural and land management strategies (Bodner et al. 2008, Schwärzel et al. 2011).

Infiltration through soil is determined by soil structure, moisture and the degree of biological activity (Angers and Caron 1998, Bronick and Lal 2005). The spatial variation, size and connectivity of pores formed by earthworms and plant roots play a key role in determining the rate of influx through soil (Edwards and Bohlen 1996, Angers and Caron 1998, Beven and Germann 2013). In addition to the already known seasonal dynamics of earthworm activity (Eisenhauer et al. 2009b), earthworms also vary within depth depending on the ecological type: endogeic, epigeic and anecic (Bouché 1977) with burrows ranging from 2 to 11 mm in diameter (Ehlers 1975, Syers and Springett 1983). Because of the different feeding and burrowing strategies, endogeic and epigeic earthworm mainly increase the infiltration in the topsoil, while anecic species enhance water flow to deeper soil strata (Shuster et al., 2002). As reported by Van Schaik et al. (2013), earthworm macropore numbers decreased with depth (10, 30 and 50 cm), except for larger pores (> 6 mm in diameter). But these macropores had a smaller hydrological effectiveness compared to those at a depth of 10 and 30 cm.

Plant diversity can influence water infiltration through several mechanisms. First, earthworm abundance and/or biomass have been reported to be positively related to plant species richness (Zaller and Arnone 1999, Spehn et al. 2004), which may induce changes in the number of macropores and have an influence water movement in the soil (Bardgett et al. 2001). Second, increasing species richness is associated with higher above- and belowground plant productivity (Tilman et al. 2001, Spehn et al. 2002). The differences in the vertical distribution of roots and rooting strategies due to variations in plant species richness, plant functional groups and soil texture (Coupland and Johnson 1965, Fargione and Tilman 2005, Schenk 2005) have pronounced effects on water fluxes through the soil profile. Several studies have shown that in root profiles root density declines exponentially with increasing depth (Schenk and Jackson 2002, Schenk 2005). However, root effects can strongly differ. Growing roots mainly clog soil pores causing reduced Infiltration capacity, while decaying roots can create vertical channels in the soil increasing the infiltration capacity (Barley 1954, Gish and Jury 1983).

The Ecotron experiment provides the possibility of analyzing soil hydraulic properties under controlled environmental conditions and almost identical functional group composition in several depths. Soil texture has often been related to hydraulic conductivity, but as shown in previous studies of the Jena Experiment, biotic factors play a more important role for the infiltration capacity at the soil surface (Chapter 4) The general objective of this study was to investigate to which extent biotic factors, such as plant species richness, plant root biomass, earthworm biomass, soil moisture and soil texture, play a role on the infiltration capacity of different macropore sizes at several depths (soil surface, within rooting zone and below rooting zone).

We measured infiltration capacity at two diversity levels (4 and 16 species) in plots containing all functional groups (small herbs, tall herbs, legumes and grasses) with almost the

same proportions. We measured infiltration at several depths (top, within the rooting zone, below the main rooting zone). In order to distinguish whether the effects were due to biotic (earthworms, root biomass and/or plant biomass) and/or abiotic factors (texture, initial moisture content), we extracted and counted earthworms in the infiltration area after the infiltration experiments, determined texture, measured initial moisture content at each depth, as well as measured above- and belowground biomass. We conducted infiltration measurements at several matric potentials in order to determine whether changes in infiltration capacity (hydraulic conductivity) are due to alterations in large or small soil pores. The infiltration through soil is controlled by macropores connected to the soil surface (Van Schaik et al. 2013) suppressing or promoting the direction and velocity at which water flows through the profile. Accounting for the variability of the soil properties it is crucial to understand the interactions between soil and biotic parameters, as well as their effects on water flow through the soil. With this study we want to find out which factors improve macropore flow through deeper depths. For irrigation and soil management it is important to consider what roles the factors on infiltration at several depths play. The main question of this field study was:

(i) Do the observed factors influencing soil hydraulic properties at the soil surface also affect infiltration into deeper soil strata? What factors are important drivers for the infiltration at several depths?

6.3 Material and Methods

6.3.1 Experimental design

In 2011 excavated soil cores from the experimental field site to a depth of 2.20 m were transported to CNRS Ecotron of Montpellier (France). The monoliths originate from a temperate grassland site, the Jena Experiment, located in the floodplain of the Saale river near Jena (Thuringia, Germany; 50°55´N, 11°35´E, 130 m above sea level). The Ecotron experiment provides the possibility to study ecosystems processes and organism under controlled environmental. The CNRS of Montpellier (France) Ecotron consists of transparent and confined Teflon domes for analyzing elementary functions under simplified conditions. Therefore, complex patterns in the real field community can be simplified. Under the same environmental condition and near the same functional group composition, we measured soil hydraulic properties and other important soil and biotic parameters to compare with the results from the field site. Additionally, we focused on the spatial variability of the infiltration capacity along the soil profile of the various factors and the resulting interactions between abiotic and biotic factors at a depth of 0, 20 and 60 cm. Because one of the 12 monoliths was broken, our measurements were conducted on 11 of the 12 monoliths.

6.3.2 Infiltration measurement

For in situ infiltration measurements we used a hood infiltrometer (UGT, Müncheberg, Germany; method described in Schwärzel & Punzel, 2007). With the in situ technique it is possible to determine the water flow through different pore size classes and consequently quantify the role of soil texture, moisture, earthworms or plant roots without destroying the measurement environment. We conducted two measurements per monolith at three different soil depths.

A hood with a diameter of 24 cm was placed with the open side on the undisturbed soil surface. The contact between the soil and hood was sealed with wet sand. We conducted measurements at increasingly negative matric potentials (Ψ_M), beginning with Ψ_M =0 m and reducing it stepwise by 0.02 m until the bubble point of the soil was reached. The bubble point refers to the matric potentials upon which a pore channel allows for penetration of air into the hood and therefore the maximum applicable matric potential at this location. For a specific matric potential (Ψ_M) the equivalent diameter (de) of the largest soil pore conducting water can be estimated after Jarvis et al. (1987). At Ψ_M = 0 m the soil is saturated and the entire pore spectrum is potentially active. At Ψ_M = -0.02 m the largest active pores correspond to de =1.5 mm and at Ψ_M = -0.04 m to de = 0.7 mm. At each pressure level we recorded infiltration capacity until they were constant in time. This steady infiltration capacity was used for further analysis. Infiltration capacity at a given matric potential is directly linked to hydraulic conductivity (Wooding 1968). The flow conditions in natural soils are far from ideal, with anisotropic behaviour, heterogeneous initial soil water contents, and flow dynamics that do not correspond to the Richards equation near soil saturation. Therefore, we refrained from deriving hydraulic conductivity from our infiltration capacity, for example via Wooding´s formula (1968). Instead, we worked with the observed Infiltration capacity, considering those as a surrogate for the rate of the soil to conduct water at the applied matric potential. We measured infiltration capacity on plots with similar absence/presence of grass and legumes in response to variations in soil texture, initial soil moisture, earthworm biomass, target plant and weed shoot biomass, root biomass, and plant diversity at soil depths of 0, 25 and 55 cm. In order to alleviate the effects of soil heterogeneity, we used two infiltration experiments per treatment plot. Overviews of all measured variables for explaining infiltration capacity are given in Table 6.1.

Table 6.1: Overview of parameters measured including measured depth and unit (for more details see text).

Variables	Depths (cm)	unit
Texture (sand, silt, clay)	10,20,30,60	%
Soil organic carbon	0-30 (5 cm steps)	%
Bulk density	0-30 (5 cm steps)	g/cm³
Earthworm biomass	0-10, 25-35, 55	g/m²
Plant biomass	Soil surface	g/m²
Root biomass	0-5, 5-10, 20-30, 30-40, 40-60	g/m²

6.3.4 Soil texture and moisture

The grain size distribution (soil texture) was determined from soil cores at 10, 20, 30 and 60 cm depth according to DIN/ISO 11277 (DIN ISO 2002). The volumetric soil water content (in m^3/m^3) was determined with a FDR probe (ML2x Theta Probe, Delta-T Devices, Cambridge, United Kingdom). The device was inserted from the top to a depth of 6 cm (length of the prongs) into the soil surrounding the hood before the infiltration experiment. The average of three measurements was used for further analysis.

6.3.5 Biotic parameters (earthworm biomass, above shoot and below biomass)

At depths of 0 and 20 cm earthworms were collected by handsorting. An area of 0.3 m² and 10 cm deep was excavated and transferred into boxes. Earthworms were collected immediately, stored and transported at approximately 4°C in closed plastic bags containing moistened filter paper. The earthworms were identified to species and weighed. At 60 cm deep it was not possible to dig out soil for handsorting because anecic earthworms were able to move downwards. Therefore, we used the mustard extraction method for the determination of earthworm biomass. Therefore, 25 g of mustard powder was mixed with 5 l of water by shaking 24 h before extraction. Before the application of the mustard solution to the soil surface another 5 l of water was added and mixed intensively. Afterwards, 2.5 l of the mustard solution was sprinkled onto each macrocosm, repeated twice at 10 min intervals. After a total extraction time of 30 min all collected earthworms were rinsed in fresh water and stored in separate plastic bags containing moistened filter paper at 4°C (see above).

We analyzed earthworm biomass per soil depth (0, 25 and 55cm). Additionally, we summed up the earthworm biomass at soil depth 0 and 25 cm, 25 and 60 cm, and for all depths (0, 25 and 55 cm), first because of using different extraction methods, and second because of the

tremor caused by digging possible facilitate the movement of anecic earthworms into deeper soil layers.

Community biomass was recorded in each plot in 20 x 50 cm rectangles shortly before the infiltration measurements started. Two randomly allocated samples were taken. Plant material was cut to a height of 3 cm aboveground. Plant and weed biomass were sorted into plant functional groups, dried (70° C, 48 h) and weighed. Root biomass was taken with a 35 mm root corer with 3 replicates per macrocosm up to a depth of 60 cm. Cores were divided into 6 layers (0-5, 5-10, 10-20, 20-30 and 40-60 cm). Layers pooled per macrocosm and washed with tap water. Root biomass was dried at 65° C for 48h minimum before weighing.

6.3.6 Soil bulk density and organic carbon content

Shortly before the excavation of the lysimeters in November in 2011, three samples next to the excavation area were taken using a split tube sampler with an inner diameter of 4.8 cm (Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands). After drying at 40°C the soil samples were segmented depth resolutions from 5 cm up to 30 cm. All soil samples were passed through a sieve with a mesh size of 2 mm. The samples were then dried at 105°C and weighed to calculate the bulk density [g/cm^3].

Total carbon concentration was analyzed on ball-milled subsamples (time 4 min, frequency 30 s^{-1}) by an elemental analyzer at 1150°C (Elementaranalysator vario Max CN; Elementar Analysensysteme GmbH, Hanau, Germany) before and after incubation. For the calculation of organic carbon the difference between elemental analyses of the total carbon concentration and soil inorganic carbon concentration was determined (Steinbeiss et al. 2008).

6.3.7 Statistical analysis

Statistical analyses were performed with a linear model using the statistical software R 2.6.2 (R Development Core team, http.//www.R-project.org). On infiltration capacity at soil depths of 0, 25 and 55 cm, we tested the effects of the explanatory variables plant species richness (SR; 4 and 16 species), soil texture (sand and clay, in %), earthworm biomass (BM ew, g/m^2), root biomass (BM root, g/m^3) and total plant aboveground biomass (BM above, g/m^2). To identify the most important predictors of infiltration capacity we used the Akaike Information Criterion (AIC) (Burnham and Anderson 1998). For the infiltration capacity in each depth, variables from all depths (0, 25 and 60 cm) were tested. The model with the lowest AIC containing one of the best fitting

variables was selected, and in a further step, the respective model was extended by additionally fitting one of the rest variables in an alternative model until the AIC could not be improved furthermore. Additionally, we used linear regression to test correlations between the biotic and

abiotic variables. We did not test the effects of the plant functional groups because of their similar representation among the plots.

6.4 Results

6.4.1 Vegetation parameters (plant species richness, above- and belowground biomass)

For all soil depths infiltration capacity did not significantly differ between 4 and 16 plant species (Figure 6.1) at all supplied matric potentials (Figure 6.2). Root biomass between 20-30 cm marginally decreased infiltration capacity at a depth of 0 cm (Table 6.2) and was marginally higher for 16 plant species compared to 4 (t-test, p=0.078; Fig. 6.2A). At the soil surface species richness significantly affected bulk density (t-test, p=0.006), while for soil organic carbon, a trend was observed (t-test, p=0.060). Additionally, between 25-30 cm of depth plant species richness marginally affected bulk density (t-test, p=0.086) (Fig. 6.3C, D). Aboveground biomass did not affect the infiltration capacity at 0 and 55 cm, while a negative trend at 25 cm deep was observed (r=-0.532, p=0.092).

6.4.2 Soil structural parameters (bulk density and soil organic carbon)

With increasing depth the bulk density increases and the soil organic carbon decreases (Fig. 6.3B, C). Because of the high correlation of bulk density and soil organic carbon (r=-0.895, p=0.001), for our analysis at the soil surface we used soil bulk density. In 25 cm none of the structural parameters correlate with the infiltration capacity. In 55 cm no data for bulk density and soil organic carbon content was available. Additionally, bulk density and soil organic carbon content above (0-30 cm) did not correlate with infiltration capacity in 55 cm.

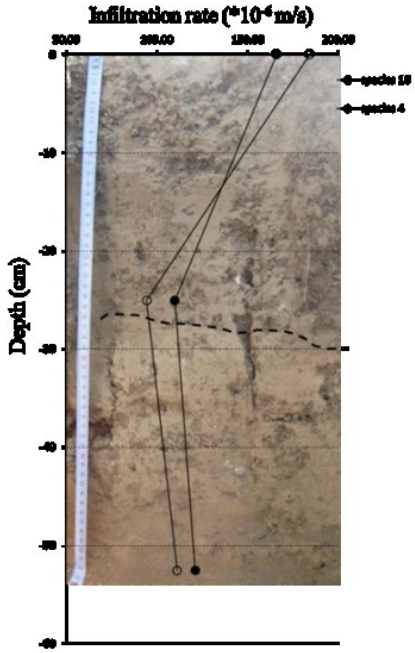

Figure 6.1: Variation of infiltration capacity (mean) through the profile for all plots separated into 4 and 16 plant species richness. Soil profile shown for macrocosm B4A18; dotted line indicates the assumed Ap horizon.

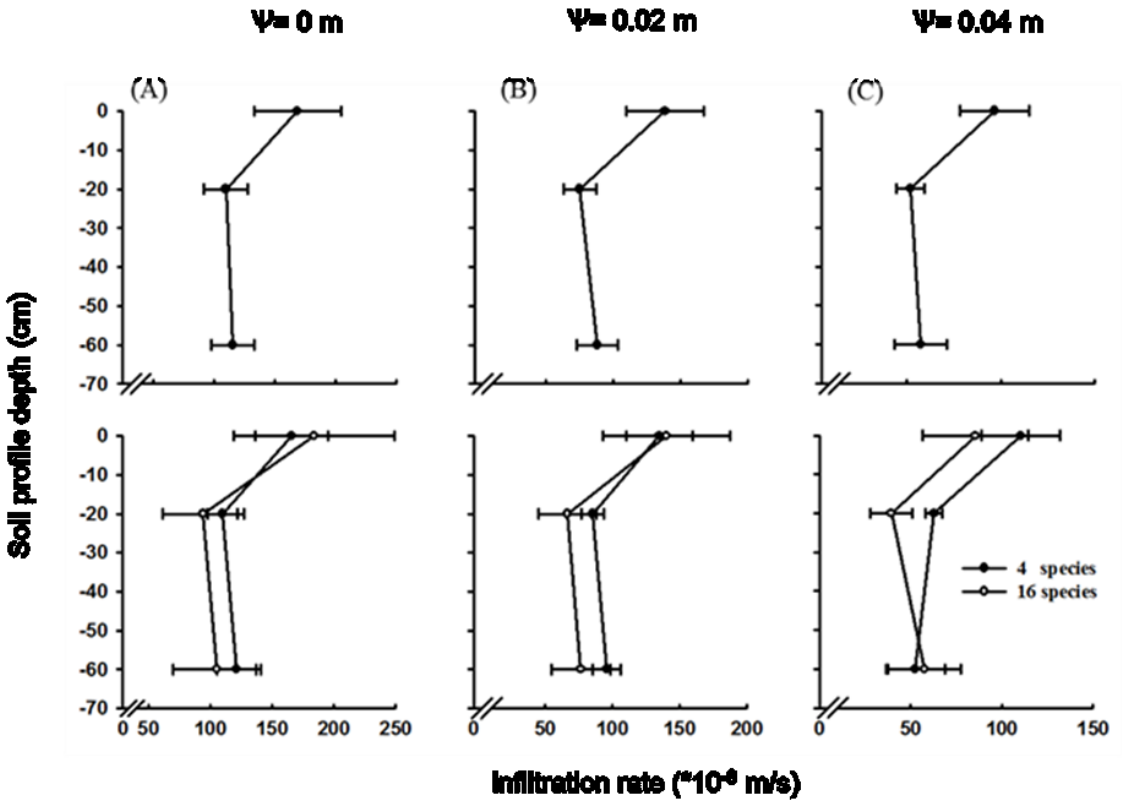

Figure 6.2: Soil profile of infiltration capacity (*10^{-6} m/s) from 0 to 60 cm for the matric potential (A) 0 m ,(B) 0.02 m and (C) 0.04 m as indicated. Upper section shows the mean for data samples and lower section shows the mean values separated by plant species richness as indicated. The standard errors of the measurements were included in the diagrams.

Figure 6.3: Variation of A) root biomass (mg*cm^{-3}), B) bulk density (g*cm^{-3}) and C) soil organic carbon content (%) through the profile for all plots separated into 4 and 16 plant species richness, soil profile shown for macrocosm B4A04. Mean with ± Standard error.

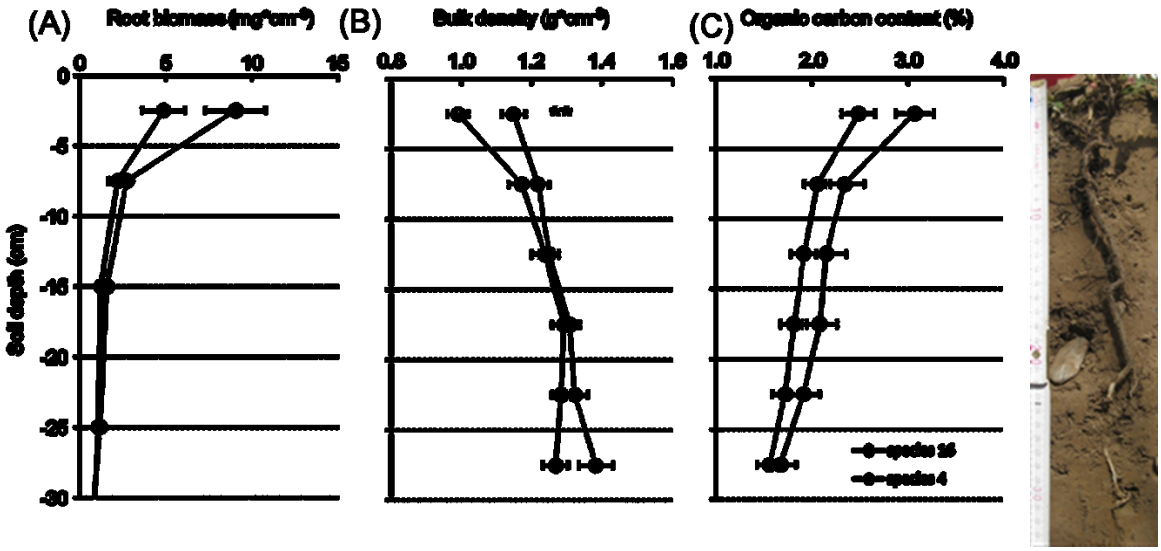

Table 6.2: Person correlation (r) coefficients for infiltration capacity of ΨM=0, -0.02 and -0.04 m including important variables from the model selection.

Variables	Depth (cm)	r (Ψ_M= 0 m)	p	r (Ψ_M= 0.02 m)	p	r (Ψ_M= 0.04 m)	p
Earthworm biomass							
	0-10	0.652	**0.030 ***	**0.620**	**0.042 ***	0.496	0.121
Root biomass							
	0-5	0.263	0.435	0.391	0.235	0.406	0.215
	5-10	-0.346	0.297	-0.415	0.204	-0.451	0.164
	10-20	-0.351	0.289	-0.267	0.427	-0.312	0.351
	20-30	-0.575	*0.064*	**-0.607**	**0.048**	-0.558	*0.074*

Significant effects are marked in bold. * p≤0.05, ** < 0.01, *** p=0.001

6.4.3 Earthworms

Because of different applied extraction methods and the movement of earthworms during digging, the differences between the depths were not comparable. In sum the earthworm biomass did not differ between the plant species. For analyzing the effects of earthworms on the infiltration capacity the biomass was tested between 0 and 25 cm, as well as between 25 and 55 cm for the infiltration. Additionally, also the impact of earthworm biomass separated for each depth on the infiltration capacity at 0, 25 and 55 cm was tested. Because of the small samples size a separation into ecological groups and therefore analyzing the effect on infiltration capacity was not possible (some values with zero). At the soil surface earthworm biomass

extraction from the upper layer significantly correlated with the infiltration capacity at the soil surface (Table 6.2). Earthworm biomass correlated marginally with the bulk density at 0-5 cm depth (r=-0.55, p=0.079) and significant with the bulk density in 5-10 (r = -0.75, p = 0.008). Additionally, earthworm biomass correlated with soil organic carbon at 0-5 cm depth (r=0.66, p=0.025), 5-10 cm depth (r=0.70, p=0.024). Infiltration capacity for pores larger or equal than 1.5 mm increased significantly with total earthworm biomass (Ψ_M = 0, p = 0.030 and Ψ_M = 0.02m, p = 0.042). At the depths of 25 and 55 cm the earthworm biomass did not affect the infiltration capacity.

6.4.4 Explanatory variables in 0, 25 and 55 cm depth

The most parsimonious model explaining the variation of infiltration capacity at the soil surface contained earthworm biomass (total biomass) and root biomass at 20-30 cm for larger macropores (Ψ_M = 0 and 0.02 , respectively > 1.5 mm and = 1.5 mm in diameter) (Table 6.3). The infiltration capacity increased significantly with increasing earthworm biomass and and decreased with root biomass. For smaller macropores (Ψ_M = 0.04m, <0.7 mm) none of the observed variables could improve the model. For subsoil layers (25 and 55 cm), none of the measured variables correlated to the infiltration capacity, respectively improved the model. Additionally, soil texture and moisture did not affect the infiltration capacity at depths of 0, 25 and 55 cm.

6.4.5 Infiltration patterns and variability

The infiltration capacity at saturation decreased from 0 to 25 cm by 57 % and increased marginally from 25 to 55 cm by 14 % for 4 and 16 plant species (Fig. 6.1). For smaller macropores the infiltration capacity also decreased from 0 to 25 cm and increased slightly from 25 to 55cm (Fig. 6.2). For all applied matric potentials, plant species richness did not significantly affect the infiltration capacity at several depths (Fig. 6.2 lower part). To investigate the variability of infiltration capacity we compared the standard deviation of infiltration for all samples and also separated samples of 4 and 16 plant species. At saturation the variation of infiltration at saturation was highest at the soil surface and decreased up to a depth of 55 cm. The variation was lowest at 55 cm deep compared to 25 cm deep. For Ψ_M =0.02 and 0.04 m the variation was also highest at the soil surface and decreased to 25 and 55 cm (Table 6.4), while the variation was lowest at 25 cm compared to 55 cm

Tab. 6.3: Summary of best explanatory variables for the infiltration capacity (*10 $^{-6}$ m/s) at 0 cm depth for various Ψ_M (0, 0.02 and 0.04 m). Soil moisture (Moisture in %), earthworm biomass (in 0-10 cm depth) and root biomass in 20-30 cm depth (BM root, g/m²).

0cm	Ψ_M= 0 m	Ψ_M = 0.02 m	Ψ_M = 0.04 m
all species richness			
Mean (*10^{-6} m/s)	175.80	138.18	96.53
SD	120.87	95.05	60.59
Min/Max	50.43/457.74	40.38/ 329.42	33.78/ 194.99
20 cm			
all species richness			
Mean (*10^{-6} m/s)	101.35	74.84	50.02
SD	60.01	40.56	24.15
Min/Max	29.19/ 239.92	17.07/148.27	9.64/ 87.84
60 cm			
all species richness			
Mean (*10^{-6} m/s)	115.65	88.14	57.36
SD	58.27	50.41	46.44
Min/Max	35.56/ 233.25	16.38/198.82	4.54/ 142.17

Bold font indicates significant effects. Arrows indicate an increase (↑) or decrease (↓) of the infiltration capacity.

To test if patterns at the soil surface layer are dependent on deeper soil layers, we used the Spearman rank correlation coefficient (r_S) and Pearson correlation coefficient (r) to compare topsoil (0 cm), with rooting zone (25 cm) and below rooting zone (55 cm). We did not find any significant correlations between the infiltration capacity at 0 cm compared to 25 and 55 cm, and 25 to 55 cm (data not shown).

Tab. 6.4: Mean, Standard deviation (SD) and minimum (min) and maximum (max) values of infiltration capacity (*10^{-6} m/s) for all plots at several matric potentials (0, 0.02 and 0.04m).

Depth 0 cm		Ψ_M **= 0 m**			AIC
	Variable	t-value	p-value		
Intercept		3.721	0.006		139.65
1st	Earthworm biomass	4.105	**0.003**	↑	135.11
2nd	BM root (20-30 cm)	-3.654	**0.006**	↓	123.69
R²	0.785				
		Ψ_M **= 0.02 m**			
Intercept		3.841	0.005		132.97
1st	Earthworm biomass	-3.686	**0.006**	↑	128.55
2nd	BM root (20-30 cm)	-3.607	**0.007**	↓	117.61
R²	0.762				

6.5 Discussion

6.5.1 Factors explaining infiltration at the soil surface

In this study, measurements of infiltration capacity in several depths allows to obtaining information of factors affecting infiltration capacity through the soil profile. Infiltration capacity at the soil surface was mainly driven by earthworm biomass at matric potentials 0 and 0.02 m (≥ 1.5 mm pore size diameter), with infiltration capacity increasing with earthworm activity. Indeed, most earthworm burrows are larger than 2 mm in diameter (Edwards and Bohlen 1996). This explains why only water flow through larger pores (≥1.5 mm), but not through smaller pores was affected by the biomass of earthworms (Tab. 6.2).

This finding supports previous result measured in 2011 (Chapter 4) and at the first glance differs from the measurement taken in 2012 (Chapter 5) at the field site. However, in fact this result is not contradicting at all, but highlighting the considerable influence on earthworm population dynamics and the presumably consequently different effect on infiltration capacity. Other studies have shown that the earthworm population depends on soil moisture conditions (Lavelle 1988, Edwards and Bohlen 1996). Our measurements in 2012 at the field site showed that under dry soil conditions (soil moisture content: 17.85 ± 4.29%) earthworm biomass was reduced compared to earthworm biomass in the year 2011 with wet soil conditions (soil moisture content: 33.71 ± 4.29%; Chapter 5). However, in 2011 we could observe a significant effect of earthworm biomass on the infiltration. In the Ecotron Experiment similar soil moisture conditions (soil moisture content: 29.70 ± 2.56%) compared to 2011 leading probably to the more pronounced effect of earthworm biomass on infiltration capacity. This finding supports results from Berry and Jordan (2001) which shown that under high soil moisture content (30%) earthworms developed faster and yielded in a higher biomass compared to earthworms in drier soil conditions (20% and 25%). This support the fact, that under wet soil moisture conditions, earthworm activity is increased and thus affecting infiltration capacity.

In this experiment bulk density and soil organic carbon between 5-10 cm deep were correlated to the earthworm biomass. Generally, it is believed that earthworms have a positive effect on the water flow through soils by changing the soil structure such as bulk density and soil organic carbon content (Six et al. 2004, Bronick and Lal 2005). At the field site no correlation between earthworm biomass and the soil bulk density (0-5 cm) was observed in the same year (Chapter 5). This may be on the one hand caused by the much moister soil conditions in the Ecotron compared to the field site, causing higher earthworm activity. On the other hand, the extraction method at the Ecotron is also much more efficient compared to the octet method used in the field (Eisenhauer et al. 2008b). Therefore, a correlation between earthworms and bulk density could also have been undetected at the field size. In general our results highlight that, while both earthworms and bulk density play an important role for infiltration capacity,

their interrelation, could not yet be explained. It may by driven by earthworm presence and population dynamics.

Bulk density was however related to species diversity, while soil carbon content as well as root biomass (factors that explained bulk density and infiltration capacity in the field in 2012, Chapter 5) only showed a trend, It is however partly in line with the results in 2012, where plant species richness affects improved soil structural parameters. However the link between soil structural parameter on the infiltration was not observed, while soil structural parameters between 5-10 cm soil deep affected earthworm biomass, which in turn affected the infiltration capacity. Despite the low sample size, the results give a hint that at the soil surface biotic factors play an important role for the infiltration capacity. Further investigations are needed to obtain a clear picture of the combined effects and interactions of earthworms and soil structural parameters on the infiltration capacity.

6.5.2 Factors explaining infiltration capacity over the depth profile

Infiltration capacity at deeper layers was lower and varied much less compared to the topsoil. As shown above, a great deal of variation in infiltration capacity originates from biotic factors. The small variation of infiltration capacity at depth indicates that these factors are no more relevant. The bulk density was increased at 25 cm depth, indicating soil compaction (plough pan), which can be a result of the destruction of inter-aggregate pores and may be responsible for the reduced infiltration capacity. This is in agreement with (Horn et al. 1994). The boundary between top and subsoil was also marked by a color change and reduced root biomass (Figure 6.2). This zone is likely the result of ploughing before the establishment of the Jena experiment which was formerly agricultural land (Roscher et al. 2004). At and below this zone, bulk density increased, while soil organic carbon and root biomass decreased resulting in a decreased infiltration capacity increasing soil depth (Figure 6.1 and 6.2). Since the field site was not ploughed for the preceding 10 years, this denser layer is probably an old plough pan. In our experiment this layer was found at approximately 30 cm of depth. Generally, plough pans have high bulk densities with a reduced number of macropores and low connectivity of pores which reduced root growth and earthworm activity (Goss et al. 1984, Reicosky and Archer 2007, Nawaz et al. 2013). This supports the idea that the compacted layer (old plough pan) at around 25 cm of soil depth hampered penetration of earthworms and plant roots and thereby eliminated possible biotic influences, which affect infiltration capacity. Surprisingly, not even texture parameters explained the variation of infiltration capacity at the depths of 25 and 55 cm. Even a decade after the conversion of arable land into grassland, soil compaction caused by ploughing, reduced infiltration capacity at 30 cm below the soil surface.

6.6 Conclusion

The aim of this chapter was to identify drivers of infiltration in different soil depths (soil surface, within the rooting zone and below the rooting zone) in a grassland biodiversity experiment that was formerly used as agricultural land. Our study shows that infiltration at the soil surface was correlated with earthworm biomass, which was interrelated to soil structural parameters such as bulk density and soil organic carbon at 5-10 cm depth. The different soil moisture conditions in the field and in the plot of the Ecotron experiment probably lead to increased activity of earthworms, which in turn also affected infiltration. Remarkably, in greater depths none of the observed factors in the experiment played an important role for the measured infiltration capacity.

Grasslands cover approximately one quarter of the world land area, contribute a high percentage to the world agricultural area and store around 20% of the global terrestrial soil carbon stocks (Ramankutty et al. 2008, Conant 2012). For grassland management and the minimization of surface run-off and soil erosion, after 10 years of conversion from arable land into grassland, at and below the observed compacted layer, biotic effects that impacted infiltration at the soil surface are suppressed. When applying hydrological models we have to be aware that anthropogenic impacts resulting in a compacted layer (plough pan) affects vertical water flow besides above all other soil properties.

Chapter
7

Effects of soil depth on the estimation of saturated hydraulic conductivity using pedotransfer functions (PTFs)

7 Effects of soil depth on the estimation of saturated hydraulic conductivity using pedotransfer functions (PTFs)

7.1 Abstract

Saturated hydraulic conductivity (K_s) is a crucial input parameter for modeling water flow and solution transport through soils. Due to the spatial and temporal variation of K_s it is difficult to measure. Based on these difficulties and when measured hydraulic conductivity is not available, indirect methods such as pedotransfer functions (PTFs) were developed to use easy to measure soil data. We evaluated the performance of various common published PTFs for estimating K_s using available input data such as soil texture, bulk density and soil organic carbon content. We compared the derived K_s with measured K_s values taken in a lysimeter study (Ecotron Experiment, Montpellier, France) at several depths (soil surface, within the rooting zone, below the main rooting zone). The measured Ks values were obtained by using a hood infiltrometer. At the soil surface the best regression model for estimating K_s based on two input parameters (earthworm biomass at the soil surface and root biomass in 20-30 cm depth). At deeper soil layers (25 and 55 cm) all PTFs underestimated the mean values for all depths. Regarding the root mean squared (RMSE) and Nash Sutcliffe Efficiency (NSE) values, all applied PTFs used in this study, except to the Jabro model at the soil surface, are inadequate for estimating K_s. For a sufficient application in hydrological models, estimation of K_s could be improved by taken into account macroporosity in the PTFs.

7.2 Introduction

For understanding and modeling water flow and chemical transport in the vadose zone, agriculture and environmental processes and how much water will runoff and causes soil erosion, hydraulic conductivity is an important physical soil property (Shouse and Mohanty 1998). Generally, the determination of soil saturated hydraulic conductivity (K_s) is based on direct and indirect methods. For the direct measurement of hydraulic conductivity, field observations have shown that hydraulic conductivity is mainly controlled by the properties of the porous media, such as size and connectivity of structural pores (Alaoui et al. 2011), and on the measuring method (Durner and Lipsius 2006), soil type (Wösten and Van Genuchten 1988), and on spatial variability (Russo and Bresler , Mallants et al. 1997). Next to these difficulties direct methods are time consuming and expensive (Schaap et al. 1998). Additionally, due to the soil heterogeneity and experimental error, results of these measurements are sometimes unreliable (Schaap et al. 1998).

Based on these difficulties and when measured hydraulic conductivity is not available, indirect methods such as pedotransfer functions (PTFs) were developed to use easy to measured

soil data such as texture, bulk density and organic matter content for estimating hydraulic properties (Hu et al. 2008). In summary, many efforts have been made to develop PTFs at large scales at the soil surface (see review Wösten et al., 2001). In this study, we therefore investigate the usability of available soil properties such as soil texure (sand, silt and clay content), bulk density and soil organic carbon to predict K_s at the soil surface, within the rooting zone and below the rooting zone. The objective of this study was to determine the applicability of some recommended models in the literature, such as the Rosetta (Schaap et al. 1998), Jabro (1992) and Vereecken (1990) PTFs, to calculate hydraulic conductivity for different soil textures and at several depths. Additionally, we compared a derived model created with the best explanatory variables at the soil surface. Furthermore, the differences between measured and calculated values of Ks were evaluated using two statistical parameters: the mean square deviation (RSME) and the Nash Sutcliffe Efficiency (NSE) parameter (Nash and Sutcliffe 1970, Tietje and Tapkenhinrichs 1993). The main aim of this study was to answer the following question:
(i) Can we predict observed saturated hydraulic conductivity using the pedotransfer functions (PTFs) at several depths?

7.3 Material and Methods

7.3.1 Experimental design

The monoliths originate from a temperate grassland site (Jena Experiment) located in the floodplain of the Saale river near Jena (Germany; 50°55´N, 11°35´E, 130 m NN) (Roscher et al. 2004). For more details about the conditions and experimental Ecotron station in Montpellier see chapter 6.3.1.

7.3.2 Hydraulic conductivity

For the assessment of saturated hydraulic conductivity (K_s) we used a hood infiltrometer (UGT, Müncheberg, Germany; method described in Schwärzel and Punzel (2007)). For each macrocosm two measurements at each depth were conducted. For the calculation of hydraulic conductivity see Chapter 2.2.2 Equation 1.3-1.9. For the measurement procedure see Chapter 6.3.2.

7.3.3 Soil parameters

The grain size distribution (soil texture) was determined from soil cores at depths of 10, 30 and 60 cm according to DIN/ISO 11277 (DIN ISO 2002). The determination of soil bulk density and soil organic carbon content is described in detail in chapter 6.3.6. The soil organic matter content is taken to be equal to 1.72 times the organic carbon content (in %).

7.3.4 Models for estimating

Several published PTFs for K_s were used in this study (Table 7.1). Based on the availability of the input data (texture, bulk density and soil organic carbon) four different PTFs were chosen, beginning with a model based on neural network methods containing only soil texture as input data (Rosetta SSC). For Rossetta SSC-BD bulk density was added. The model by Jabro (1992) predicts saturated hydraulic conductivity of soil using silt, clay content and bulk density. Sand content did not play a significant role for predicting hydraulic conductivity and therefore was not included in the end model. Vereecken (1990) relates K_s to soil properties such as clay, sand, and soil organic matter, as well as bulk density via empirical equations and multivariate regression analysis.

7.3.5 Performance of models

In order to examine the performance of the PTFs, we compared calculated K_s with measured K_s values at each depth. We used R^2, root mean square error (RMSE) and the Nash Sutcliffe efficiency (NSE). The RSME gives the mean difference between measured and calculated K_s values and is calculated by (Tietje and Tapkenhinrichs 1993):

$$\text{RMSD}=\sqrt{\frac{1}{n}\sum_{i=1}^{n}(x_i - y_i)^2} \qquad \text{(Equation 7.1)}$$

where x_i is the measured K_s value, y_i is the calculated K_s value obtained with various models, and n is the number of measurements.

The NSE compares the measured and the calculated K_s value and is calculated as (Nash and Sutcliffe 1970):

$$\text{NSE}=1-\left[\frac{\sum_{i=1}^{n}(x_i-y_i)^2}{\sum_{i=1}^{n}(x_i-x_i^{mean})^2}\right] \qquad \text{(Equation 7.2)}$$

where x_i^{mean} is the average of measured K_s values. The NSE determines the relative magnitude of residual variance compared to the measured data variance, which indicates the fitting of observed versus modelled values at the 1:1 line. The values can range from $-\infty$ to 1. A value of 1 corresponds to a perfect match of modeled to measured values. Values between 0 and 1 indicate that the model calculations are as accurate as the mean of the measured data. When the measured data is a better predictor than the calculated data, then the efficiency is less than zero indicating unacceptable performance.

Table 7.1: Pedotransfer functions and derived model for estimating Ks.

Author	PTF mathematical expression
1.Schaap (1999, Rosetta SSC)	Rosetta neural network requiring percentage sand, silt and clay
2. Schaap (1999, Rosetta SSC-BD)	Rosetta neural network requiring percentage sand, silt, clay and bulk density
3. Jabro (1992)	Log(Ks) (cm h^{-1})= 9.56 - 0.81 (log silt) - 1.09 (log clay) - 4.64 (ρ_d)
4. Vereecken (1990)	Ks(cm d^{-1})=exp (20.62 - 0.96 (ln clay) - 0.66 (ln sand) - 0.46 (ln OM) – 8.43(ρ_d))
5. derived model	Ks= 203.60 + 4.41 * ew biomass -140.37 * BM root

ρd = bulk density, ew biomass = earthworm biomass in 0-10 cm, OM=organic matter, BM root = root biomass in 20-30 cm soil depth

7.4 Results

7.4.1 K_s model analysis

Based on the presence of the layer condition such as color, bulk density, soil organic carbon content and root abundance we could determine three distinct layers: topsoil, plough pan and subsoil (see chapter 6). Correlation tests showed that soil infiltration at saturation was highly significant to earthworm biomass and plant root biomass, but not to texture (clay, silt and sand content) (see chapter 6, Tab. 6.1). Using stepwise regression, the best model included two variables: earthworm biomass at the soil surface and root biomass between 20-30 cm. The regression results showed that these variables significantly explained the hydraulic conductivity at the soil surface (Tab. 7.2). The predicted and observed K_s were plotted on a 1:1 line (Fig. 7.1). A linear trendline showed that observed and calculated data were highly correlated (R^2=0.57, p=0.023). For the subsoil layers, none variables explained the infiltration capacity and therefore we could not develop a model.

7.4.2 Puplished PTFs and model comparison

Based on available input data from the Ecotron experiment (bulk density (ρ_d)), organic matter (OM), silt (Si), clay (C) and sand (S)) various published PTFs for estimating K_s were evaluated in this study (Tab. 7.1). Table 7.2 contains an overview of necessary input parameters for the PTFs compared to this study. In order to evaluate the performance of the chosen PTFs and the derived model in predicting K_s, the estimates were compared to the measured K_s values at each depth (Tab. 7.3). The table shows the mean values for K_s with associated minimum (Min) and maximum (Max) values at the various depths. Calculated and measured values decreased with increasing depth. At the soil surface, the derived model using parameters from the soil surface is slightly the best model for predicting Ks at this layer (R^2=0.457, p=0.023).

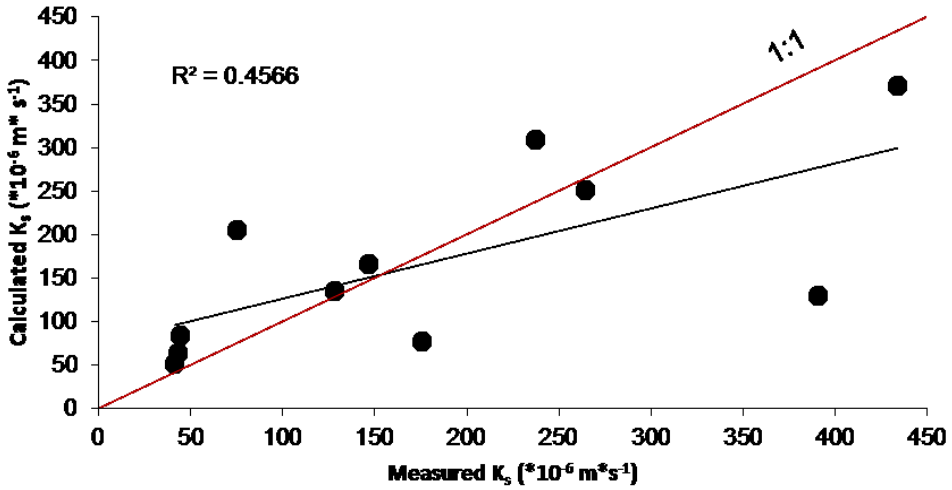

Figure 7.1: Linear regression between calculated and measured values of saturated hydraulic conductivity (K_s, * 10^{-6} m * s^{-1}) at the soil surface. Calculated values were obtained with the derived model (see Table 7.1).The red plotted line is the 1:1 and the black plotted line the correlation line.

Also the model after Jabro (1990) using bulk density and soil texture (silt and clay) explained some variation of the hydraulic conductivity (R^2=0.415, p=0.032). All PTFs underestimated the mean values for all depths, while the Jabro PTF best performed the mean value of K_s at deeper soil layers (Tab. 7.3), but clearly underestimated the minimum and maximum. Therefore the model performance was inadequate. However, for deeper soil layers none of the used models is an acceptable model and could not estimate K_s. The results showed that for the Rosetta SCC and SCC-BD models the RMSD between measured and calculated values of K_s was 2.21*10^{-4} m* s^{-1} and 2.51*10^{-4} m* s^{-1}, and the NSE were -0.06 and -0.01 respectively. Next to a very low R^2 (data not shown), both statistical parameters suggesting inadequate estimations of K_s. Using Vereecken´s model the RSMD between measured and calculated values was 2.07 * 10^{-4} m* s^{-1}, NSE was 0.06, R^2 was 0.315,which were slightly better than values obtained with the Rosetta model. The Jabro model showed some improvements with RSMD of 1.65*10^{-4} m* s^{-1}, NSE of 0.406, and the R^2 was 0.415. Finally, using the derived model, which includes the input variables earthworm biomass at the soil surface and root biomass between 20-30cm soil depth, yielded an RSMD of 9.85 * 10^{-5} m* s^{-1}, an NSE of 0.789 and an R^2 of 0.457. This model estimated values of K_s with the smallest RSMD and largest NSE at the soil surface. For the deeper soil layers R^2 was very low and the NSE was negative for all tested models (data not shown). The most negative values were for the Rosetta SCC model, followed by the Rosetta SCC-BD model and then followed by the Vereecken´s model. The NSE for the Jabro model was improved, but also negative, implying that all models were inadequate for estimating K_s in deeper soil strata. Because soil organic carbon and bulk density were not available at 55 cm soil depth we could not applied the Rosetta SCC-BD, Jabro and Vereecken´s model.

Table 7.2: Measured values of saturated hydraulic conductivity (K_s), bulk density (ρ_d), soil organic carbon content (SOC) sand, silt and clay of the three soil layers (0, 25 and 55cm) depths for the 11 macrocosm

Soil properties	Soil depth (cm)	Min	Max	Mean	Median	Variance
K_s (m s^{-1})	0	$4.11 * 10^{-5}$	$4.34 * 10^{-4}$	$1.80 * 10^{-4}$	$1.47 * 10^{-4}$	$1.9 * 10^{-8}$
	25	$2.13 * 10^{-5}$	$1.68 * 10^{-4}$	$5.95 * 10^{-5}$	$5.21 * 10^{-5}$	$1.8 * 10^{-9}$
	55	$2.12 * 10^{-5}$	$1.03 * 10^{-4}$	$6.13 * 10^{-5}$	$6.52 * 10^{-5}$	$7.8 * 10^{-10}$
ρ_d (g m^{-3})	0-5	0.87	1.24	1.06	1.05	0.012
	10-15	1.08	1.35	1.24	1.26	0.006
	20-25	1.20	1.40	1.30	1.30	0.005
	25-30	1.15	1.52	1.32	1.32	0.012
SOC (%)	0-5	2.05	3.59	2.80	2.65	0.274
	20-25	1.25	2.39	1.82	1.78	0.136
	25-30	1.10	2.19	1.62	1.61	0.117
Sand (%)	0-5	5.30	50.66	20.86	13.44	133.42
	20-25	34.30	70.94	54.74	57.98	135.21
	25-30	2.45	39.78	16.45	13.66	128.94
Silt (%)	0-5	33.00	69.00	54.27	58.00	133.42
	20-25	6.31	50.58	20.93	14.08	251.31
	25-30	38.00	68.00	55.46	56.00	77.68
Clay (%)	0-5	15.00	37.00	24.74	26.00	41.02
	20-25	15.11	30.76	24.33	27.10	40.93
	25-30	15.10	28.40	20.91	21.90	15.39

Table 7.3: Overview of comparison of models

Models	Model R^2	Min	Mean	Max
0 cm depth				
Rosetta SSC	ns	$1.26 * 10^{-6}$	$1.58 * 10^{-6}$	$2.27 * 10^{-6}$
Rosetta SSC-BD	ns	$3.54 * 10^{-6}$	$2.03 * 10^{-5}$	$1.78 * 10^{-5}$
Jabro (1992)	R^2=0.415, p=0.033	$1.92 * 10^{-6}$	$5.04 * 10^{-5}$	$3.77 * 10^{-4}$
Vereecken (1990)	R^2=0.315, p=0.079	$4.38 * 10^{-6}$	$1.53 * 10^{-5}$	$4.49 * 10^{-5}$
derived model	R^2=0.457, p=0.023	$5.17 * 10^{-5}$	$1.67 * 10^{-4}$	$3.71 * 10^{-4}$
Measured		$4.11 * 10^{-5}$	$1.80 * 10^{-4}$	$4.34 * 10^{-4}$
25 cm depth				
Rosetta SSC	ns	$1.27 * 10^{-6}$	$1.60 * 10^{-6}$	$2.28 * 10^{-6}$
Rosetta SSC-BD	ns	$1.49 * 10^{-6}$	$2.88 * 10^{-6}$	$6.32 * 10^{-6}$
Jabro (1992)	ns	$2.52 * 10^{-6}$	$1.74 * 10^{-5}$	$7.47 * 10^{-5}$
Vereecken (1990)	ns	$1.20 * 10^{-6}$	$1.17 * 10^{-5}$	$4.53 * 10^{-5}$
Measured		$2.11 * 10^{-5}$	$5.94 * 10^{-5}$	$1.68 * 10^{-4}$
55 cm depth				
Rosetta SSC	ns	$1.33 * 10^{-6}$	$1.51 * 10^{-6}$	$1.80 * 10^{-6}$
Measured		$2.19 * 10^{-5}$	$6.13 * 10^{-5}$	$1.03 * 10^{-4}$

7.5 Discussion

This study evaluated the application of various Pedotransfer functions (PTFs, Table 7.1) at several soil depths (soil surface, within rooting zone, below the rooting zone). In our study PTFs generally underestimated the real K_s at the soil surface and were inadequate at predicting the K_s in deeper soil layers (Tab. 7.3). The calculated hydraulic conductivity matched observations better, when bulk density and soil organic carbon are included, such as in the PTFs after Jabro (1992) and Vereecken (1990). Probably because of the high correlation of bulk density and soil organic matter (data not shown), adding soil organic matter in the Vereecken model (1990) did not improve model estimation compared to the Jabro model. Furthermore, other studies have shown that additional variables such as, water content at defined potentials, can improve the accuracy of the prediction (Aimrun and Amin 2009, Alvarez-Acosta et al. 2012), but these extra variables also increase the amount of effort to obtain and requires their availability (Tietje and Tapkenhinrichs 1993, Minasny et al. 1999). In our study we were not able to test the improvement using water content at defined potential, because it not available.

The regression model shows that the relatively high measured K_s is affected, next to bulk density, by earthworms and root biomass (at the depth interval of 20-30 cm). This may be partly, because both earthworm and root biomass carry information on pore connectivity. On the other hand, soil texture, bulk density and soil organic matter only provide information on pore space but not on how pores are connectivity (Sobieraj et al. 2001).

7.6 Conclusion

The tested PTFs predicted K_s very poorly. Next to the high spatial variation of hydraulic conductivity, the variation in pore structure is probably an important source of uncertainty for the estimation. For all depths the used PTFs underestimated K_s. The performance of the PTFs was improved by including additional data such as bulk density and soil organic matter. The best regression model for estimating Ks at the soil surface is a two parameter regression model (earthworm biomass at the soil surface and root biomass between 20-30 cm soil deep). At and below the assumed plough layer predictions using texture, bulk density and soil organic carbon content failed to predict K_s.

Chapter

8

General discussion

8 General discussion

This thesis evaluated the main direct and indirect mechanisms by which plant community, earthworms, soil structural parameters, soil texture and soil moisture and earthworms affect infiltration capacity in a biodiversity grassland experiment (The Jena Experiment). There is little research on understanding how these interrelated factors might influence vertical soil water fluxes by modifying soil hydraulic properties. In order to improve the understanding of factors affecting water flow through soil and their possible interactions I conducted two field surveys (Chapter 4, chapter 5) along the relevant plant species gradient at The Jena Experiment field site. In the third experiment we measured infiltration capacity on 11 monoliths with two diversity levels (4 and 16 plant species), originating from The Jena Experiment site at several depths in the CNRS Ecotron, Montpellier (chapter 6 and 7). . In this thesis, I distinguish between abiotic soil factors (texture), which are constant in time, and biotic factors (soil fauna, ecosystem structure), which change dynamically depending on environmental factors. The main results of this thesis are summarized in the framework of the research questions formulated in Chapter 1 and summarized with a general perspective.

8.1 Synthesis

Soil hydraulic conductivity is an important input variable for process-based soil hydrological models (Shouse and Mohanty 1998, Li et al. 2013). For a better understanding of run-off processes, preferential flow and solution transport the characterization of factors affecting of the spatial hydraulic conductivity is important (Shukla et al. 2006). It has been suggested that presence of macropores and the connectivity of pores may influences the infiltration pattern of soil (Durner and Lipsius 2006). There are a large number of studies for understanding the water flow through, leading to controversial results. In this thesis the orthogonal design of The Jena Experiment presents the opportunity to disentangling the effect on infiltration pattern by plant species loss caused by human activity on a soil structural, texture and earthworm gradient. I used this setup to address the question:

> *(1) Which factors shape soil hydraulic properties such as infiltration capacity? – Are abiotic factors (soil texture) more important compared to biotic factors (earthworms, plant and functional diversity, root biomass) for the infiltration through soil?*

We found a relation between macropores formed by earthworms as well as structural heterogeneity expressed as soil bulk density with the infiltration capacity (Chapter 4-7).

Furthermore, results in 2012 showed that plant species richness and its increased root biomass control bulk density leading to an increase of infiltration capacity (Chapter 5).
The different effects on infiltration capacity do not contradict each other. These separated effects on infiltration capacity probably depended on seasonal changes in climate affecting the dynamical patterns of the factors that could lead also to undiscovered interactions. Soil texture and soil moisture had only subordinate effects on infiltration capacity (Chapter 4-7).

Usually, pore size distribution depends on soil type (Rawls et al. 1982), thus influences the infiltration capacity through soil. Between clayey and sandy soil there are large differences in pores size with fine pores in clayey and large pores in sandy soils, leading to a higher infiltration capacity in sandy soils. Interestingly, legumes presumably reverse this texture effect by forming additional pores resulting in a lower infiltration in sandy soils.
Biotic processes play a decisive role for explaining the variation of infiltration capacity. Soil texture and soil moisture did not influence infiltration capacity.

Biotic influences on infiltration capacity are based on shaping pore sizes. In has been shown that in many terrestrial ecosystems earthworms dominate the invertebrate biomass and are the most important decomposer groups. They improving soil structure and affect infiltration. Due to their burrowing and feeding behavior earthworms provide pathways for water flow and play an important role in the formation of macro- and microaggregates (Lee 1985, Edwards and Bohlen 1996, Six et al. 2004, Bronick and Lal 2005). For land management high Infiltration capacity contribute to reduce run-off and soil erosion (Kladivko et al. 1986). I therefore asked the question:

(2) Does earthworm activity increase infiltration capacity?
(3) How does the plant community influence earthworm activity?

The results of the study presented in Chapter 4-6 showed that with increasing earthworm biomass the infiltration capacity increases. Smaller macropores (< 1.5 mm (Chapter 4 and 5) and <0.75mm (Chapter 6)) were not affected by earthworm biomass. Interestingly, the effect of earthworm biomass on infiltration capacity was independent of the effect of bulk density on infiltration capacity. However, a positive correlation between earthworms and soil organic carbon content was found. This emphasized that earthworms probably acts on large macropores, while changes in bulk density are due to other processes (possibly soil aggregation as shown by Chappell et al. (1999) and Baumgartl and Horn (1991). Several studies suggested that with increasing plant species and functional group diversity influenced earthworm density due to the amount and quality of plant residues (Edwards and Bohlen 1996, Hector et al. 1999, Hooper et al. 2005). Only few studies found an increase of earthworm density with increasing

plant species (Zaller and Arnone 1999, Spehn et al. 2000) or no response (Gastine et al. 2003). My study shows not plant species and functional group diversity, but certain plant functional groups such as legumes and grasses affected earthworm performance (Eisenhauer and Scheu 2008a) (Chapter 4). Remarkably, in absence of earthworm growing grass root presumably clogged soil pores and thus reduced the infiltration capacity (Chapter 4). Earthworm biomass explained independently of plant species richness, soil bulk density and porosity some variation of the infiltration capacity which indicates uncoupled effects on the infiltration capacity. The responses of earthworm on plant community measures and their effect on infiltration capacity were not uniform. This suggests that the dynamic of earthworm populations which is, besides soil and ecosystem properties, also affected by the climate conditions (such as rainfall). This plays an important role for infiltration and the resulted interactions with other factors.
Infiltration capacity was affected by earthworm biomass. With increasing earthworm biomass the infiltration also increases. This effect was independent of bulk density.

Besides earthworms, microbial activity improves soil structure, leading to soil aggregates and a larger pore spectrum. Generally, it is known that biological activity is higher on higher plant species richness plots leading to higher carbon content, decreased bulk density and increased porosity (Zacharias and Wessolek 2007; Périé and Ouimet 2008). Other studies have shown that an increase in soil organic matter content lead to a higher pore development, which increased soil aggregate stability, water holding rate and water infiltration through soil (Berglund et al. 1980; Haynes and Naidu 1998; Franzluebbers 2002). The stability of soil aggregates and the pores between the aggregates improve infiltration, drainage and storage of water (Lee and Foster 1991; Bronick and Lal 2005). Also, investigations on the influence of vegetation on soil hydraulic properties are often focused on soil management or topography (Schwartz et al. 2003, Bodhinayake and Cheng Si 2004, Bodner et al. 2008). Therefore, there is no investigation on how ecosystem properties, especially species diversity, may reflect on soil hydraulic properties. I therefore investigated the following questions:

(4) Do patterns in soil organic carbon content, induced by biodiversity gradients, relate to structural parameters bulk density and porosity?
(5) Do those parameters affect infiltration capacity?

As explained above earthworms had no influence on bulk density. However, bulk density was related to plant species diversity.
Furthermore, we could show that plant species diversity influenced vertical soil water fluxes by modifying soil structural parameters such as bulk density and porosity (Chapter 5, 6). In the last 10 years soil structural parameters (here soil bulk density) correlated in more than half of the

observed years with plant species richness. This suggests that infiltration capacity is often affected by plant species diversity, whereas in some years other processes (potentially earthworms) play a more important role for explaining infiltration capacity. For example 2012 was characterized by a dry autumn and we found a more pronounced effect of plants species diversity on infiltration capacity. This was accompanied by reduced earthworm activity due the dry soil. After 10 years after conversion of an arable land into grassland, the infiltration capacity at the soil surface for higher plant species richness plots was comparable to the natural composition (reference plots-r) plots. In contrast, bare ground plots were similar to plots containing lower plant species (Fig. 8.1).

Besides earthworms, soil structural parameters such as soil bulk density and porosity affect the infiltration capacity. However, both are not correlated to each other. Plant diversity indirectly increased infiltration by improving soil structural parameters.

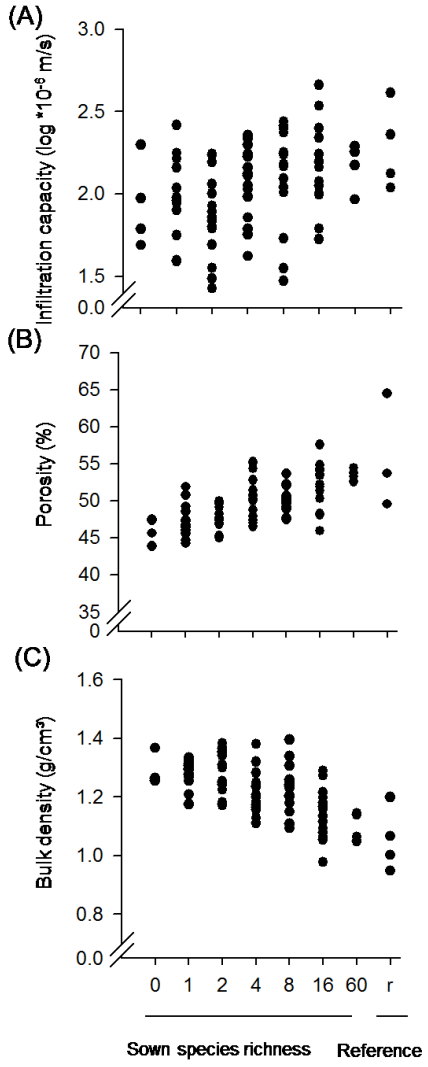

Figure 8.1: Relationship between species richness (0, 1, 2, 4, 8, 16, and 60 plant species) and Reference plots (r) for A) infiltration capacity (log*10-6 m/s), B) Porosity (%) and C) Bulk density (g/cm³).

Most of the observations were conducted at the soil surface, indicating how much water can enter the soil. The last part of this research was dedicated to understand the further heritage of the infiltrated water. Water flow in macropores formed by earthworms and plant roots are crucial for the prediction of soil run-off and soil erosion (Beven and Germann 1982, Weiler and Naef 2003). Next to the initiation of water flow into macropores at the soil surface, it has been suggested that in addition, also subsurface connected macropores could play an important role in explaining water flow through soil (Ela et al. 1992, Kladivko 2001). I therefore asked:

> *(6) Do the observed factors influencing soil hydraulic properties at the soil surface also affect infiltration into deeper soil strata? What factors are important drivers for the infiltration at several depths?*

The observed influence of biotic (earthworm and root biomass) and soil structural parameters (soil bulk density and soil organic carbon content) at the soil surface played no role at and below the plough pan (Chapter 6). Above this compacted layer we observed much greater variation in the infiltration capacity, compared to below. In our study none of the observed variables could explain the infiltration capacity in deeper soil strata. After 10 years after the conversion of arable into grassland, soil surface biotic factors, such as soil structural parameters which are affected by plant diversity and earthworms, could not counteract the compaction in 20–30 cm soil depth, caused by anthropogenic impact. In none of the observed depths, soil texture was a relevant factor for explaining infiltration capacity.

At the soil surface bulk density, earthworm biomass, soil organic carbon and root biomass were highly correlated to the infiltration capacity. At and below the plough pan none of the observed variables, neither soil texture could explain the infiltration pattern. Higher infiltration at the soil surface not implies a higher infiltration in deeper soil strata.

For the measurement of saturated hydraulic conductivity, direct methods (*in situ* or in the laboratory) are particularly difficult, expensive and time intensive (Schaap et al. 1998, Aimrun and Amin 2009). Therefore, indirect methods such as pedotransfer functions (PTFs) were developed using easy to measure soil properties such as texture, soil bulk density and soil organic matter for calculating hydraulic conductivity (Schaap et al. 2001, Wösten et al. 2001). The estimation of hydraulic conductivity is an important variable in hydrological models for evaluating water flow, water relationship for plant growth and chemical transport processes needed in agriculture and engineering applications (Shouse and Mohanty 1998, Wösten et al. 2001). I therefore asked the question:

(7) Can we predict observed saturated hydraulic conductivity using the pedotransfer functions (PTFs) at several depths?

In this study, we investigated the utility of available soil properties (texture, soil organic contant and bulk density to estimate the saturated hydraulic conductivity (K_s) at several depths. The performance of well-common known PTFs such as Rossetta, Jabro and Vereecken were tested. We calculated and compared the hydraulic conductivity conducted on 11 lysimeter, because there the depth distributions of factors that are important for the infiltration capacity (e.g. root biomass) were available, and K_s could be assessed at several depths. The best regression model for estimating the soil saturated hydraulic conductivity at the soil surface showed that biotic factors from deeper soil layers and earthworms from the topsoil (0-10 cm) play an important role. This implies that probably larger and longer connected pores up to the plough pan play an important role for the hydraulic conductivity at the soil surface. Additionally, this emphasized (as shown in Chapter 5) the independent role to bulk density of earthworms on the infiltration capacity.

At and below the old plough layer predictions using PTFs based on soil texture, bulk density and soil organic carbon content were very uncertain. At the soil surface the pedotransfer function after Jabro (1990) explained 41% of the measured variation of K_s. In general, models including bulk density could better explain the measured hydraulic conductivity. For a sufficient application in hydrological models, estimation of K_s could be improved by accounting for roots. **Predicting hydraulic conductivity near saturation remains difficult and uncertain for all soil layers. PTFs including soil structure are better in estimating soil hydraulic conductivity, but other biotic factors such as earthworms activity and roots are also important.**

8.2 General Perspectives

At present heavy rainfalls inducing flooding events occur more often leading to a higher risk of run-off and soil erosion (IPCC 2012). For soil conservation, hydraulic properties such as infiltration capacity are a very important soil quality indicator reflecting soil conditions. The change of the soil infiltration capacity by inadequate land-use and land-management is connected to a loss
of biodiversity (including plant and soil fauna diversity), resulting in negative impact on soil erosion and surface run-off (Pimentel and Kounang 1998, Tilman et al. 2002, Haines-Young 2009). A high infiltration of soil is important to reduced soil erosion and diminishes the impact of temporal flooding during high precipitation events (Mannering and Meyer 1963).

The results of this thesis show that the infiltration capacity is affected on the one hand by large macropores formed by earthworms and on the other hand by plant species diversity,

which improves soil structural parameters such as bulk density. Both effects can act together with the strength of their effects depending on other environmental conditions such as climate (Figure 8.2). For example, in 2012 we observed a strong influence of species diversity (and hence bulk density), and only a small influence of earthworms on infiltration capacity, probably in this year climate conditions suppressed earthworm activity.

The results of the thesis indicate that the positive effects of plant diversity at the soil surface were not transferred into deeper soil layers. For drainage, crop production and water management a plough layer is problematic. Further work is needed to find solutions for appropriate measures to minimize risks of subsoil compaction. Therefore, variation of the depth of ploughing, conversation tillage, incorporating a combination of plants with deep tap and fibrous roots could improve or correct the subsoil compaction (Ishaq et al. 2001, Hassan et al. 2007). For the estimation of soil hydraulic conductivity at the soil surface and the application in hydrological models information about soil structure properties are essential.

In summary, this study shows that vegetation cover and earthworms influence explain patterns of infiltration capacity, although different patterns have been observed in different years. Measurements in The Jena Experiment on several gradients were an opportunity to discover these influences, because they allowed for distinguishing interacting effects on the infiltration capacity. Within the last decades several studies have shown that grassland biodiversity supports and regulates ecosystem services such as primary productivity, nutrient cycling, stability and carbon storage (Roscher et al. 2004; Hooper et al. 2005; Cardinale et al. 2007; Steinbeiss et al. 2008; Bessler et al. 2009; Weigelt et al. 2010). Here, I show that species diversity may also provide an ecosystem service related to erosion and flood prevention by providing higher infiltration capacity, although this effect varies between years. Despite the temporal and spatial variation of infiltration capacity, my results underline that biotic influences on soil hydraulic properties over a longer period of time sustain and improve ecosystem services and functioning. This study shows that earthworms (then also legumes and grasses play a role) and plant species diversity (then soil structural parameters play a role) are relevant for explaining variation in infiltration capacity. Open questions relate to the cause for different drivers in different years (earthworms vs. productivity).

Further studies on a similar statistical plot design are necessary for observing the single and interaction effects of earthworms and bulk density and accordingly in which environmental condition one or both of these factors play a role maintaining ecosystem services and functioning.

Figure 8.2: Summary of probable and hypothetical mechanisms by which plant species richness, plant functional groups, plant roots, earthworms and soil structural parameters such as soil organic carbon, bulk

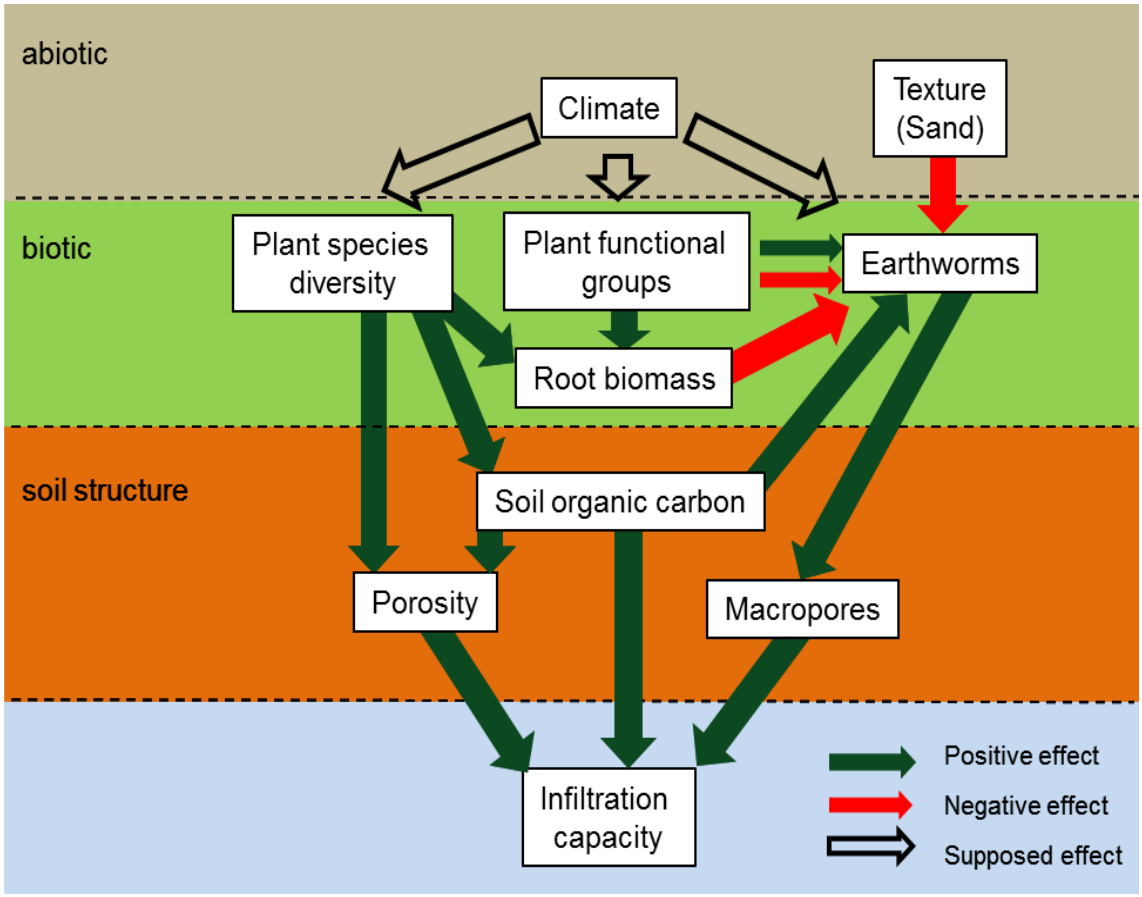

Figure 8.2: Scheme of probable and hypothetical effects of climate, soil texture, plant species richness, plant functional groups, plant roots, earthworms and soil structural parameters such as soil organic carbon and porosity on infiltration capacity.

9. References

Abbott I. and Parker C. A. (1981) Interactions between earthworms and their soil environment. Soil Biology and Biochemistry 13: 191-197.

Ad-hoc-AG Boden (2005) Bodenkundliche Kartieranleitung. 5. Auflage, Hannover.

Aimrun W. and Amin M. S. M. (2009) Pedo-transfer function for saturated hydraulic conductivity of lowland paddy soils. Paddy and Water Environment 7: 217-225.

Alaoui A., Lipiec J. and Gerke H. H. (2011) A review of the changes in the soil pore system due to soil deformation: A hydrodynamic perspective. Soil and Tillage Research 115–116: 1-15.

Altieri M. A. (1999) The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems & Environment 74: 19-31.

Alvarez-Acosta C., Lascano R. J. and Stroosnijder L. (2012) Test of the rosetta pedotransfer function for saturated hydraulic conductivity. Open Journal of Soil Science 2: 203-212.

Angers D. A. and Caron J. (1998) Plant-induced Changes in Soil Structure: Processes and Feedbacks. Biogeochemistry 42: 55-72.

Angulo-Jaramillo R., Vandervaere J.-P., Roulier S., Thony J.-L., Gaudet J.-P. and Vauclin M. (2000) Field measurement of soil surface hydraulic properties by disc and ring infiltrometers: A review and recent developments. Soil and Tillage Research 55: 1-29.

Ankeny M. D., Kaspar T. C. and Horton R. (1990) Characterization of Tillage and Traffic Effects on Unconfined Infiltration Measurements. Soil Science Society of America Journal 54: 837-840.

Archer N. A. L., Quinton J. N. and Hess T. M. (2002) Below-ground relationships of soil texture, roots and hydraulic conductivity in two-phase mosaic vegetation in South-east Spain. Journal of Arid Environments 52: 535-553.

Aslyng H. (1963) Soil physics terminology. International Union of Soil Sciences 23.

Azooz R. H. and Arshad M. A. (1996) Soil infiltration and hydraulic conductivity under long-term no-tillage and conventional tillage systems. Canadian Journal of Soil Science 76: 143-152.

Bardgett R. D., Anderson J. M., Behan-Pelletier V., Brussaard L., Coleman D. C., Ettema C., Moldenke A., Schimel J. P. and Wall D. H. (2001) The Influence of Soil Biodiversity on Hydrological Pathways and the Transfer of Materials between Terrestrial and Aquatic Ecosystems. Ecosystems 4: 421-429.

Barley K. P. (1954) Effects of Root Growth and Decay on the Permeability of A Synthetic Sandy Loam. Soil Science 78: 205-210.

Barnes P. W. and Harrison A. T. (1982) Species distribution and community organization in a Nebraska Sandhills mixed prairie as influenced by plant/soil-water relationships. Oecologia 52: 192-201.

Bastardie F., Capowiez Y., de Dreuzy J. R. and Cluzeau D. (2003) X-ray tomographic and hydraulic characterization of burrowing by three earthworm species in repacked soil cores. Applied Soil Ecology 24: 3-16.

Baumgartl T. and Horn R. (1991) Effect of aggregate stability on soil compaction. Soil and Tillage Research 19: 203-213.

Bens O., Wahl N., Fischer H. and Hüttl R. (2007) Water infiltration and hydraulic conductivity in sandy cambisols: impacts of forest transformation on soil hydrological properties. European Journal of Forest Research 126: 101-109.

Berglund E. R., Ahyoud A. and Tayaa M. H. (1980) Comparison of soil and infiltration properties of range and afforested sites in northern Morocco. Forest Ecology and Management 3: 295-306.

Berry E. C. and Jordan D. (2001) Temperature and soil moisture content effects on the growth of Lumbricus terrestris (Oligochaeta: Lumbricidae) under laboratory conditions. Soil Biology and Biochemistry 33: 133-136.

Bessler H., Temperton V. M., Roscher C., Buchmann N., Schmid B., Schulze E.-D., Weisser W. W. and Engels C. (2009) Aboveground overyielding in grassland mixtures is associated with reduced biomass partitioning to belowground organs. Ecology 90: 1520-1530.

Beven K. (1981) Micro-, Meso-, Macroporosity and Channeling Flow Phenomena in Soils. Soil Science Society of America Journal 45: 1245-1245.

Beven K. and Germann P. (1982) Macropores and water flow in soils. Water Resources Research 18: 1311-1325.

Beven K. and Germann P. (2013) Macropores and water flow in soils revisited. Water Resources Research 49: 3071-3092.

Blackburn W. H. (1975) Factors influencing infiltration and sediment production of semiarid rangelands in Nevada. Water Resources Research 11: 929-937.

Blanchart E., Lavelle P., Braudeau E., Le Bissonnais Y. and Valentin C. (1997) Regulation of soil structure by geophagous earthworm activities in humid savannas of Côte d'Ivoire. Soil Biology and Biochemistry 29: 431-439.

Blanchart E., Albrecht A., Brown G., Decaens T., Duboisset A., Lavelle P., Mariani L. and Roose E. (2004) Effects of tropical endogeic earthworms on soil erosion. Agriculture, Ecosystems & Environment 104: 303-315.

Boden A.-h.-A. (2005):Bodenkundliche Kartieranleitung. Hannover

Bodhinayake W. and Cheng Si B. (2004) Near-saturated surface soil hydraulic properties under different land uses in the St Denis National Wildlife Area, Saskatchewan, Canada. Hydrological Processes 18: 2835-2850.

Bodner G., Loiskandl W., Buchan G. and Kaul H. P. (2008) Natural and management-induced dynamics of hydraulic conductivity along a cover-cropped field slope. Geoderma 146: 317-325.

Bonsu M. (1992) A study of a texture-based equation for estimating the saturated hydraulic conductivity of an alfisol in the sudan savannah ecological zone, Ghana. Hydrological Sciences Journal 37: 599-606.

Bouché M. B. (1977) Strategies lombriciennes. Ecological Bulletins: 122-132.

Bouché M. B. and Al-Addan F. (1996) Earthworms, water infiltration and soil stability: Some new assessments. Soil Biology and Biochemistry 29: 441-452.

Bronick C. J. and Lal R. (2005) Soil structure and management: a review. Geoderma 124: 3-22.

Brown G. (1995) How do earthworms affect microfloral and faunal community diversity? Plant and Soil 170: 209-231.

Buckingham, E. (1907) Studies on the movement of soil moisture. Bulletin 38. USDA Bureau of Soils, Washington, DC.

Bundt M., Widmer F., Pesaro M., Zeyer J. and Blaser P. (2001) Preferential flow paths: biological 'hot spots' in soils. Soil Biology and Biochemistry 33: 729-738.

Burnham K. and Anderson D. (1998) Model selection and inference a practical information theoretic approach. Springer, Berlin , Heidelberg, New York

Cerdà A. (1996) Seasonal variability of infiltration rates under contrasting slope conditions in southeast Spain. Geoderma 69: 217-232.

Chan K. Y. (2004) Impact of tillage practices and burrows of a native Australian anecic earthworm on soil hydrology. Applied Soil Ecology 27: 89-96.

Chappell N. A., Ternan J. L. and Bidin K. (1999) Correlation of physicochemical properties and sub-erosional landforms with aggregate stability variations in a tropical Ultisol disturbed by forestry operations. Soil and Tillage Research 50: 55-71.

Conant R. (2012) Grassland Soil Organic Carbon Stocks: Status, Opportunities, Vulnerability. In: R Lal, K Lorenz, R F Hüttl, B U Schneider and J von Braun (eds) Recarbonization of the Biosphere. Springer Netherlands

Coupland R. T. and Johnson R. E. (1965) Rooting Characteristics of Native Grassland Species in Saskatchewan. Journal of Ecology 53: 475-507.

Darcy H. (1856) Les fontaines publiques de la ville de Dijon. V. Dalmont

Darwin C. (1882) The formation of vegetable mould through the action of worms : with observations on their habits / by Charles Darwin. J. Murray, London

Deb S. K. and Shukla M. K. (2012) Variability of hydraulic conductivity due to multiple factors. American Journal of Environmental Sciences 8: 489-502.

Dec D., Dorner J., Becker-Fazekas O. and Horn R. (2008) Effect of bulk density on hydraulic properties of homogenized and structured soils. Revista de la ciencia del suelo y nutrición vegetal 8: 1-13.

Dekker L. W. and Ritsema C. J. (1994) How water moves in a water repellent sandy soil: 1. Potential and actual water repellency. Water Resource Research 30: 2507-2517.

Dexter A. R. (1988) Advances in characterization of soil structure. Soil and Tillage Research 11: 199-238.

DIN ISO (2002) Bodenbeschaffenheit – Bestimmung der Partikelgrößenverteilung in Mineralböden – Verfahren mittels Siebung und Sedimentation. Beuth-Verlag GmbH Berlin

Duraiappah A. K., Naeem, S. (2005) Millennium Ecosystem Assessment.Ecosystems and human well-being: Biodiversity Synthesis World Resources Institute, Washington DC, US

Durner W. and Lipsius K. (2006) Determining Soil Hydraulic Properties. Encyclopedia of Hydrological Sciences. John Wiley & Sons, Ltd

Edwards C. A. and Bohlen P. J. (1996) The biology and ecology of earthworms. Chapman and Hall, London

Edwards W. M., Shipitalo M. J., Owens L. B. and Norton L. D. (1990) Effect of Lumbricus terrestris L. burrows on hydrology of continuous no-till corn fields. Geoderma 46: 73-84.

Edwards W. M., Shipitalo M. J., Traina S. J., Edwards C. A. and Owens L. B. (1992) Role of *Lumbricus terrestris* (L.) burrows on quality of infiltrating water. Soil Biology and Biochemistry 24: 1555-1561.

Ehlers W. (1975) Observations on Earthworm Channels and Infiltration on Tilled and Untilled Loess Soil. Soil Science 119: 242-249.

Eisenhauer N. and Scheu S. (2008a) Earthworms as drivers of the competition between grasses and legumes. Soil Biology and Biochemistry 40: 2650-2659.

Eisenhauer N., Straube D. and Scheu S. (2008b) Efficiency of two widespread non-destructive extraction methods under dry soil conditions for different ecological earthworm groups. European Journal of Soil Biology 44: 141-145.

Eisenhauer N., Milcu A., Sabais A. C. W. and Scheu S. (2008c) Animal Ecosystem Engineers Modulate the Diversity-Invasibility Relationship. PLoS ONE 3: e3489.

Eisenhauer N., Milcu A., Nitschke N., Sabais A., Scherber C. and Scheu S. (2009a) Earthworm and belowground competition effects on plant productivity in a plant diversity gradient. Oecologia 161: 291-301.

Eisenhauer N., Milcu A., Sabais A. C. W., Bessler H., Weigelt A., Engels C. and Scheu S. (2009b) Plant community impacts on the structure of earthworm communities depend on season and change with time. Soil Biology and Biochemistry 41: 2430-2443.

Eisenhauer N., Milcu A., Sabais A. C. W., Bessler H., Brenner J., Engels C., Klarner B., Maraun M., Partsch S., Roscher C., Schonert F., Temperton V. M., Thomisch K., Weigelt A., Weisser W. W. and Scheu S. (2011) Plant Diversity Surpasses Plant Functional Groups and Plant Productivity as Driver of Soil Biota in the Long Term. PLoS ONE 6: e16055.

Ela S. D., Gupta S. C. and Rawls W. J. (1992) Macropore and Surface Seal Interactions Affecting Water Infiltration into Soil. Soil Science Society of America Journal 56: 714-721.

Ellenberg H. and Leuschner C. (2010) Vegetation Mitteleuropas mit den Alpen: In ökologischer, dynamischer und historischer Sicht. Ulmer Verlag, Stuttgart

FAO-Unesco (1997) Soil map of the world. Revised legend with corrections and update, Wageningen

Fargione J. E. and Tilman D. (2005) Diversity decreases invasion via both sampling and complementarity effects. Ecology Letters 8: 604-611.

Flury M., Flühler H., Jury W. A. and Leuenberger J. (1994) Susceptibility of soils to preferential flow of water: A field study. Water Resources Research 30: 1945-1954.

Fonte S. J., Winsome T. and Six J. (2009) Earthworm populations in relation to soil organic matter dynamics and management in California tomato cropping systems. Applied Soil Ecology 41: 206-214.

Fornara D. A. and Tilman D. (2008) Plant functional composition influences rates of soil carbon and nitrogen accumulation. Journal of Ecology 96: 314-322.

Franzluebbers A. J. (2002) Water infiltration and soil structure related to organic matter and its stratification with depth. Soil and Tillage Research 66: 197-205.

Fuentes J. P., Flury M. and Bezdicek D. F. (2004) Hydraulic Properties in a Silt Loam Soil under Natural Prairie, Conventional Till, and No-Till. Soil Science Society of America Journal 68: 1679-1688.

Gastine A., Scherer-Lorenzen M. and Leadley P. W. (2003) No consistent effects of plant diversity on root biomass, soil biota and soil abiotic conditions in temperate grassland communities. Applied Soil Ecology 24: 101-111.

Gaston K. J. and Spicer J. I. (2004) Biodiversity: An Introduction. Wiley

Germann P. and Beven K. (1981) Water flow in soil macropores I. An experimental approach. Journal of Soil Science 32: 1-13.

Gijsman A. J. and Thomas R. J. (1996) Evaluation of some physical properties of an oxisol after conversion of native savanna into legume-based or pure grass pastures. Tropical Grasslands 30: 237-248.

Gish T. J. and Jury W. A. (1983) Effect of plant root channels on solute transport. Trans. Am. Soc. Agric. Eng. 26: 440-444.

Goss M. J., Ehlers W., Boone F. R., White I. and Howse K. R. (1984) Effects of soil management practice on soil physical conditions affecting root growth. Journal of Agricultural Engineering Research 30: 131-140.

Gotelli N. J. and Colwell R. K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391.

Grace J. (2006) Structural Equation Modeling and Natural Systems. Cambridge University Press

Grevers M. C. J. and Jong E. D. (1990) The characterization of soil macroporosity of a clay soil under ten grasses using image analysis. Canadian Journal of Soil Science 70: 93-103.

Gyssels G. and Poesen J. (2003) The importance of plant root characteristics in controlling concentrated flow erosion rates. Earth Surface Processes and Landforms 28: 371-384.

Haines-Young R. (2009) Land use and biodiversity relationships. Land Use Policy 26: S178-S186.

Hale C., Frelich L., Reich P. and Pastor J. (2005) Effects of European Earthworm Invasion on Soil Characteristics in Northern Hardwood Forests of Minnesota, USA. Ecosystems 8: 911-927.

Hassan F. U., Ahmad M., Ahmad N. and Abbasi M. K. (2007) Effects of subsoil compaction on yield and yield attributes of wheat in the sub-humid region of Pakistan. Soil and Tillage Research 96: 361-366.

Haynes R. J. and Naidu R. (1998) Influence of lime, fertilizer and manure applications on soil organic matter content and soil physical conditions: a review. Nutrient Cycling in Agroecosystems 51: 123-137.

Hector A., Schmid B., Beierkuhnlein C., Caldeira M. C., Diemer M., Dimitrakopoulos P. G., Finn J. A., Freitas H., Giller P. S., Good J., Harris R., Högberg P., Huss-Danell K., Joshi J., Jumpponen A., Körner C., Leadley P. W., Loreau M., Minns A., Mulder C. P. H., O'Donovan G., Otway S. J., Pereira J. S., Prinz A., Read D. J., Scherer-Lorenzen M., Schulze E.-D., Siamantziouras A.-S. D., Spehn E. M., Terry A. C., Troumbis A. Y., Woodward F. I., Yachi S. and Lawton J. H. (1999) Plant Diversity and Productivity Experiments in European Grasslands. Science 286: 1123-1127.

Hillel D. (1998) Environmental Soil Physics. CA Academic Press, New York

Hooper D. U., Chapin F. S., Ewel J. J., Hector A., Inchausti P., Lavorel S., Lawton J. H., Lodge D. M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A. J., Vandermeer J. and Wardle D. A. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge Ecological Monographs 75: 3-35.

Hopp H. and Slater C. S. (1948) Influence of Earthworms on Soil Productivity. Soil Science 66: 421-428.

Horn R., Taubner H., Wuttke M. and Baumgartl T. (1994) Soil physical properties related to soil structure. Soil and Tillage Research 30: 187-216.

Hu W., Shao M. A., Wang Q. J., Fan J. and Reichardt K. (2008) Spatial variability of soil hydraulic properties on a steep slope in the loess plateau of China. Scientia Agricola 65: 268-276.

IPCC (2012) Summary for policemakers. In: managing the risks of extrem events and disaster in advance climate change adaption. In: C B Field, Barros, V., Stocker, T.F., Qin, D., Dokken, D.J., Ebi, K.L., Mastrandrea, M.D., Mach, K. and P J., G.-K., Allen, S.K., Tignor, M. & Midgley, P.M.). (eds) A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change., Cambridge University Press, Cambridge, UK, and New York, NY, USA

Ishaq M., Hassan A., Saeed M., Ibrahim M. and Lal R. (2001) Subsoil compaction effects on crops in Punjab, Pakistan: I. Soil physical properties and crop yield. Soil and Tillage Research 59: 57-65.

Isselstein J., Jeangros B. and Pavlu V. (2005) Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe–a review. Agronomy Research 3: 139-151.

Jabro J. D. (1992) Estimation of saturated hydraulic conductivity of soils from particle size distribution and bulk density data. Transactions of the ASAE 35: 557-560.

Jarvis N. J., Leeds-Harrison P. B. and Dosser J. M. (1987) The use of tension infiltrometers to assess routes and rates of infiltration in a clay soil. Journal of Soil Science 38: 633-640.

Jarvis N. J. and Messing I. (1995) Near-Saturated Hydraulic Conductivity in Soils of Contrasting Texture Measured by Tension Infiltrometers. Soil Science Society of America Journal 59: 27-34.

Joschko M., Söchtig W. and Larink O. (1992) Functional relationship between earthworm burrows and soil water movement in column experiments. Soil Biology and Biochemistry 24: 1545-1547.

Kladivko E. J., Mackay A. D. and Bradford J. M. (1986) Earthworms as a Factor in the Reduction of Soil Crusting. Soil Science Society of America Journal 50: 191-196.

Kladivko E. J. (2001) Tillage systems and soil ecology. Soil and Tillage Research 61: 61-76.

Kluge G. and Müller-Westermeier G. (2000) Das Klima ausgewählter Orte der Bundesrepublik Deutschland: Jena. Berichte des Deutschen Wetterdienstes 213, Offenbach/ Main

Knoop W. T. and Walker B. H. (1985) Interactions of Woody and Herbaceous Vegetation in a Southern African Savanna. Journal of Ecology 73: 235-253.

Kohler-Milleret R., Bayon R.-C., Chenu C., Gobat J.-M. and Boivin P. (2013) Impact of two root systems, earthworms and mycorrhizae on the physical properties of an unstable silt loam Luvisol and plant production. Plant and Soil: 1-15.

Kördel W., Egli H. and Klein M. (2008) Transport of pesticides via macropores (IUPAC Technical Report). Pure Appl. Chem. 80: 105-160.

Kulli B., Gysi M. and Flühler H. (2003) Visualizing soil compaction based on flow pattern analysis. Soil and Tillage Research 70: 29-40.

Kutílek M. (2004) Soil hydraulic properties as related to soil structure. Soil and Tillage Research 79: 175-184.

Lachnicht S. L., Parmelee R. W., McCartney D. and Allen M. (1997) Characteristics of macroporosity in a reduced tillage agroecosystem with manipulated earthworm populations: Implications for infiltration and nutrient transport. Soil Biology and Biochemistry 29: 493-498.

Lamandé M., Hallaire V., Curmi P., Pérès G. and Cluzeau D. (2003) Changes of pore morphology, infiltration and earthworm community in a loamy soil under different agricultural managements. CATENA 54: 637-649.

Lavelle P. (1988) Earthworm activities and the soil system. Biology and Fertility of Soils 6: 237-251.

Lavelle P., Blanchart E., Martin A., Spain A. V. and Martin S. (1992) Impact of Soil Fauna on the Properties of Soils in the Humid Tropics. Soil Sci Soc Am, Madison, WI

Lavelle P., Lattaud C., Trigo D. and Barois I. (1995) Mutualism and biodiversity in soils. Plant and Soil 170: 23-33.

Lavelle P. (1997) Faunal activities and soil processes: Adaptive strategies that determine ecosystem function. Advances in Ecological Research Volume 27: 93-132.

Lee K. and Foster R. (1991) Soil fauna and soil structure. Soil Research 29: 745-775.

Lee K. E. (1985) Earthworms : their ecology and relationships with soils and land use. Academic Press, Sydney [etc.]

Li X., Zhang Q. and Ye X. (2013) Effects of spatial information of soil physical properties on hydrological modeling based on a distributed hydrological model. Chinese Geographical Science 23: 182-193.

Lin H. S., McInnes K. J., Wilding L. P. and Hallmark C. T. (1999) Effects Of Soil Morphology On Hydraulic Properties I. Quantification Of Soil Morphology. Soil Science Society of America Journal 63: 948-954.

Lipiec J., Kuś J., Słowińska-Jurkiewicz A. and Nosalewicz A. (2006) Soil porosity and water infiltration as influenced by tillage methods. Soil and Tillage Research 89: 210-220.

Logsdon S. D. and Cambardella C. A. (2000) Temporal Changes in Small Depth-Incremental Soil Bulk Density 1 Instrument information is provided for the benefit of the reader and does not imply endorsement by the USDA. Soil Science Society of America Journal 64: 710-714.

Logsdon S. D. and Karlen D. L. (2004) Bulk density as a soil quality indicator during conversion to no-tillage. Soil and Tillage Research 78: 143-149.

Loreau M. and Hector A. (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412: 72-76.

Luxmoore R. J. (1981) Micro-, meso-, and macroporosity of soil. Soil Sci. Soc. Am. J. 45: Medium: X; Size: Pages: 671.

Luxmoore R. J. (1991) On preferential flow and its measurement

Mallants D., Mohanty B. P., Vervoort A. and Feyen J. (1997) Spatial analysis of saturated hydraulic conductivity in a soil with macropores. Soil Technology 10: 115-131.

Mannering J. V. and Meyer L. D. (1963) The Effects of Various Rates of Surface Mulch on Infiltration and Erosion1. Soil Science Society of America Journal 27: 84-86.

Marquard E., Weigelt A., Temperton V. M., Roscher C., Schumacher J., Buchmann N., Fischer M., Weisser W. W. and Schmid B. (2009) Plant species richness and functional composition drive overyielding in a six-year grassland experiment. Ecology 90: 3290-3302.

Meek B. D., Rechel E. A., Carter L. M. and DeTar W. R. (1989) Changes In Infiltration Under Alfalfa As Influenced By Time And Wheel Traffic. Soil Science Society of America Journal 53: 238-241.

Meek B. D., Rechel E. R., Carter L. M., DeTar W. R. and Urie A. L. (1992) Infiltration rate of a sandy loam soil: effects of traffic, tillage, and plant roots. Soil Science Society of America Journal 56: 908-913.

Messing I. and Jarvis N. J. (1990) Seasonal variation in field-saturated hydraulic conductivity in two swelling clay soils in Sweden. Journal of Soil Science 41: 229-237.

Messing I. and Jarvis N. J. (1993) Temporal variation in the hydraulic conductivity of a tilled clay soil as measured by tension infiltrometers. Journal of Soil Science 44: 11-24.

Milcu A., Partsch S., Langel R. and Scheu S. (2006) The response of decomposers (earthworms, springtails and microorganisms) to variations in species and functional group diversity of plants. Oikos 112: 513-524.

Milcu A., Partsch S., Scherber C., Weisser W. W. and Scheu S. (2008) Earthworms and legumes control litter decompostion in a plant diversity gradient. Ecology 89: 1872-1882.

Miller F. (1989) Matric water potential as an ecological determinant in compost, a substrate dense system. Microbial Ecology 18: 59-71.

Minasny B., McBratney A. B. and Bristow K. L. (1999) Comparison of different approaches to the development of pedotransfer functions for water-retention curves. Geoderma 93: 225-253.

Mitchell A. R., Ellsworth T. R. and Meek B. D. (1995) Effect of root systems on preferential flow in swelling soil. Communications in Soil Science and Plant Analysis 26: 2655-2666.

Mohanty B. P., Ankeny M. D., Horton R. and Kanwar R. S. (1994) Spatial analysis of hydraulic conductivity measured using disc infiltrometers. Water Resources Research 30: 2489-2498.

Mytton L. R., Cresswell A. and Colbourn P. (1993) Improvement in soil structure associated with white clover. Grass and Forage Science 48: 84-90.

Nash J. E. and Sutcliffe J. V. (1970) River flow forecasting through conceptual models part I - A discussion of principles. Journal of Hydrology 10: 282-290.

Nawaz M., Bourrié G. and Trolard F. (2013) Soil compaction impact and modelling. A review. Agronomy for Sustainable Development 33: 291-309.

Oades J. M. (1993) The role of biology in the formation, stabilization and degradation of soil structure. Geoderma 56: 377-400.

Obi M. E. (1999) The physical and chemical responses of a degraded sandy clay loam soil to cover crops in southern Nigeria. Plant and Soil 211: 165-172.

Oelmann Y., Wilcke W., Temperton V. M., Buchmann N., Roscher C., Schumacher J., Schulze E.-D. and Weisser W. W. (2007) Soil and Plant Nitrogen Pools as Related to Plant Diversity in an Experimental Grassland. Soil Science Society of America Journal 71: 720-729.

Paoletti M. G. (1999) The role of earthworms for assessment of sustainability and as bioindicators. Agriculture, Ecosystems & Environment 74: 137-155.

Papadopoulos A., Mooney S. J. and Bird N. R. A. (2006) Quantification of the effects of contrasting crops in the development of soil structure: an organic conversion. Soil Use and Management 22: 172-179.

Parker K. C. (1991) Topography, Substrate, and Vegetation Patterns in the Northern Sonoran Desert. Journal of Biogeography 18: 151-163.

Pérès G., Cluzeau D., Curmi P. and Hallaire V. (1998) Earthworm activity and soil structure changes due to organic enrichments in vineyard systems. Biology and Fertility of Soils 27: 417-424.

Pérès G., Cluzeau D., Menasseri S., Soussana J. F., Bessler H., Engels C., Habekost M., Gleixner G., Weigelt A., Weisser W. W., Scheu S. and Eisenhauer N. (2013) Mechanisms linking plant community properties to soil aggregate stability in an experimental grassland plant diversity gradient. Plant and Soil.

Périé C. and Ouimet R. (2008) Organic carbon, organic matter and bulk density relationships in boreal forest soils. Canadian Journal of Soil Science 88: 315-325.

Pfiffner L. and Luka H. (2007) Earthworm populations in two low-input cereal farming systems. Applied Soil Ecology 37: 184-191.

Pimentel D. and Kounang N. (1998) Ecology of Soil Erosion in Ecosystems. Ecosystems 1: 416-426.

Pinheiro J. C. and Bates D. M. (2000) Mixed-effects models in S and S-Plus. Springer, New York

Pohl M., Alig D., Körner C. and Rixen C. (2009) Higher plant diversity enhances soil stability in disturbed alpine ecosystems. Plant and Soil 324: 91-102.

Poier K. R. and Richter J. (1992) Spatial distribution of earthworms and soil properties in an arable loess soil. Soil Biology and Biochemistry 24: 1601-1608.

Pucheta E., Bonamici I., Cabido M. and Díaz S. (2004) Below-ground biomass and productivity of a grazed site and a neighbouring ungrazed exclosure in a grassland in central Argentina. Austral Ecology 29: 201-208.

Ramankutty N., Evan A. T., Monfreda C. and Foley J. A. (2008) Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. Global Biogeochemical Cycles 22: GB1003.

Rawls W. J., Brakensiek D. L. and Saxto K. E. (1982) Estimation of soil water properties. Transactions of the ASAE 25: 1316-1320.

Reicosky D. C. and Archer D. W. (2007) Moldboard plow tillage depth and short-term carbon dioxide release. Soil and Tillage Research 94: 109-121.

Reynolds W. D., Bowman B. T., Brunke R. R., Drury C. F. and Tan C. S. (2000) Comparison of Tension Infiltrometer, Pressure Infiltrometer, and Soil Core Estimates of Saturated Hydraulic Conductivity. Soil Science Society of America Journal 64: 478-484.

Richards L. A. (1931) Capillary conduction of liquids through porous mediums Physics 1: 318-333.

Roscher C., Schumacher J., Baade J., Wilcke W., Gleixner G., Weisser W. W., Schmid B. and Schulze E.-D. (2004) The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. Basic and Applied Ecology 5: 107-121.

Rowell D. L. (1994) Soil science: methods and applications. Longman Scientific & Technical

Russo D. and Bresler E. Soil Hydraulic Properties as Stochastic Processes: I. An Analysis of Field Spatial Variability. Soil Science Society of America Journal 45: 682-687.

Salehi A., Ghorbanzadeh N. and Kahneh E. (2013) Earthworm biomass and abundance, soil chemical and physical properties under different poplar plantations in the north of Iran. Journal of Forest Science 59: 223-229.

Salverda A. P. and Dane J. H. (1993) An examination of the Guelph permeameter for measuring the soil's hydraulic properties. Geoderma 57: 405-421.

Saxton K. E., Rawls W. J., Romberger J. S. and Papendick R. I. (1986) Estimating Generalized Soil-water Characteristics from Texture. Soil Science Society of America Journal 50: 1031-1036.

Schaap M. G., Leij F. J. and van Genuchten M. T. (1998) Neural Network Analysis for Hierarchical Prediction of Soil Hydraulic Properties. Soil Science Society of America Journal 62: 847-855.

Schaap M. G., Leij F. J. and van Genuchten M. T. (2001) rosetta: a computer program for estimating soil hydraulic parameters with hierarchical pedotransfer functions. Journal of Hydrology 251: 163-176.

Schenk H. J. and Jackson R. B. (2002) The global biogeography of roots. Ecological Monographs 72: 311-328.

Schenk H. J. (2005) Vertical Vegetation Structure Below Ground: Scaling from Root to Globe. Springer Berlin Heidelberg

Scheu S. (2003) Effects of earthworms on plant growth: patterns and perspectives: The 7th international symposium on earthworm ecology · Cardiff · Wales · 2002. Pedobiologia 47: 846-856.

Schjønning P., Munkholm L. J., Moldrup P. and Jacobsen O. H. (2002) Modelling soil pore characteristics from measurements of air exchange: the long-term effects of fertilization and crop rotation. European Journal of Soil Science 53: 331-339.

Schmidt O. and Curry J. (1999) Effects of earthworms on biomass production, nitrogen allocation and nitrogen transfer in wheat-clover intercropping model systems. Plant and Soil 214: 187-198.

Schumm S. A. and Lusby G. C. (1963) Seasonal variation of infiltration capacity and runoff on hillslopes in western Colorado. Journal of Geophysical Research 68: 3655-3666.

Schwartz R. C., Evett S. R. and Unger P. W. (2003) Soil hydraulic properties of cropland compared with reestablished and native grassland. Geoderma 116: 47-60.

Schwärzel K. and Punzel J. (2007) Hood Infiltrometer - A New Type of Tension Infiltrometer. Soil Science Society of America Journal 71: 1438-1447.

Schwärzel K., Carrick S., Wahren A., Feger K.-H., Bodner G. and Buchan G. (2011) Soil Hydraulic Properties of Recently Tilled Soil under Cropping Rotation Compared with Two-Year Pasture. Vadose Zone Journal 10: 354-366.

Seyfried M. S. and Wilcox B. P. (1995) Scale and the Nature of Spatial Variability: Field Examples Having Implications for Hydrologic Modeling. Water Resources Research 31: 173-184.

Shipitalo M. J. and Protz R. (1988) Factors Influencing the Dispersibility of Clay in Worm Casts. Soil Science Society of America Journal 52: 764-769.

Shipitalo M. J., Edwards W. M. and Redmond C. E. (1994) Comparison of Water Movement and Quality in Earthworm Burrows and Pan Lysimeters. J. Environ. Qual. 23: 1345-1351.

Shipitalo M. J., Nuutinen V. and Butt K. R. (2004) Interaction of earthworm burrows and cracks in a clayey, subsurface-drained, soil. Applied Soil Ecology 26: 209-217.

Shouse P. J. and Mohanty B. P. (1998) Scaling of near-saturated hydraulic conductivity measured using disc infiltrometers. Water Resour. Res. 34: 1195-1205.

Shukla M. K., Lal R. and Ebinger M. (2006) Determining soil quality indicators by factor analysis. Soil and Tillage Research 87: 194-204.

Shuster W. D., Subler S. and McCoy E. L. (2002) The influence of earthworm community structure on the distribution and movement of solutes in a chisel-tilled soil. Applied Soil Ecology 21: 159-167.

Simmonds L. P. and Nortcliff S. (1998) Small scale variability in the flow of water and solutes, and implications for lysimeter studies of solute leaching. Nutrient Cycling in Agroecosystems 50: 65-75.

Six J., Paustian K., Elliott E. T. and Combrink C. (2000) Soil Structure and Organic Matter I. Distribution of Aggregate-Size Classes and Aggregate-Associated Carbon. Soil Science Society of America Journal 64: 681-689.

Six J., Bossuyt H., Degryze S. and Denef K. (2004) A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. Soil and Tillage Research 79: 7-31.

Slater C. S. and Hopp H. (1947) Relation of fall protection to earthworm populations and soil physical conditions. Proceedings of the National Academy of Sciences 12: 508-511.

Slater C. S. (1957) Cylinder infiltrometers for determining rates of irrigation. Soil Science Society of America Journal 21: 457-460.

Smit H. J., Metzger M. J. and Ewert F. (2008) Spatial distribution of grassland productivity and land use in Europe. Agricultural Systems 98: 208-219.

Sobieraj J. A., Elsenbeer H. and Vertessy R. A. (2001) Pedotransfer functions for estimating saturated hydraulic conductivity: implications for modeling storm flow generation. Journal of Hydrology 251: 202-220.

Soto B., Basanta R., Benito E., Perez R. and Diaz-Fierros F. (1994) Runoff and erosion from burnt soils in northwest Spain. In: M Sala, Rubio JL. (ed) Soil erosion and degradation as a consequence of forest fires. Geoforma, Logroño, Spain

Spehn E., Joshi J., Schmid B., Alphei J. and Körner C. (2000) Plant diversity effects on soil heterotrophic activity in experimental grassland ecosystems. Plant and Soil 224: 217-230.

Spehn E. M., Scherer-Lorenzen M., Schmid B., Hector A., Caldeira M. C., Dimitrakopoulos P. G., Finn J. A., Jumpponen A., O'Donnovan G., Pereira J. S., Schulze E. D., Troumbis A. Y. and Körner C. (2002) The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. Oikos 98: 205-218.

Spehn E. M., Hector A., Joshi J., Scherer-Lorenzen M. and Schmid B. (2004) Ecosystem effects of biodiversity manipulations in European grasslands. Grassland Science in Europe Volume 9. vdf Hochschulverlag AG an der ETH Zurich, Zürich

Steinbeiss S., Beßler H., Engels C., Temperton V. M., Buchmann N., Roscher C., Kreutziger Y., Baade J., Habekost M. and Gleixner G. (2008) Plant diversity positively affects short-term soil carbon storage in experimental grasslands. Global Change Biology 14: 2937-2949.

Stirzaker R. J., Passioura J. B. and Wilms Y. (1996) Soil structure and plant growth: Impact of bulk density and biopores. Plant and Soil 185: 151-162.

Stockdill S. M. J. (1966) The role of earthworm in pasture production and moisture conservation. Proceedings of the 28th Conference of the Zealand Grassland Association 13: 68-83.

Syers J. K. and Springett J. A. (1983) Earthworm ecology in grassland soils. In: J E Satchell (ed) Earthworm Ecology. Springer Netherlands

Thielemann U. (1986) The octet-method for sampling earthworm populations. Pedobiologia 29: 296-302.

Thompson S. E., Harman C. J., Heine P. and Katul G. G. (2010) Vegetation-infiltration relationships across climatic and soil type gradients. J. Geophys. Res. 115: G02023.

Tietje O. and Tapkenhinrichs M. (1993) Evaluation of Pedo-Transfer Functions. Soil Science Society of America Journal 57: 1088-1095.

Tietje O. and Hennings V. (1996) Accuracy of the saturated hydraulic conductivity prediction by pedo-transfer functions compared to the variability within FAO textural classes. Geoderma 69: 71-84.

Tilman D. (1996) Biodiversity: Population Versus Ecosystem Stability. Ecology 77: 350-363.

Tilman D., Reich P. B., Knops J., Wedin D., Mielke T. and Lehman C. (2001) Diversity and Productivity in a Long-Term Grassland Experiment. Science 294: 843-845.

Tilman D., Cassman K. G., Matson P. A., Naylor R. and Polasky S. (2002) Agricultural sustainability and intensive production practices. Nature 418: 671-677.

Tippkötter R. (1983) Morphology, spatial arrangement and origin of macropores in some hapludalfs, West Germany. Geoderma 29: 355-371.

Trojan M. D. and Linden D. R. (1992) Microrelief and Rainfall Effects on Water and Solute Movement in Earthworm Burrows. Soil Science Society of America Journal 56: 727-733.

van Eekeren N., de Boer H., Hanegraaf M., Bokhorst J., Nierop D., Bloem J., Schouten T., de Goede R. and Brussaard L. (2010) Ecosystem services in grassland associated with biotic and abiotic soil parameters. Soil Biology and Biochemistry 42: 1491-1504.

van Schaik L., Palm J., Klaus J., Zehe E. and Schröder B. (2013) Linking spatial earthworm distribution to macropore numbers and hydrological effectiveness. Ecohydrology: n/a-n/a.

Vereecken H. (1995) Estimating the unsaturated hydraulic conductivity from theoretical models using simple soil properties. Geoderma 65: 81-92.

Vereecken H., Meas, J., Feyen, J. (1990) Estimating Unsaturated Hydraulic Conductivity from Easily Measured Soil Properties. Soil Science 149: 1-12.

Visa N. (1992) Earthworm community response to tillage and residue management on different soil types in southern Finland. Soil and Tillage Research 23: 221-239.

Wainer H. (1976) Robust Statistics: A Survey and Some Prescriptions. Journal of Educational and Behavioral Statistics 1: 285-312.

Ward A. D. and Trimble S. W. (2004) Environmental hydrology. CRC Press, Boca Ratan

Ward R. C. and Robinson M. (1990) Principles of Hydrology. McGraw-Hill Ryerson, Limited

Watson K. W. and Luxmoore R. J. (1986) Estimating Macroporosity in a Forest Watershed by use of a Tension Infiltrometer. Soil Science Society of America Journal 50: 578-582.

Weiler M. and Naef F. (2003) An experimental tracer study of the role of macropores in infiltration in grassland soils. Hydrological Processes 17: 477-493.

Weltzin J. F., Loik M. E., Schwinning S., Williams D. G., Fay P. A., Haddad B. M., Harte J., Huxman T. E., Knapp A. K., Lin G., Pockman W. T., Shaw M. R., Small E. E., Smith M. D., Smith S. D., Tissue D. T. and Zak J. C. (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53: 941-952.

Wen Y.-W., Tsai Y.-W., Wu D. B.-C. and Chen P.-F. (2013) The Impact of Outliers on Net-Benefit Regression Model in Cost-Effectiveness Analysis. PLoS ONE 8: e65930.

Wooding R. A. (1968) Steady Infiltration from a Shallow Circular Pond. Water Resources Research 4: 1259-1273.

Wösten J., Lilly A., Nemes A. and Le Bas C. (1998) Using existing soil data to derive hydraulic parameters for simulation models in enviromental studies and in land use planning. DLO-Staring Centre

Wösten J. H. M. and van Genuchten M. T. (1988) Using texture and other soil properties to predict the unsaturated soil hydraulic functions. Soil Science Society of America Journal 52: 1762-1770.

Wösten J. H. M., Pachepsky Y. A. and Rawls W. J. (2001) Pedotransfer functions: bridging the gap between available basic soil data and missing soil hydraulic characteristics. Journal of Hydrology 251: 123-150.

Wuest S. B. (2001) Earthworm, infiltration, and tillage relationships in a dryland pea–wheat rotation. Applied Soil Ecology 18: 187-192.

Wurst S. and Jones T. H. (2003) Indirect effects of earthworms (Aporrectodea caliginosa) on an above-ground tritrophic interaction. Pedobiologia 47: 91-97.

Yeates G. W., Shepherd T. G. and Francis G. S. (1998) Contrasting response to cropping of populations of earthworms and predacious nematodes in four soils. Soil and Tillage Research 48: 255-264.

Zacharias S. and Wessolek G. (2007) Excluding Organic Matter Content from Pedotransfer Predictors of Soil Water Retention. . Soil Science Society of America Journal 71: 43-50.

Zachmann J. E., Linden D. R. and Clapp C. E. (1987) Macroporous infiltration and redistribution as affected by earthworms, tillage and residue. Soil Science Society of America Journal 51: 1580-1586.

Zachmann J. E. and Linden D. R. (1989) Earthworm Effects on Corn Residue Breakdown and Infiltration. Soil Science Society of America Journal 53: 1846-1849.

Zaller J. G. and Arnone J. A., III (1999) Earthworm responses to plant species' loss and elevated CO2 in calcareous grassland. Plant and Soil 208: 1-8.

Zartman R. E., Moffet C. A., Wester D. B., Sosebee R. E., Fish E. B. and Jaynes W. F. (2012) Influence of Surface Biosolids Application on Infiltration. Applied and Environmental Soil Science 2012.

Zehe E. and Flühler H. (2001) Slope scale variation of flow patterns in soil profiles. Journal of Hydrology 247: 116-132.

Zund P. R., Pillai-McGarry U., McGarry D. and Bray S. G. (1997) Repair of a compacted Oxisol by the earthworm Pontoscolex corethrurus (Glossoscolecidae, Oligochaeta). Biology and Fertility of Soils 25: 202-208.

Zuur A. F., Ieno E. N. and Elphick C. S. (2010) A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1: 3-14.

10. Appendix

Appendix Table A1: Calculated values (in %) for all Plots (plotcode indicated plot number at The Jena Experiment field site) in 10, 20, 30, 40, 60, 80 and 100 cm depth for clay

clay10	clay20	clay30	clay40	clay60	clay80	clay100	plotcode
15.60	16.50	15.30	14.10	15.10	18.40	15.50	B1A01
13.80	14.50	14.90	13.80	16.30	18.90	15.60	B1A02
14.50	15.10	15.20	14.40	16.00	16.10	12.70	B1A03
13.30	14.00	15.10	14.30	15.20	15.60	14.40	B1A04
13.60	14.30	15.70	16.00	15.30	15.10	11.70	B1A05
15.40	15.60	15.70	14.40	16.70	18.50	17.60	B1A06
14.80	15.30	15.10	15.70	17.50	16.80	15.30	B1A07
14.10	14.10	15.30	13.40	18.20	22.10	17.00	B1A08
13.70	14.50	15.80	13.50	19.10	27.10	15.90	B1A09
14.20	14.20	15.90	16.00	16.80	20.40	16.80	B1A11
14.00	15.80	17.50	15.60	16.50	16.50	15.90	B1A12
15.30	16.60	19.20	19.10	17.10	21.90	12.40	B1A13
16.80	17.40	17.70	18.80	18.20	19.80	9.60	B1A14
16.10	16.40	16.90	17.10	15.60	18.00	12.60	B1A15
16.50	17.00	17.60	18.80	18.00	20.30	19.60	B1A16
18.10	18.40	17.70	19.60	19.40	25.30	20.10	B1A17
18.70	18.70	16.50	19.60	19.90	24.10	22.90	B1A18
20.60	18.60	17.10	18.20	21.20	21.60	22.40	B1A19
20.60	17.50	16.60	17.30	20.70	25.40	17.70	B1A20
16.80	16.80	16.40	17.90	21.00	27.90	19.30	B1A21
16.90	16.90	16.10	17.40	18.10	22.40	19.20	B1A22
13.70	17.60	19.90	16.50	17.20	28.20	26.10	B2A01
15.60	19.70	21.00	19.10	21.30	24.50	22.90	B2A02
20.50	21.90	20.80	19.10	21.70	20.20	11.50	B2A03
23.20	22.70	22.10	20.90	21.80	21.20	8.60	B2A04
20.40	19.60	21.00	19.60	20.80	21.90	18.50	B2A05
20.90	20.40	19.90	21.30	22.70	26.60	25.70	B2A06
21.90	23.40	21.90	24.60	25.00	29.30	27.50	B2A08
23.30	23.60	21.60	25.10	26.00	31.50	27.50	B2A09
22.60	22.50	18.20	24.40	23.80	25.80	25.60	B2A10
21.90	21.30	16.50	23.90	22.10	23.70	20.90	B2A11
21.20	21.20	20.80	20.40	22.10	26.80	25.70	B2A12
20.20	23.90	23.10	23.90	24.60	24.60	23.00	B2A13
20.20	21.40	20.10	22.80	23.20	21.20	20.90	B2A14
21.30	20.90	22.20	22.70	21.60	24.10	17.50	B2A15
21.80	20.80	20.90	21.70	19.70	22.30	19.40	B2A16
21.30	20.50	19.40	21.40	23.30	26.70	26.10	B2A17
22.30	22.80	23.00	24.90	28.40	30.70	31.00	B2A18
22.50	23.80	24.50	27.80	26.50	30.90	26.20	B2A19
23.90	24.30	22.30	27.10	27.00	27.50	25.70	B2A20
24.70	24.70	21.30	24.90	24.60	24.80	25.90	B2A21
22.90	22.90	19.80	26.40	23.60	23.10	24.50	B2A22
24.00	24.00	21.80	22.40	28.10	22.10	21.80	B3A01
24.00	24.00	24.20	23.60	26.70	24.70	24.10	B3A02
21.40	22.50	22.20	23.40	25.80	25.70	25.60	B3A03
22.70	23.30	23.40	23.00	26.80	26.40	24.10	B3A04

clay10	clay20	clay30	clay40	clay60	clay80	clay100	plotcode
24.30	24.50	22.40	22.00	26.80	25.50	21.90	B3A05
24.80	24.30	22.90	25.00	27.80	26.10	17.50	B3A06
23.70	23.10	21.20	26.30	27.50	24.90	21.60	B3A07
21.10	21.10	22.10	27.60	29.20	22.40	20.50	B3A08
22.00	22.40	25.70	27.50	26.50	22.10	18.40	B3A09
21.20	21.20	23.40	24.80	23.00	22.20	19.40	B3A11
21.00	21.00	23.40	23.20	25.00	20.90	19.90	B3A12
19.80	19.80	20.90	19.60	19.80	16.80	20.00	B3A13
23.60	23.60	23.20	23.80	21.90	24.00	20.20	B3A14
23.60	23.60	23.90	23.80	22.80	27.80	24.70	B3A15
24.70	24.70	24.20	22.20	25.00	27.40	22.60	B3A16
23.70	23.70	23.40	23.60	25.00	27.70	21.00	B3A17
24.20	23.50	22.60	26.10	29.60	23.80	21.40	B3A19
22.60	22.50	22.30	27.10	27.00	18.00	16.90	B3A20
20.70	20.90	22.00	24.50	25.80	22.50	18.10	B3A21
22.30	22.30	25.50	26.70	21.90	21.50	16.80	B3A22
20.20	20.10	22.90	23.60	22.20	17.60	17.60	B3A23
21.70	21.60	22.90	23.30	22.50	18.80	18.30	B3A24
21.90	21.90	21.20	20.50	16.50	17.10	18.80	B4A01
23.00	23.00	23.60	21.80	17.80	20.80	13.30	B4A02
23.40	23.40	25.20	22.00	20.80	17.80	16.50	B4A03
22.70	22.70	23.40	24.40	22.80	18.40	15.50	B4A04
23.30	23.30	22.20	20.90	20.00	20.30	14.40	B4A06
24.00	24.00	23.00	21.80	20.80	19.90	16.60	B4A07
24.10	24.10	23.40	23.50	21.90	19.40	18.50	B4A08
24.50	24.50	20.60	16.90	19.50	24.10	19.70	B4A09
24.30	24.30	23.00	20.10	20.50	22.70	23.90	B4A10
24.60	24.60	24.10	22.00	22.60	22.40	13.80	B4A11
23.70	23.70	22.80	23.00	22.50	20.60	17.00	B4A12
20.20	20.20	22.00	19.80	20.20	23.30	27.30	B4A13
24.00	24.00	23.50	21.20	18.30	21.50	24.60	B4A14
24.00	24.00	24.10	22.60	19.50	20.00	18.30	B4A15
22.40	22.40	23.60	23.00	22.70	20.90	18.40	B4A16
22.80	22.80	23.50	21.30	23.10	26.90	28.30	B4A17
22.50	22.50	24.80	22.90	21.40	24.80	24.70	B4A18
22.00	22.00	24.00	23.70	19.90	17.70	16.60	B4A19
22.10	22.10	24.30	21.20	20.40	16.70	18.90	B4A20
21.90	21.90	24.10	23.50	22.90	26.90	29.40	B4A21
21.90	21.90	23.40	23.30	20.70	23.00	24.90	B4A22
21.00	21.00	25.10	23.40	18.80	17.60	22.00	B4A23

Appendix Table 2: Calculated values (%) for all Plots (plotcode indicated plot number at The Jena Experiment field site) in 10, 20, 30, 40, 60, 80 and 100 in cm depth for sand

sand10	sand20	sand30	sand40	sand60	sand80	sand100	plotcode
44.80	40.80	46.20	43.10	34.30	33.20	41.30	B1A01
48.40	45.20	42.50	41.90	32.40	25.40	31.70	B1A02
47.70	45.10	42.70	41.20	36.80	30.10	37.50	B1A03
45.10	42.20	40.90	42.30	40.30	37.80	39.10	B1A04
44.50	41.80	40.70	37.60	42.50	32.60	41.60	B1A05
40.50	40.80	42.20	37.40	39.40	26.80	30.90	B1A06
39.30	42.80	45.00	35.50	31.80	23.70	30.50	B1A07
41.30	43.40	44.10	40.40	22.30	21.80	25.60	B1A08
44.10	45.00	45.00	43.20	21.70	13.70	28.00	B1A09
43.00	43.00	40.10	38.30	24.40	19.50	31.10	B1A11
38.00	35.60	41.40	38.70	35.00	27.80	44.90	B1A12
35.80	33.20	31.90	31.30	33.20	26.60	48.50	B1A13
38.20	36.10	35.00	32.50	34.00	28.00	59.00	B1A14
38.00	35.60	35.10	33.90	37.50	32.70	46.70	B1A15
39.40	36.80	35.30	32.80	35.00	25.30	33.50	B1A16
34.80	33.40	35.90	28.00	31.30	15.50	27.40	B1A17
36.20	35.60	38.00	29.00	22.30	16.90	20.60	B1A18
32.90	33.60	37.60	30.90	16.90	17.50	24.80	B1A19
38.90	38.10	38.30	36.10	23.60	16.70	24.60	B1A20
39.20	39.20	37.80	34.40	20.50	20.60	24.00	B1A21
35.20	35.20	31.20	32.50	29.80	16.90	25.80	B1A22
31.80	33.30	37.30	37.60	35.60	12.90	21.40	B2A01
30.00	30.30	31.10	30.80	25.50	18.80	32.50	B2A02
22.30	22.00	22.90	23.30	18.10	19.30	56.60	B2A03
20.60	20.60	21.70	22.70	20.20	18.20	62.90	B2A04
31.60	30.60	25.90	22.90	21.70	20.20	28.70	B2A05
27.10	25.80	21.90	23.80	17.80	15.90	19.50	B2A06
21.40	20.10	29.50	16.70	13.90	15.60	18.80	B2A08
21.90	21.80	26.50	19.40	14.30	12.20	15.60	B2A09
23.80	23.00	28.30	19.00	18.00	17.10	15.20	B2A10
26.50	23.70	18.80	21.40	21.50	20.20	22.90	B2A11
26.90	26.90	30.60	30.30	28.80	17.20	15.60	B2A12
19.90	20.70	23.30	23.90	23.30	19.10	17.60	B2A13
17.00	17.50	18.90	15.00	15.30	17.40	14.60	B2A14
24.70	25.10	17.00	14.90	15.90	16.40	25.10	B2A15
21.30	21.10	17.60	20.20	16.10	12.20	19.20	B2A16
16.60	16.30	17.70	18.00	12.70	11.10	14.80	B2A17
16.10	16.10	17.20	14.80	9.80	11.10	13.80	B2A18
15.80	15.50	22.40	11.00	11.80	10.70	18.70	B2A19
15.10	15.30	22.70	10.80	9.90	14.80	17.20	B2A20
13.90	14.00	18.30	15.50	18.50	19.90	14.20	B2A21
15.40	14.90	13.90	13.20	21.90	22.60	19.20	B2A22
21.40	21.40	21.40	27.30	21.90	24.70	27.50	B3A01
19.80	19.80	19.90	24.90	21.40	15.80	22.30	B3A02
21.30	21.30	20.10	20.50	17.30	12.80	11.20	B3A03
20.00	19.90	19.20	19.60	9.90	10.20	14.10	B3A04
18.80	18.50	21.90	21.30	8.10	16.90	19.90	B3A05

sand_10	sand_20	sand_30	sand_40	sand_60	sand_80	sand_100	plotcode
17.10	16.80	19.70	15.40	9.00	15.60	29.30	B3A06
14.40	14.40	16.10	10.50	11.20	15.50	31.20	B3A07
17.60	19.40	16.30	9.80	10.30	21.30	32.90	B3A08
11.40	13.80	14.90	6.90	13.10	23.60	28.60	B3A09
16.20	16.70	12.70	11.40	16.50	18.70	23.60	B3A11
14.80	15.30	13.50	15.60	15.20	18.80	17.90	B3A12
14.90	14.90	18.00	15.50	16.50	19.00	12.30	B3A13
17.00	17.00	15.80	12.20	13.30	12.00	14.60	B3A14
19.60	19.60	19.30	15.50	12.30	14.40	12.60	B3A15
17.10	17.10	18.80	17.40	11.20	8.00	18.50	B3A16
19.20	19.20	19.60	17.40	9.70	10.90	24.90	B3A17
14.60	14.80	14.70	15.20	7.10	17.10	31.30	B3A19
11.40	13.30	15.50	8.30	14.00	24.50	38.60	B3A20
15.80	18.40	17.60	12.50	14.90	23.70	33.50	B3A21
16.50	17.70	12.70	6.80	20.40	24.60	27.60	B3A22
14.10	14.50	15.60	13.00	17.90	20.60	20.30	B3A23
13.50	13.50	13.90	14.80	18.00	18.50	17.70	B3A24
21.30	21.30	12.30	14.60	12.30	21.30	20.50	B4A01
19.30	19.30	9.90	7.40	15.00	13.20	26.80	B4A02
16.00	16.00	9.00	10.60	12.20	13.90	27.40	B4A03
15.30	15.30	17.80	12.00	11.00	14.80	33.40	B4A04
16.60	16.60	9.40	10.20	7.60	19.20	23.80	B4A06
12.30	12.30	9.70	7.90	12.30	11.80	23.20	B4A07
13.00	13.00	11.30	8.10	10.00	15.00	21.00	B4A08
11.20	11.20	14.70	13.60	6.60	8.20	15.90	B4A09
9.70	9.70	7.30	4.60	10.60	8.10	7.50	B4A10
8.50	8.50	6.20	5.20	8.30	7.30	17.80	B4A11
10.90	10.90	7.90	7.00	10.20	12.00	13.20	B4A12
19.30	19.30	11.90	7.70	7.30	10.60	7.00	B4A13
8.40	8.40	7.20	5.90	14.10	12.20	6.60	B4A14
8.80	8.80	7.80	5.60	11.10	8.70	9.20	B4A15
9.80	9.80	9.10	7.20	10.10	8.10	14.30	B4A16
7.30	7.30	6.60	15.10	3.80	5.40	6.20	B4A17
6.20	6.20	6.20	7.70	7.40	4.10	4.70	B4A18
8.00	8.00	9.30	6.00	7.30	12.90	8.60	B4A19
7.90	7.90	7.90	11.30	9.80	10.10	5.00	B4A20
10.40	10.40	9.40	10.10	4.80	6.10	7.00	B4A21
7.20	7.20	8.20	13.70	7.40	6.20	4.80	B4A22
10.30	10.30	6.50	8.00	9.90	5.90	9.00	B4A23

Appendix Table 3: Calculated values (in %) for all Plots (plotcode indicated plot number at The Jena Experiment field site) in 10, 20, 30, 40, 60, 80 and 100 in cm depth for silt

silt10	silt20	silt30	silt40	silt60	silt80	silt100	plotcode
39.60	42.70	38.50	42.80	50.60	48.40	43.20	B1A01
37.80	40.30	42.60	44.30	51.30	55.70	52.70	B1A02
37.80	39.80	42.10	44.40	47.20	53.80	49.80	B1A03
41.60	43.80	44.00	43.40	44.50	46.60	46.50	B1A04
41.90	43.90	43.60	46.40	42.20	52.30	46.70	B1A05
44.10	43.60	42.10	48.20	43.90	54.70	51.50	B1A06
45.90	41.90	39.90	48.80	50.70	59.50	54.20	B1A07
44.60	42.50	40.60	46.20	59.50	56.10	57.40	B1A08
42.20	40.50	39.20	43.30	59.20	59.20	56.10	B1A09
42.80	42.80	44.00	45.70	58.80	60.10	52.10	B1A11
48.00	48.60	41.10	45.70	48.50	55.70	39.20	B1A12
48.90	50.20	48.90	49.60	49.70	51.50	39.10	B1A13
45.00	46.50	47.30	48.70	47.80	52.20	31.40	B1A14
45.90	48.00	48.00	49.00	46.90	49.30	40.70	B1A15
44.10	46.20	47.10	48.40	47.00	54.40	46.90	B1A16
47.10	48.20	46.40	52.40	49.30	59.20	52.50	B1A17
45.10	45.70	45.50	51.40	57.80	59.00	56.50	B1A18
46.50	47.80	45.30	50.90	61.90	60.90	52.80	B1A19
40.50	44.40	45.10	46.60	55.70	57.90	57.70	B1A20
43.40	44.00	45.80	47.70	58.50	51.50	56.70	B1A21
47.90	47.90	52.70	50.10	52.10	60.70	55.00	B1A22
54.50	49.10	42.80	45.90	47.20	58.90	52.50	B2A01
54.40	50.00	47.90	50.10	53.20	56.70	44.60	B2A02
57.20	56.10	56.30	57.60	60.20	60.50	31.90	B2A03
56.20	56.70	56.20	56.40	58.00	60.60	28.50	B2A04
48.00	49.80	53.10	57.50	57.50	57.90	52.80	B2A05
52.00	53.80	58.20	54.90	59.50	57.50	54.80	B2A06
56.70	56.50	48.60	58.70	61.10	55.10	53.70	B2A08
54.80	54.60	51.90	55.50	59.70	56.30	56.90	B2A09
53.60	54.50	53.50	56.60	58.20	57.10	59.20	B2A10
52.60	55.00	64.70	54.70	56.40	56.10	56.20	B2A11
51.90	51.90	48.60	49.30	49.10	56.00	58.70	B2A12
59.90	55.40	53.60	52.20	52.10	56.30	59.40	B2A13
62.80	61.10	61.00	62.20	61.50	61.40	64.50	B2A14
54.00	54.00	60.80	62.40	62.50	59.50	57.40	B2A15
56.90	58.10	61.50	58.10	64.20	65.50	61.40	B2A16
62.10	63.20	62.90	60.60	64.00	62.20	59.10	B2A17
61.60	61.10	59.80	60.30	61.80	58.20	55.20	B2A18
61.70	60.70	53.10	61.20	61.70	58.40	55.10	B2A19
61.00	60.40	55.00	62.10	63.10	57.70	57.10	B2A20
61.40	61.30	60.40	59.60	56.90	55.30	59.90	B2A21
61.70	62.20	66.30	60.40	54.50	54.30	56.30	B2A22
54.60	54.60	56.80	50.30	50.00	53.20	50.70	B3A01
56.20	56.20	55.90	51.50	51.90	59.50	53.60	B3A02
57.30	56.20	57.70	56.10	56.90	61.50	63.20	B3A03
57.30	56.80	57.40	57.40	63.30	63.40	61.80	B3A04
56.90	57.00	55.70	56.70	65.10	57.60	58.20	B3A05

silt10	silt20	silt30	silt40	silt60	silt80	silt100	plotcode
58.10	58.90	57.40	59.60	63.20	58.30	53.20	B3A06
61.90	62.50	62.70	63.20	61.30	59.60	47.20	B3A07
61.30	59.50	61.60	62.60	60.50	56.30	46.60	B3A08
66.60	63.80	59.40	65.60	60.40	54.30	53.00	B3A09
62.60	62.10	63.90	63.80	60.50	59.10	57.00	B3A11
64.20	63.70	63.10	61.20	59.80	60.30	62.20	B3A12
65.30	65.30	61.10	64.90	63.70	64.20	67.70	B3A13
59.40	59.40	61.00	64.00	64.80	64.00	65.20	B3A14
56.80	56.80	56.80	60.70	64.90	57.80	62.70	B3A15
58.20	58.20	57.00	60.40	63.80	64.60	58.90	B3A16
57.10	57.10	57.00	59.00	65.30	61.40	54.10	B3A17
61.20	61.70	62.70	58.70	63.30	59.10	47.30	B3A19
66.00	64.20	62.20	64.60	59.00	57.50	44.50	B3A20
63.50	60.70	60.40	63.00	59.30	53.80	48.40	B3A21
61.20	60.00	61.80	66.50	57.70	53.90	55.60	B3A22
65.70	65.40	61.50	63.40	59.90	61.80	62.10	B3A23
64.80	64.90	63.20	61.90	59.50	62.70	64.00	B3A24
56.80	56.80	66.50	64.90	71.20	61.60	60.70	B4A01
57.70	57.70	66.50	70.80	67.20	66.00	59.90	B4A02
60.60	60.60	65.80	67.40	67.00	68.30	56.10	B4A03
62.00	62.00	58.80	63.60	66.20	66.80	51.10	B4A04
60.10	60.10	68.40	68.90	72.40	60.50	61.80	B4A06
63.70	63.70	67.30	70.30	66.90	68.30	60.20	B4A07
62.90	62.90	65.30	68.40	68.10	65.60	60.50	B4A08
64.30	64.30	64.70	69.50	73.90	67.70	64.40	B4A09
66.00	66.00	69.70	75.30	68.90	69.20	68.60	B4A10
66.90	66.90	69.70	72.80	69.10	70.30	68.40	B4A11
65.40	65.40	69.30	70.00	67.30	67.40	69.80	B4A12
60.50	60.50	66.10	72.50	72.50	66.10	65.70	B4A13
67.60	67.60	69.30	72.90	67.60	66.30	68.80	B4A14
67.20	67.20	68.10	71.80	69.40	71.30	72.50	B4A15
67.80	67.80	67.30	69.80	67.20	71.00	67.30	B4A16
69.90	69.90	69.90	63.60	73.10	67.70	65.50	B4A17
71.30	71.30	69.00	69.40	71.20	71.10	70.60	B4A18
70.00	70.00	66.70	70.30	72.80	69.40	74.80	B4A19
70.00	70.00	67.80	67.50	69.80	73.20	76.10	B4A20
67.70	67.70	66.50	66.40	72.30	67.00	63.60	B4A21
70.90	70.90	68.40	63.00	71.90	70.80	70.30	B4A22
68.70	68.70	68.40	68.60	71.30	76.50	69.00	B4A23

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Curriculum vitae

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Eduaction

09/1994-07/2002	Albert-Schweitzer-Gymnasium 7 in Erfurt, Degree: General qualification for university entrance
08/2002-07/2005	Apprenticeship as a survey technician, Erfurt

Scientific Career

11/2010-11/2013	PhD student at the Friedrich-Schiller University Jena under the supervision of Jun.-Prof- Anke Hildebrandt
PhD Thesis:	"*Does ecosystem diversity affect soil hydraulic properties? Investigation of the biotic and abiotic factors on Infiltration capacity in a grassland biodiversity experiment"*
10/2005-09/2010	Study of Biology at the Friedrich-Schiller-University Jena, Germany
Diploma thesis:	„*Regulation of Jasmonic acid and12-Oxophytodienacid (OPDA) release upon herbivory in A.thaliana*"

Work experience

10/2009-02/2010	Tutor for Mathematics and tatistics for Biologists at the Friedrich-Schiller-
und 10/2008-02/2009	University Jena, Germany
03/2009-08/2009	Student research assistant for interactions between *Nicotiana attenuata* and Mykorrhiza at the Max-Planck-Institut for chemical ecology, Jena
09/2007	Student research assistant in the working group „Multitrophische Interaktionen" at the institute for ecology, Jena
04/2007-06/2007	Student research assistant for field work at The Jena Experiment field site

Further Qualifications

08.07.2013	Course: "Structural Equation Modelling-A gentle introduction", Graduierten Akademie, Jena

26.11.2012	Course: “How to deal with missingness?-Analysis of incomplete datasets”, Graduierten Akademie, Jena
16.-18.04.2012	Course: Introduction to Biodiversity Sciences (basic and applied plant and animal biology/ecology)-Higrade
30.01.-2.02.2012	Course: Ecological data evaluation (R), Higrade
02.-07.10.2011	Summer School on Flow and Transport in Terrestrial Systems, Heidelberg
10.-11.05.2011	Course: Multivariate statistics using R –Higrade
14.-18.03.2011	Course: Applied Statistics and Data Analysis-Higrade
30.03.-01.04./2011	Introduction to Hydrological Processes, Water Resources Management and Aquatic Ecosystems (2011)-Higrade
14.-18.03.2011	Course: Applied Statistics and Data Analysis, International Max Planck Research School for Global Biochemical Cycles (IMPRS), Jena
30.04./07.05.2010	Courses Statistics in a nutshell: Design and Analysis of Experiments (I); Questionnaires and Surveys (II), Graduierten Akademie , Jena
03/2008	Traineeship: „Praktische Einführung in GPS und GIS“ at the Institute for ecology, Jena
08/2007	Traineeship at the Verein zur Förderung der ökologischen Bildung e.V., Erfurt

Other skills and interests

Seit 2012	Board member in the choir Chorissimo, Jena
2007 bis heute	Singer in the choir Chorissimo, Jena
2003-2005	voluntary danceteacher (CVJM)
2000-2005	volunteer at the CVJM choir (Christlicher Verein Junger Menschen), Erfurt

Awards

2013	First place for Poster Award with the title "Key soil and plant community characteristics govering soil hydraulic properties in a grassland biodiversity experiment" at the Biohydrology Conference at the University Koblenz-Landau.

Publications

Schäfer, M., Fischer, C., Meldau, S., Seebald, E., Oelmüller, R., Baldwin, I. T. (2011). Lipase activity in insect oral secretions mediates defense responses in Arabidopsis thaliana. Plant Physiology.

Schäfer, M.,Fischer, C., Baldwin, I.T. and Meldau, S. (2011). Grasshopper oral secretions increase salicylic acid and abscic acid levels in wounded leaves of Arabidopsis thaliana. Plant signaling & Behaviour.

In Preparation

Fischer, C., Roscher, C., Jensen, B.,Eisenhauer, E., Baade, J. Attinger, A.,Scheu, S., Weisser, W.W., Hildebrandt, A.(in prep.). How do earthworm, soil texture and plant composition affect infiltration in managed grasslands along a plant diversity gradient?

Fischer, C. Tischer,J., Roscher,C., Eisenhauer, N., Raveneck, J., Gleixner, G. Attinger, S., Jensen, B. , de Kroon, H., Mommer, L., Hildebrandt, A.(in prep.). Soil and plant community characteristics governing soil hydraulic properties in a grassland biodiversity experiment.

Posters

Fischer, C., Roscher, C., Merkel, B.,Eisenhauer, E., Baade, J. Attinger, A.,Scheu, S., Hildebrandt, A.(2012). Infiltration capacity as affected by soil texture, plant community composition and earthworms in a grassland plant diversity experiment. Eurosoil (Bari, Italy).

Fischer, C. Tischer,J., Roscher,C., Eisenhauer, N., Raveneck, J., Gleixner, G. Attinger, S., Jensen, B. , de Kroon, H., Mommer, L., Hildebrandt, A.(2013). Key soil and plant community characteristics govering soil hydraulic properties in a grassland biodiversity experiment. Biohydrology (Landau, Germany).

Presentations

Fischer, C., Roscher, C., Jensen, B.,Eisenhauer, E., Baade, J. Attinger, A.,Scheu, S., Hildebrandt, A.(2012) How do soil texture, plant community composition and earthworms affected the Infiltration capacity in a grassland plant diversity experiment depending on season? EGU (Vienna, Austria).

Fischer, C. Tischer,J., Roscher,C., Eisenhauer, N., Raveneck, J., Gleixner, G. Attinger, S., Jensen, B. , de Kroon, H., Mommer, L., Hildebrandt, A. (2013) Factors affecting Infiltration capacity in a grassland plant diversity experiment, MPI for biogeochemistry colloquium (Jena, Germany).

Fischer, C., Roscher, C., Jensen, B., Eisenhauer, E., Baade, J. Attinger, A.,Scheu, S., Weisser, W.W., Hildebrandt, A.(2013) What factors influence water infiltration through soil? HIGRADE fall conference (Leizig, Germany).

Supervisions

Julia Kästner (2011) Infiltration capacity as affected by soil texture, plant community composition and earthworms in a grassland plant diversity experiment. Praktikumsbericht, Friedrich-Schiller-Universität Jena.

Jana Tischer (2012) Zusammenhang zwischen Bodeneigenschaften und Biodiversität. Projektbericht, Friedrich-Schiller-Universität Jena.

Wenke Stoll (2013) Vergleich von FDR- und TDR- Sonden zur Bestimmung des Bodenwassergehaltes auf dem Jena Biodiversitätsexperiment. Bachelor thesis, Friedrich-Schiller-Universität Jena.

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Ort, Datum Christine Fischer

Selbständigkeitserklärung

Ich erkläre, dass ich die vorliegende Dissertation selbständig und nur unter Verwendung der angebenen Hilfmittel, persönlichen Mitteilungen und Quellen angefertigt habe.

Ort, Datum

Christine Fischer