Termites and Ants in Burkina Faso (West Africa)

- Taxonomic and functional diversity along land-use gradients

- Ecosystem services of termites in the traditional Zaï system

Dissertation zur Erlangung des

naturwissenschaftlichen Doktorgrades

der Julius-Maximilians-Universität Würzburg

vorgelegt von

Dorkas Tabitha Kaiser

geboren in Stuttgart

Würzburg 2014

Eingereicht am:

Mitglieder der Promotionskommission:

Vorsitzender: Prof. Dr. Thomas Dandekar

Gutachter: Prof. Dr. K. Eduard Linsenmair

Gutachter: Prof. Dr. Souleymane Konaté

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Doktorurkunde ausgehändigt am:

To my family

especially my mother Margot Kaiser-Braue
my husband Bernd Helle
and my aunt Doris Jahn-Kotzem

In Hamburg lebten zwei Ameisen,
Die wollten nach Australien reisen.
Bei Altona auf der Chaussee
Da taten ihnen die Beine weh,
Und da verzichteten sie weise
Dann auf den letzten Teil der Reise.

Joachim Ringelnatz (1883–1934)

ZUSAMMENFASSUNG

Die Folgen von Lebensraumveränderungen für die Lebensqualität der Bevölkerung sind vermutlich besonders extrem in Burkina Faso. Das Land liegt in einem für Dürren sehr anfälligen Gebiet von Westafrika. Die Kleinbauern, welche die Hauptproduzenten für Lebensmittel der Region sind, können besonders betroffen sein, wenn Verluste der biologischen Vielfalt zu Veränderungen in den Ökosystemfunktionen führen, da viele von degradierten Flächen für die landwirtschaftliche Produktion abhängen.

Das Hauptziel der vorliegenden Arbeit war daher, die funktionellen Merkmale derjenigen Bodenorganismen zu charakterisieren, die im Untersuchungsgebiet von entscheidender Bedeutung für ertragreiche und ausgewogene Böden sind: Termiten und Ameisen. Sie sind wahre Ökosystem-Ingenieure, deren Aktivität den Lebensraum verändert. Durch Bodenumwälzung während des Baus von biogenen Strukturen unterschiedlicher Größe und Natur (Hügel, Nester, unterirdischer Gänge, Schutzschichten aus Erde, sogenannte „soil-sheetings“, Furagierlöcher, etc.) bewegen sie riesige Bodenmassen und haben enorme Auswirkungen auf die Bodenstruktur. Dies wirkt sich wiederrum positiv auf die Bodenfruchtbarkeit, die Stabilität, die Bodenbelüftung und die Wasserinfiltration aus, und bietet so auch Lebensraum für andere Arten. In den afrikanischen Ländern südlich der Sahara sind Ameisen und Termiten die einzige nennenswerte aktive Bodenmakrofauna während des gesamten Jahres. In der Sub-Sahelregion von Burkina Faso sind während der Trockenzeit Termiten die einzigen aktiven Primärzersetzer. Da keine Informationen über den Artenreichtum der Termiten- und Ameisen-Fauna in Burkina Faso vorlagen, setzte ich in der Dissertation zwei Schwerpunkte: Im ersten Teil, einer Grundlagenstudie, erfasste ich die lokale Termiten und Ameisenfauna in verschiedenen Landnutzungssystemen und untersuchte deren quantitative und qualitative Reaktion auf sich ändernde Umweltbedingungen, die aus dem zunehmenden Einfluss des Menschen resultieren ("funktionelle Reaktionsmerkmale"). Im zweiten und anwendungsbezogenen Teil befasste ich mich mit dem Einfluss der für die Regeneration degradierter Böden wichtigen biogenen Strukturen ("funktionelle Wirkungsmerkmale").

Es wurden zwei für die Untersuchungsregion typische traditionelle Landwirtschaftsformen ausgewählt. Jede stellte einen Landnutzungsgradienten dar, der vier verschiedene Habitate umfasste, welche sich in der Stärke des anthropogenen Einflusses unterschieden, ursprünglich aber den gleichen Anfangszustand hatten. Der erste Nutzungsgradient in Ouahigouya (Provinz Yatenga, Sub-Sahel-Zone) – namens Zaï – war ein zeitlicher Querschnitt durch eine traditionelle Boden- und Wasserschutztechnik zur Regeneration stark verkrusteter, degradierter Böden. Der zweite Nutzungsgradient nahe der Stadt Fada N’Gourma (Provinz Gourma, Nord-Sudan Region) war ein Landwirtschaftstyp, der Fruchtfolge und Brachzeiten für das Nährstoffmanagement nutzte.

Zur Erhebung der Termiten- und Ameisen-Diversität in semi-ariden (Agrar-) Ökosystemen existierte kein Standardprotokoll; zwei international akzeptierte Protokolle bildeten die Grundlage für das neu überarbeitete und kombinierte Protokoll „RAP“ zur schnellen Erhebung der Termiten- und Ameisenfauna: Das ALL-Protokoll für Ameisen der Laubstreuschicht von Agosti and Alonso (2000) und das Transektprotokoll für Termiten in tropischen Wäldern von Jones and Eggleton (2000). In meiner Untersuchung wurden zwischen 2004 und 2008 während der Regenzeit in jedem der Untersuchungsgebiete drei bis vier Transekte abgesammelt.

Das RAP-Protokoll erwies sich als sehr effektive Methode, um die taxonomische und funktionelle Vielfalt von Termiten und Ameisen zu beschreiben, zu vergleichen und zu überwachen. Zwischen 70% und 90% der geschätzten Gesamtartenzahl wurden auf allen Ebenen (Transekte, Lebensräume, Regionen) gesammelt.

Insgesamt wurden in beiden Regionen 65 Ameisenarten (25 Gattungen) und 39 Termitenarten (13 Gattungen) gesammelt. Dies sind bislang die ersten Nachweise für Burkina Faso. Die Daten weisen auf eine hohe Sensitivität von Termiten und Ameisen gegenüber einer Landnutzungsintensivierung hin. Mit zunehmendem anthropogenem Einfluss nahm die Artenvielfalt in der Nord-Sudanregion stark zu. Insgesamt wurden 53 Ameisenarten (23 Gattungen) und 31 Termitenarten (12 Gattungen) gefunden. Sehr vielversprechende Ergebnisse wurden bezüglich des Erholungspotenzials der Bodenarthropoden-Diversität im Zaï-System gesammelt; die Vielfalt beider Taxa nahm in mit zunehmender Lebensraumsanierung stark zu: Insgesamt wurden 41 Ameisenarten (16 Gattungen) und 33 Termitenarten (11 Gattungen) dieser Region gefunden. Entlang der Landnutzungsgradienten zeigten sich signifikante Unterschiede im Vorkommen von Termiten und Ameisen. So bewiesen bei Termiten beispielsweise die Pilzzüchter die größte Anpassungsfähigkeit an die unterschiedlichen Bewirtschaftungspraktiken. Die größten Unterschiede zwischen den Lebensräumen wurden bei den boden- und den grasfressenden Termiten beobachtet. In stark vom Menschen beeinflussten Lebensräumen fehlten ganze funktionelle Gruppen, beispielsweise kamen in der degradierten Fläche der Sub-Sahelregion weder Bodenfresser noch Grasfresser oder Holzfresser vor. Mehrere Umweltparameter wurden identifiziert, welche einen großen Teil der Veränderungen in der Zusammensetzung der Arthropoden-Gemeinschaften entlang der Gradienten signifikant erklärten; sie lassen auf eine große Bedeutung der strukturellen Habitat-Komplexität (Vegetationsstruktur) und den damit verbundenen mikroklimatischen Schwankungen (Temperatur- und Feuchtigkeit), der Nahrungsverfügbarkeit und der Bodenstruktur schließen. Die Termitenvielfalt in der Sub-Sahelzone korrelierte stark mit dem Überschirmungsgrad, dem Sandgehalt im Oberboden und der Verfügbarkeit von Streu. Ihre Vielfalt in der Nord-Sudanregion korrelierte stark mit der kumulierten Gehölzpflanzen-Grundfläche, dem Tongehalt und dem organischen Material im Oberboden. Die identifizierten Parameter für die Ameisen-Gemeinschaften im Zaï-System waren die Höhe der Bäume, der Sandgehalt im Oberboden und die Luftfeuchte. Ihre Vielfalt in der Nord-Sudanregion korrelierte stark mit dem Überschirmungsgrad, dem Trockengewicht der verfügbaren Streu und der Baumhöhe.

Um die relative Bedeutung von Termiten und Ameisen für die Bodenumwälzung beurteilen zu können, erfasste ich im zweiten Teil der Arbeit zunächst die natürlichen Schwankungen im Trockengewicht der in jedem Untersuchungsgebiet oberirdisch vorhandenen biogenen Strukturen.

Die Ergebnisse veranschaulichen eindrucksvoll, dass:

1. Termiten in allen Untersuchungsgebieten die Hauptumwälzer, Ameisenstrukturen dagegen von untergeordneter Bedeutung für die Bioturbation waren;
2. Regenwürmer und grasfressende Termiten in der regenreicheren Nord-Sudanregion wesentlich zur Bodenumwälzung beitrugen;
3. die Gesamtmasse der umgewälzten Erde von Jahr zu Jahr schwankte, die relative Bedeutung beider Taxa für die Bioturbation jedoch ziemlich konstant war;

4. in der Sub-Sahelzone die wichtige Funktion der Bodenumwälzung vollständig von pilzzüchtenden *Macrotermes*- und *Odontotermes*-Arten übernommen wird, die zusammen große Mengen von feinkörnigem Bodenmaterial an die Oberfläche transportieren. Dadurch sank mit zunehmender Habitat-Rehabilitation der Gehalt an grobkörnigem Bodenmaterial in den oberen Bodenschichten und reicherte sich zunehmend in den tieferen Horizonten an.

Im anwendungsbezogen Teil der Arbeit konzentrierte ich mich daher auf die Bioturbationsleistung pilzzüchtender Termiten in den vier Hauptstadien des Zaï-Systems: der degradierten Fläche (Ausgangsstadium der vier Sukzessionsstadien), dem Hirsefeld, dem jungen und dem alten Zaï-Wald. In jedem dieser vier Sukzessionsstadien wurde die Furagiertätigkeit von pilzzüchtenden Termiten folgendermaßen angeregt: Es wurden neun Versuchsblöcke installiert, mit je vier Unterquadraten mit einer Fläche von 1 m^2. Drei der Unterquadrate wurde mit unterschiedlichen, lokal verfügbaren organischen Materialien bedeckt (mit *Aristida kerstingii* Stroh, *Bombax costatum* Holz, Kompost), eines blieb als Kontrolle ohne organisches Material. Das vierwöchige Experiment wurde zweimal durchgeführt (Regenzeit 2005, Trockenzeit 2006). Dabei wurden die Untersuchungsflächen regelmäßig auf Termitenaktivität überprüft und die Zunahme der "soil-sheetings" kartiert.

Nach vier Wochen wurde:

i. Die gesamte Termitenerde gesammelt, luftgetrocknet und für jede Gattung getrennt gewogen;
ii. die Furagierlöcher gezählt und ihr Durchmesser vermessen;
iii. in ausgewählten Flächen die Wasserinfiltrationsrate gemessen;
iv. die physikalisch-chemischen Eigenschaften der Sheeting-Erde analysiert.

Sobald das Stroh in einem Unterquadrat abgetragen war, wurde nach den betreffenden Messungen (s. oben i. und ii.) neues aufgebracht.

Der Vergleich der Ergebnisse beider Durchläufe zeigte deutlich, dass Stroh der attraktivste Köder war. Für jedes Gramm abgetragenes Stroh wurden von *Odontotermes* etwa 12 g, von *Macrotermes* etwa 4 g Erde an die Oberfläche gebracht. *Odontotermes* war die einzige Gattung, die in der degradierten Fläche von organischem Material angelockt wurde. Sie ist damit der entscheidende primäre physikalische Ökosystem-Ingenieur im Zaï-System, der den Restaurierungsprozess anstößt. Mit zunehmender Habitatsanierung nahm die Menge der umgewälzten Erde stark zu: In den 36 Unterquadraten der degradierten Fläche bewegte *Odontotermes* insgesamt 31,8 Tonnen Erde pro Hektar und Monat Trockenzeit, in denen der Hirsefelder insgesamt 32,4 Tonnen. Beide Gattungen zusammen bewegten im jungen Zaï-Wald insgesamt 138,9 Tonnen, im alten Wald 215,5 Tonnen Erde pro Hektar und Monat Trockenzeit. In jedem Sukzessionsstadium waren sowohl die Bodenumwälzung als auch die Anzahl der Furagierlöcher in den Versuchsflächen mit Stroh am größten, gefolgt von denen mit Kompost, dann denen mit Holz und zuletzt den Kontrollflächen. Die Furagiertätigkeit der pilzzüchtenden Termiten führte zu einer starken Zunahme der Makroporosität des Oberbodens. Nach einem Monat induzierter Fraßaktivität stieg im Mittel die Anzahl der Furagierlöcher pro Quadratmeter von 142 in der degradierten Fläche auf 921 Löcher im alten Zaï Wald. Die bei der Nahrungssuche gegrabenen Gänge und Löcher führten zu einem signifikanten Anstieg der Wasserinfiltrationsrate, im Mittel um den Faktor 2–4. Nur wenige vergleichbare Zahlen konnten in der Literatur gefunden werden. Bei den Untersuchungen von Mando and Miedema (1997) im Norden von Burkina Faso wälzten die beiden Gattungen nach Mulchen mit einem Holz-Stroh-Gemisch Sheetings mit einem Trockengewicht von insgesamt 20 Tonnen je Hektar und Monat Trockenzeit um. Im Senegal wurden in Versuchsflächen mit starker Furagieraktivität rund 10 Tonnen Erde bewegt (Rouland et al. 2003).

Laboranalysen ergaben, dass sich Sheeting-Erde stark sowohl von der entsprechenden Kontroll-Erde unterschied als auch dem überdeckten Futtertyp und ebenso zwischen den beiden Gattungen. Dabei unterschied sich Sheeting-Erde von *Odontotermes* in mehr Parametern als Sheeting-Erde von *Macrotermes*, und Sheetings aus der Trockenzeit unterschieden sich in mehreren Parametern und in stärkerem Maße als Sheetings aus der Regenzeit. Der Gehalt an organischem Material, an Kohlenstoff und Stickstoff war in allen Trockenzeit-Sheetings deutlich erhöht, in der Regenzeit vor allem in Sheetings, die über Kompost gebaut wurden. Die Analyse der Korngrößenverteilung ließ darauf schließen, dass beide Gattungen Erde aus dem Oberboden und aus tieferen Horizonten in unterschiedlichen Mischungsverhältnissen nutzten. Dies bestätigt Beobachtungen von Jouquet et al. (2006).

Zusammenfassend lässt sich sagen, dass die vorliegende Untersuchung zu einem besseren Verständnis der funktionellen Reaktionsmerkmale von Termiten und Ameisen auf sich ändernde Umweltparameter beiträgt, die aus dem zunehmenden Einfluss des Menschen resultieren. Das RAP-Protokoll erwies sich als eine einfach zu erlernende und sehr effektive Methode, um die taxonomische und funktionelle Vielfalt von Termiten und Ameisen in semi-ariden Savannen und Agrarökosystemen repräsentativ zu charakterisieren, zu vergleichen und zu überwachen. Das Experiment erbrachte schlüssige Beweise für die Bedeutung pilzzüchtender Termiten (insbesondere *Odontotermes* und *Macrotermes*-Arten) für die Sanierung vollständig degradierter und verkrusteter Böden, und für eine nachhaltige landwirtschaftliche Produktion in der Sub-Sahelzone in Westafrika.

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ABSTRACT

The consequences of habitat change for human well-being are assumed to be especially extreme in Burkina Faso. The country is located in a highly drought-sensitive zone of West Africa, and small-scale subsistence farmers may be especially affected if losses of biodiversity lead to changes in ecosystem functioning; many depend on more or less degraded lands for agricultural production.

The overall aim of the present thesis consequently was to characterize the functional traits of soil-organisms which are crucial for a productive and balanced soil environment in the study region – termites and ants. They are true ecosystem engineers whose activity alters the habitat. Through soil-turnover in the course of constructing biogenic structures of varying size and nature (mounds, nests, galleries, soil-sheetings, foraging-holes), they bioturbate huge amounts of soil masses and exert massive effects on soil structure, positively influencing the fertility, stability, aeration and water infiltration rate into soils; and they provide habitats for other species. In sub-Saharan Africa, ants and termites are the only active soil macrofauna during the long dry season; in the sub-Sahel zone of Burkina Faso, termites even represent the only active, quantitatively remarkable decomposers all year round. Since no information was available about the actual diversity of the focal arthropods, I divided the thesis in two main parts: In the first part, a baseline study, I assessed the local termite and ant fauna, and investigated their quantitative and qualitative response to changing habitat parameters resulting from increasing human impact (‘functional response traits’). In the second and applied part, I addressed the impact of the biogenic structures which are important for the restoration of degraded soils (‘functional effect traits’).

Two traditional agricultural systems characteristic for the study region were selected. Each system represented a land-use intensification gradient comprising four distinct habitats now differing in the magnitude of human intervention but formerly having the same initial state. The first disturbance gradient, the temporal cross-section of a traditional soil water conservation technique to restore degraded heavily encrusted, barren soil named Zaï in Ouahigouya (Yatenga province, sub-Sahel zone); the second disturbance gradient, an agriculture type using crop rotation and fallow as nutrient management techniques near Fada N’Gourma (Gourma province, North-Sudanese zone).

No standard protocol existed for the assessment of termite and ant diversity in semi-arid (agro-) ecosystems; two widely accepted standard protocols provided the basis for the newly revised and combined rapid assessment protocol ‘RAP’: the ALL protocol for leaf litter ants of Agosti and Alonso (2000), and the transect protocol for termites in tropical forests of Jones and Eggleton (2000). In each study site, three to four replicate transects were conducted during the rainy seasons (2004—2008).

The RAP-protocol turned out to be very effective to characterize, compare and monitor the taxonomic and functional diversity of termites and ants; between 70% and 90% of the estimated total species richness were collected on all levels (transects, habitats, regions). Together in both regions, 65 ant species (25 genera) and 39 termite species (13 genera) were collected. These findings represent the first records for Burkina Faso. The data indicate a high sensitivity of termites and ants to land-use intensification. The diversity strongly decreased with increasing anthropogenic impact in the North-Sudan region. In total, 53 ant species (23 genera) and 31 termite species (12 genera) were found. Very promising results concerning the recovery potential of the soil-arthropods’ diversity were gathered in the Zaï system. The diversity of both taxa strongly increased with increasing habitat rehabilitation – in total, 41 ant species (16 genera) and 33 termite species (11 genera) were collected. For both taxa significant differences could be noted in the shape of the density variations along the gradient. For instance termites: Fungus-growers showed the greatest adaptability to different management practices. The greatest variations between the habitats were observed in soil and grass-feeding termites. Whole functional groups were missing in heavily impacted habitats, e.g. soil-, grass-, and wood-feeders were absent in the degraded site in the sub-Sahel zone. Several environmental parameters could be identified which significantly explained a great part of the variations in the composition of the arthropods' communities; they indicate the importance of the habitats' structural complexity (vegetation structure) and concomitant effects on diurnal temperature and moisture fluctuations, the availability of food sources, and the soil-structure. The diversity of termites in the sub-Sahel region was strongly correlated with the crown-cover percentages, the topsoils' sand-content, and the availability of litter; in the North-Sudan region with the cumulated woody plant basal area, the topsoils' clay- and organic matter-content. The parameters identified for ant communities in the Zaï system, were the height of trees, the topsoils' clay-content and air humidity; in the North-Sudan region the habitats' crown-cover percentages, the quantity of litter and again the height of trees.

In the second part of the thesis, I first rapidly assessed the (natural) variations in the amount of epigeal soil-structures along the two disturbance gradients in order to judge the relative importance of termites and ants for soil-turnover. The results illustrated impressively that a) in all study sites, termites were the main bioturbators while ant structures were of minor importance for soil turn-over; b) earthworms and grass-feeding termites contributed significantly to soil turn-over in the more humid North-Sudan region; and c) the bioturbated soil mass varied between seasons and years, however, the relative importance of the different taxa seemed to be fairly constant. In the sub-Sahel zone, fungus-growing *Odontotermes* and *Macrotermes* species fully take over the important function of bioturbation, leading to the transport of huge amounts of fine-textured soil material to the surface; with increasing habitat restoration, coarse fragments decreased in the upper horizons and became concentrated deeper along the soil profile.

Consequently, in the applied part, I concentrated on the bioturbation activity of fungus-growing termites in the four main stages of the Zaï system: crusted bare soil (initial stage), millet field, young and old forest. In each of the four Zaï sites nine experimental blocks (each comprising four plots of $1m^2$) were used to stimulate the foraging activity of fungus-growing termites with different, locally available organic materials (*Aristida kerstingii* hay, *Bombax costatum* wooden blocks, compost and a control without any organic amendment). The experiment was conducted twice for the duration of four weeks (rainy season 2005, dry season 2006). The plots were regularly checked and the increase of the area covered by sheetings chronologically followed. After four weeks a) all sheeting-soil was collected, air dried and separately weighed according to the different genera, and b) the foraging-holes were counted and their diameter measured. Additionally, c) ponded water infiltration was measured in selected plots, and d) the physicochemical properties of sheeting-soil were analyzed. In case of complete consumption of the offered hay during the experimental 4-weeks-duration, the same procedure (a, b) was followed before adding new hay to the respective plot.

The comparison between the different plots, sites and seasons revealed clearly that hay was the most attractive bait; for each gram of hay removed, *Odontotermes* brought about 12 g soil to the surface, *Macrotermes* 4 g. *Odontotermes* was the only genus attracted by organic material to the degraded area, and was therefore the decisive primary physical ecosystem engineer in the Zaï system, initiating the restoration process. The mass of soil bioturbated in the course of foraging increased strongly from the degraded, barren towards the most rehabilitated reforested site. Combining all 36 experimental plots per Zaï stage, *Odontotermes* bioturbated 31.8 tons of soil per hectare and month dry season in the degraded area, and 32.4 tons ha^{-1} mon^{-1} in the millet fields; both genera moved 138.9 tons ha^{-1} mon^{-1} in the young and 215.5 tons ha^{-1} mon^{-1} in the old Zaï forest. Few comparable figures were found in the literature. In northern Burkina Faso, both genera constructed 20 tons of sheetings ha^{-1} mon^{-1} after mulching with a straw-wood mixture (Mando & Miedema 1997), and in Senegal, around 10 tons ha^{-1} mon^{-1} were moved in heavily foraged plots (Rouland et al. 2003). Within a site, soil turn-over and the number of foraging holes created was always highest in hay, followed by compost, then by wood and in the end control. The fungus-growers' foraging-activity was leading to an enormous increase in surface pore space – after one month of induced foraging activity in hay-plots, the median number of foraging-holes increased from 142 m^{-2} in the degraded site up to 921 m^{-2} in the old Zaï forest. The creation of subterranean galleries and macropores significantly increased the water infiltration rate by a mean factor 2–4.

Laboratory analyses revealed that sheeting-soil differed strongly from the respective control soil as well as between the seasons, the food-type covered, and the two genera. *Odontotermes*-sheetings differed in more parameters than *Macrotermes*-sheetings, and dry season sheetings differed in more parameters (and more strongly) than rainy season sheetings. In the present study, soil organic matter, carbon and nitrogen contents were significantly increased in all dry season sheetings; in the rainy season mainly in those built on compost. Texture analysis pointed out that both genera used topsoil and soil from deeper horizons in varying mixture ratios, thereby supporting findings of Jouquet et al. (2006).

To summarize, the present thesis contributes to a better understanding of the functional response traits of termites and ants to changing environmental parameters resulting from increasing human impact. The RAP-protocol represents an easy-to-learn and very effective method to representatively characterize, compare and monitor the taxonomic and functional diversity of termites and ants. The experiment has provided conclusive evidence of the importance of the consideration of fungus-growing termites (particularly *Odontotermes* and *Macrotermes* species) when aiming to restore infertile, degraded and crusted soils and to maintain a sustainable agricultural production in the Sahel-Sudanese zone of West Africa.

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1 GENERAL INTRODUCTION AND STUDY OUTLINE

This first chapter provides an overview on the broader context and summarizes the current state of knowledge of the topics dealt with in this thesis. I then name the main study aims, I introduce the interdisciplinary research project 'BIOTA West Africa' within the framework of which the present study was conducted and end with a short outline of the subsequent chapters.

1.1. THEMATIC BACKGROUND

The anthropogenic footprint on ecosystems and biodiversity is more notable now than at any other point in history (Millennium Ecosystem Assessment 2005). Human activities are changing the environment on local and global scales, thereby affecting both managed and unmanaged ecosystems (e.g. Millennium Ecosystem Assessment 2005; Pimentel et al. 1992). Many of these changes can have dramatic consequences for ecosystem properties, the biotic structure, the composition of ecological communities and ecosystem functioning (e.g. Cardinale et al. 2012; Geissen et al. 2009; Hooper et al. 2005; Marquard et al. 2009; Mujeeb Rahman et al. 2011; Winqvist et al. 2011). Today, the fastest changes are taking place in developing countries.

Agricultural processes are thereby particularly affecting ecosystems (Millennium Ecosystem Assessment 2005) and have been a leading cause of loss of global biodiversity (Green et al. 2005). However, crop production will even have to increase by 70%–100% until 2050 to meet the growing food and feed demand driven by human population growth (FAO 2009; Godfray et al. 2010). At the same time, food producers are experiencing greater competition for land, water, and energy resources, and the urgent requirement to increase soil fertility and the sustainability of agricultural production (Godfray et al. 2010; National Research Council 2010; Pretty et al. 2010).

Particularly existential are the consequences in sub-Saharan Africa (SSA) where millions of people depend on agriculture for their livelihoods and where the agricultural productivity in general is especially low (Batjes 2001). As a result, vast areas in the Sahel-Sudanese zones of West Africa already became converted into infertile, crusted barren soils. The problem of land degradation – defined as a long-term decline in ecosystem function and measured in terms of net primary productivity – increases worldwide (Bai et al. 2008). It was estimated that 65% of SSA's agricultural land is degraded (Brady 1990). However, the opinions about the accuracy of the numbers and the correctness of the methodology followed to assess the global and local status of degradation vary greatly (e.g Mazzucato & Niemeijer 2001; Somé et al. 1992).

The causes of land degradation are many – among the most important factors are overgrazing, combined with unsustainable agriculture and climatic variability (http://www.cbd.int/). These various impacts interact in a complex and sometimes unpredictable way. Arid, semi-arid and dry lands are particularly prone to the ravages of desertification. According to the 'United Nations Environment Programme' (UNEP), desertification directly affects about 70% of the total dryland area, and one-sixth of the world's people (http://www.cbd.int/). Reich et al. (2001) estimated that 50% of the total area in Burkina Faso, is highly to very highly vulnerable to desertification and 38% moderately vulnerable; only 12% of the total area was assumed to have a low vulnerability.

The limited availability of fertile land is pushing the farmers to rely on degraded lands for agricultural production (Drechsel et al. 2005). Such land is characterized by a tremendous loss of water through runoff due to the degraded, sealed soil surface which impedes water infiltration and root growth. Further characteristics are nutrient depletion, reduced biodiversity and very low to zero primary production (e.g. Maatman et al. 1998; Mando et al. 1999). The conventional techniques used to rehabilitate those lands are limited and too costly for small-scale subsistence farmers who are the major food producers in the Sahel-Sudanese zone of West Africa. Traditional techniques of managing land for agriculture, some dating back thousands of years, have served an important function in keeping human settlements in harmony with the natural resources on which people depend (Jarvis et al. 2008). Therefore, renewal of traditional knowledge may serve as an efficient approach to fertility management, even more if the methods are optimally adapted to the respective ecological and socio-economic conditions and demands (Jarvis et al. 2008; Marchal 1983; Roose 1994).

One approach to develop more sustainable agriculture is to maintain or restore natural ecosystem services that reduce dependence on human inputs to agricultural systems (e.g. Evans et al. 2011; Hooper et al. 2005; Montgomery 2007). The ecological services provided by biodiversity, in particular those promoted by soil organisms, are crucial for a productive and balanced (soil) environment (Altieri 1999; Cardinale et al. 2012; Pretty et al. 2010). Chapuis-Lardy et al. (2011) claimed further research efforts should be directed at investigating macrofauna-mediated processes in agricultural systems because these are potentially important for enhancing soil Phosphorous availability to cultivated plants.

Agro-ecologists claim the collapse can be reversed by restoring community homeostasis through the addition or enhancement of biodiversity (e.g. Cardinale et al. 2012). If correctly assembled in time and space biodiversity can lead to sustainable agro-ecosystems capable of supporting their own soil fertility, crop protection and productivity (Altieri 1999; Pretty et al. 2010). Their agricultural productivity may be especially affected if losses of biodiversity lead to changes in ecosystem functioning as most farmers have limited access to inputs (Giller et al. 1997).

Consequently, a key task is to identify the soil organisms (taxa) capable of carrying out the ecological services needed in the region of focus and then to determine and promote the practices[1] that will strengthen these components (Altieri 1999).

1.2. THE CONCEPT OF ECOSYSTEM ENGINEERING

Ecologists have long recognized that organisms can have important impacts on physical and chemical processes occurring in the environment. Aristotle called earthworms the "plows and intestines of the earth" (Bohlen & Lal 2002) and in 1881, Darwin dedicated an entire book to the effects of earthworms on soil formation and concluded that earthworms play a decisive role in world history (Darwin 1881). Numerous examples of these types of organismal effects on the abiotic environment had been reported in ecological publications (e.g. see Lee & Wood 1971; Lobry de Bruyn & Conacher 1990; Wood et al. 1983) until Jones et al. (1994) proposed the concept of 'ecosystem engineering'.

The authors defined physical ecosystem engineering by organisms as the "physical modification, maintenance, or creation of habitats" (Jones et al. 1997). Ecosystem engineers are, by definition, organisms whose presence or activity physically alters their biotic or abiotic surroundings and directly or indirectly change the availability of resources (other than themselves) to other organisms (Jones et al. 1994; Jones et al. 1997). Important ecosystem engineers are thus capable to expand the distributional range of other taxa by reducing the limiting abiotic and/or biotic stresses and often form the basis for community development (Crain & Bertness 2006).

One of the most prominent examples for an engineer whose presence (i.e. physical structure) alters the habitat (‘autogenic engineer’) is a tree. A tree significantly modifies and creates habitats for other organisms. To name only a few of the numerous examples given in the literature: branches, bark, roots and leaf surfaces provide shelter and living space (see for example Brühl et al. 1998; Delabie et al. 2007; Floren & Linsenmair 2000; Hölldobler & Wilson 1990; Roisin et al. 2006; Yanoviak et al. 2008); the canopy provides shade, modifies microclimatic soil conditions and reduces the impact of wind or rain (Callaway 1997; Moro et al. 1997); and root growth affects soil structure, increases aeration and affects water infiltration (Smiles 1988; Tisdall & Oades 1982).

Typical examples for an engineer who alters the physical environment by producing so-called 'biogenic structures' i.e. by its activity (‘allogenic engineers’) are earthworms and beavers.

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[1] Such practices might for example increase the diversity and abundance of soil organisms by enhancing resource availability or improving habitat conditions.

The beavers' (*Castor* sp.) dam-building activity can alter the hydrology of an entire water-body. By modifying nutrient cycle and the availability of resources for plants and animals, the beaver influences species richness and the composition of flora and fauna (Jones et al. 1997; Wright et al. 2002).

It should be noted that the ecosystem engineering concept overlaps with other concepts or terms used in the ecological literature. Examples are 'ecological engineer' which is used interchangeably with 'ecosystem engineer', 'dominant species', 'foundation species' or 'keystone-species'. For a more thorough definition of each term and differences between them please refer to the review published recently by Cottee-Jones and Whittaker (2012) and the references therein.

1.3. 'BIODIVERSITY–ECOSYSTEM FUNCTION PARADIGM'

The accelerated loss of biodiversity (or community composition changes) driven by anthropogenic actions has put the question whether diversity has effects on ecosystem functioning or not, in the focus of current research. The 'Biodiversity–Ecosystem Function Paradigm' (BEFP) was coined by Naeem (2002), emphasizing the actuality of the 'ecosystem engineering concept'. Without denying the influence of the environment on organisms, the BEFP sees the environment primarily as a function of diversity, underlining the active role of the biota in governing environmental conditions. "A specific ecosystem function is seen as a function of biodiversity and the functional traits of the organisms involved, associated biogeochemical processes, and the abiotic environment" (Scherer-Lorenzen 2005). A review of scientific evidences for links between biodiversity and ecosystem functioning pointing out the uncertainties was given by Hooper et al. (2005). The authors point out, that an understanding of how changes in biodiversity influence ecosystem properties and thus ecosystem services requires an understanding of the 'functional traits' of the species involved. By definition, 'functional response traits' determine how species respond to habitat change while 'functional effect traits' determine how species affect ecosystem processes or properties (Hooper et al. 2005). Response and effect traits may or may not be correlated with one another.

Understanding the links among the species' functional response and effect traits is therefore vital to an understanding of the dynamics of ecosystem functioning in a changing world and the services it provides for human well-being (Hooper et al. 2005; Lavorel & Garnier 2002).

1.4. SOIL ECOSYSTEM ENGINEERS IN THE STUDY REGION

Termites (Isoptera) and ants (Hymenoptera, Formicidae) are among the soil organisms best adapted to arid and semi-arid conditions and they are of key ecological importance for the dynamics and functioning of ecosystems (Evans et al. 2011; Jones et al. 1994; Lal 1988). In sub-Saharan Africa, ants and termites represent the only active soil macrofauna during the dry season that is for more than seven months of the year (Rouland et al. 2003; Schuurman

2006). The study of Mando and Brussaard (1999) in the sub-Sahel zone of Burkina Faso even revealed that termites were the only active decomposers all year round. Ants and termites are considered as true allogenic engineers whose activity alter the habitat and they appear to replace earthworms as soil ecosystem engineers in drylands (Evans et al. 2011; Lee & Foster 1991).

Termites and ants differ from the majority of soil organisms since many species modify the soil to create an environment suitable for their own purposes. They move through the soil and build different organo-mineral structures (so-called 'biogenic structures') with specific physicochemical and microbiological properties (Lavelle et al. 1997): mounds, nests, subterranean galleries (also called 'tunnels'), soil-sheetings constructed by foraging termites over the food source as protection against direct sun-radiation and predators, foraging holes, etc.

The role of termites and ants in ecosystems was reviewed by several authors (e.g. see Bignell & Eggleton 2000; Del Toro et al. 2012; Hölldobler & Wilson 1990; Lal 1988; Lavelle et al. 1997; Lee & Wood 1971; Lobry de Bruyn & Conacher 1990; Sileshi et al. 2010; Wood 1988). Through soil-turnover ('bioturbation') in the course of constructing their biogenic structures, ants and most notably termites bioturbate huge amounts of soil masses and exert massive effects on soil structure, essentially and positively influencing the fertility, stability, aeration and water infiltration rate into soils and they provide habitats for other species. According to Lavelle et al. (1997) in most tropical soils, surface horizons are mainly composed of an accumulation of these biogenic structures. Aside from their quantitative significance, the impact of these biogenic structures on soil functioning is very diverse; their properties depend on the type of the structure, the engineer species, its diet and the soil type (e.g. Bayen 2010; Grohmann 2010; Konaté et al. 1999; Lee & Wood 1971; Siegle 2009).

The results from various analyses of termite-modified soil compared with unmodified soil can be summarised as follows (e.g. Al-Houty 1998; Black & Okwakol 1997; Holt & Lepage 2000; Jouquet et al. 2002; Jouquet et al. 2004; Jouquet et al. 2011; Lobry de Bruyn & Conacher 1990): Concerning the physical soil properties, termites generally remove fine grained material from deep soil horizons, often leaving coarser material to form sub-soil, gravel or "stone layers"; this process increases over time. Their foraging-holes as well as the subterranean galleries and chambers greatly influence soil macroporosity, water flow and storing properties and soil aeration – and similar effects are caused by burrowing of ants (Folgarait 1998). The chemical composition of various termite constructions is mainly determined by soil particle selection and the extent of saliva and faeces admixture. Mounds and nests form a significant bank of nutrients that are temporarily withheld from plant growth (e.g. see review of Sileshi et al. 2010). Organic compounds, particularly those of C, N, in some cases P, and exchangeable cations are more abundant in termite nest structures than in the surrounding soils. The time for release depends on their longevity and the degree of erosion.

Most research on pedoturbation relates to the process of erosion of dead mounds and the re-distribution and deposition of eroded particles on the soil surface (e.g. Bonell et al. 1986;

Lee & Wood 1971; summarized in Lobry de Bruyn & Conacher 1990), only few on live mounds (e.g. Grohmann 2010). There are, however, little data for the mass of the above ground runways or soil-sheetings although it is recognised that surface sheetings may have a more important impact (on soil turnover and soil properties) than nests (Rouland et al. 2003). In contrast to mounds which can persist for decades, soil-sheetings erode easily and are often replaced thereby directly influencing the local physico-chemical soil properties (Bagine 1984; Holt & Lepage 2000; Wood 1988).

Unlike termites, ants do not cement the excavated subsoil material together nor mould it into a cohesive mound (Nye 1955). Therefore, soil material excavated by ants is easily eroded by rain and in open areas also by wind. Despite the fact, that ants occur in exceptionally high densities, to our knowledge there are no data available to draw any valid conclusions e.g. regarding the amount of soil turn-over (Lal 1988).

Termites and ants can have either negative effects on agricultural systems due to the spread of a few pest species, or – and more importantly – beneficial effects on soil properties. The processes they promote via their feeding and nesting behaviors are crucial for the long-term balance of soil nutrients and for the creation of the soil itself. In fact, it is increasingly recognized that soil fauna such as termites and ants are a key consideration for land rehabilitation (Ouédraogo et al. 2008) and that the ecosystem services they provide represent a potential alternative to high priced inputs via mechanical treatment or fertilizers (Evans et al. 2011; Mando & Van Rheenen 1998).

Rather than using mechanical methods like soil tillage to control crusting, triggering termite activity by applying mulch is a more sustainable and affordable option for small-scale farmers in the sub-Sahelian region of Burkina Faso (Ouédraogo et al. 2008). Even on bare crusted soils, soil water infiltration rate can thus be improved and the re-establishment of plants can be enhanced (e.g. Mando & Miedema 1997; Ouédraogo et al. 2008). In an experiment conducted by Evans et al. (2011) in arid Australia, crop yields were increased in the presence of termites and ants. However, surprisingly few studies have been reported on the utilization of termite and ant activity for the management of soil fertility in agro-ecosystems or for the rehabilitation of degraded soils. More research is needed to improve traditional systems and to restore the natural agrosylvopastoral processes and, above all, soil fertility in semiarid degraded areas (Roose et al. 1999).

A very promising example for a traditional soil restoration method in semi-arid West Africa, which is making use of the positive effects termites exert on soil properties, is the Zaï practice (e.g. David 2003; Kaboré & Reij 2004a, b; Laguemvare 2003; Roose et al. 1999). Zaï is (in short) a very complex soil restoration system using organic matter localization, termites to bore channels in the crusted soils, runoff capture in microwatersheds, and seed-hole cropping of sorghum or millet. Roose et al. (1999) tested the Zaï-system with (and without) different kinds of compost in two types of soil. Not only could the production of cereal grains be increased (5-7 fold increase compared to control treatments), but also a diverse flora be re-introduced that may help to restore degraded soils during the fallow period. This traditional system has the potential of a very wide application in Africa (Roose et al. 1999) and could also play an important role in carbon sequestration in these regions, as it seems suitable for reforestation even of the most severely degraded, crusted soils. Presently, Zaï is, despite its high efficiency and its very positive long-term effects, still only applied in north-western Burkina Faso. A comparable technique called 'Tassa' is used in some parts of Niger and Mali (Slingerland & Sork 2000).

Surprisingly, no studies were conducted, how to optimise the system by manipulating the biological component, the termite fauna, e.g. by selective attraction of specific species (or functional groups) or by fastening the successional dynamic. Chapuis-Lardy et al. (2011) stress that field studies should aim to better understand the volume of soil impacted and the dynamics of the biogenic structures produced.

1.5. MONITORING OF TERMITE AND ANT COMMUNITIES

Because of the important role these soil-arthropods have for ecosystem functioning, monitoring of ants and termites is considered crucial in order to assess changes in their diversity, distribution and abundance triggered by direct and indirect human impact and global climate change. Over the world, Brown (1991) scored ants and termites second and third in importance for ecological analysis and monitoring after butterflies (Lepidoptera).

In general, their stationary nesting habits and high level of ecological specialization, their sensitivity to habitat disturbance including land use change combined with short generation times, the small size and high abundance make termites and ants ideal candidate taxa for biological indicators of natural environmental variability and anthropogenic disturbance (e.g. Jones & Eggleton 2000; King et al. 1998; Lawton et al. 1998; Lobry de Bruyn 1999; Perfecto et al. 2003). They also meet three of the criteria for good biological indicators of Noss (1990): they are sufficiently sensitive to provide an early warning for change, distributed over a wide geographical area, and capable of providing a continuous assessment over a wide range of stresses (Peck et al. 1998). However, the existing knowledge is largely fragmentary since most of the studies on termite diversity so far focussed mainly on forest ecosystems, mostly neglecting savanna ecosystems.

Globally, over 2600 termite species in about 281 genera are described in the Order Isoptera. There are over 660 known termite species in Africa (Kambhampati & Eggleton 2000) but the numbers are likely to be underestimated because the taxonomy of African termites is notoriously difficult, and many new species are yet to be described. Termites are divided into lower and higher termites. The lower termites of Africa belong to the families Kalotermitidae, Termopsidae, Rhinotermitidae and Hodotermitidae (Kambhampati & Eggleton 2000). The majority of lower termites are wood feeders. All higher termites belong to the family Termitidae. They show considerable variation in feeding and nesting habits as well as their social organization. In contrast to the lower termites, Termitidae typically lack eukaryotic flagellate protista. They are not limited to feed wood; some feed exclusively on soil, while others cultivate and consume cellulolytic fungi. More than 90% of all known species in Africa (>600 species) are higher termites (Kambhampati & Eggleton 2000). All specimens collected in the present study belonged to five subfamilies within the higher termites (Amitermitinae, Apicotermitinae, Termitinae, Macrotermitinae and Nasutitermitinae). Fungus-growers (all belonging to the Macrotermitinae) will be in the focus of the applied part of the present dissertation. They evolved a mutualistic ectosymbiosis with fungi of the genus *Termitomyces* (Basidiomycotina). The fungus helps the termites to degrade the plant-derived material (e.g. wood, dry grass, dung, leaf litter) on which they live (e.g. Johnson et al. 1981; Koné et al. 2011). It grows on a special structure in the nest, the fungus comb, maintained by the termites through continuous addition of predigested plant substrate while the older comb material is consumed (Rouland-Lefèvre 2000). Due to this agricultural symbiosis, Macrotermitinae have become major decomposers of the Old World tropics (Aanen et al. 2002).

Ants (Hymenoptera: Formicidae) are the most diverse group of social insects: more than 12,500 species in 21 subfamilies and 283 genera have been described, and about the same number are presumed to be still discovered, especially in the tropics (Bolton et al. 2007; Ward 2009). They display various adaptive strategies and specializations – seed harvesting, herding and milking of other invertebrates, communal nest weaving, cooperative hunting in packs, social parasitism, slave-making and agriculture of fungi (only in the Neotropics) (Ward 2012). They play important roles in food webs at different levels – as herbivores in the Neotropics (Hölldobler & Wilson 1990), effective seed dispersers (e.g. Giladi 2006; Mossop 1989) and they often act as plant protection against herbivores (e.g. Heil et al. 2001; Vandermeer et al. 2002). Ants are major invertebrate predators (Dyer 2002; Philpott et al. 2008). They are among the most important predators of termites; many genera of ants feed only on termites and numerous ant species (e.g. genus *Pachycondyla*) feed either only on termites or incorporate termites in their diet (Hölldobler & Wilson 1990; Longhurst 1977; Longhurst et al. 1978).

Local species richness and the composition of assemblages vary between ecosystems and are strongly influenced by climate, altitude, habitat characteristics and historical factors (site history). The local species pool is also constrained by the composition of the regional species pool which again was influenced by long-term historical factors (Bignell & Eggleton 2000). This makes generalizations about taxonomic and functional community composition difficult. However there are some general trends. In general, species richness declines with distance from the equator, probably due to a drop in insolation and rainfall (Coaton & Sheasby 1972; Eggleton 2000). This decline in diversity is generally accompanied by a reduction of abundance and biomass however termites can remain functionally important in subtropical ecosystems, especially rangelands and agroecosystems (Bignell & Eggleton 2000). However, for African savannas only little information is available on the effects of natural climate and anthropogenic usage gradients on the diversity of termite species and changes in their community structure (Wood 1996) and even less information exist on the effects of anthropogenic usage gradients on the ecosystem services provided by termites.

Since ecosystem engineers affect other communities through environmentally mediated interactions, their impact is likely to shift across environmental stress gradients – impacts of land-use are thus likely to have significant consequences for soil processes and ecosystem functioning (Crain & Bertness 2006). Termite communities are generally very sensitive to land-use practices that modify the availability of organic resources and the rate of perturbations (e.g. Ayuke et al. 2011; Davies et al. 1999; Davies et al. 2003; Eggleton et al. 2002; Okwakol 2000). It has been demonstrated that ant communities respond predictably to disturbance (e.g. Andersen 1990; Bestelmeyer & Wiens 2001; Floren & Linsenmair 2001; Kone et al. 2012; Peck et al. 1998). Changes in community composition may thereby occur at a taxonomical level (species up to whole families that disappear), a quantitative (changes in biomass or density) or an ecological one (changes or the complete loss of functional groups). Functional groups are similar to the guild concept (Blondel 2003; Root 1967). Mostly the terms 'guild' and 'functional group' are more or less synonymously used to describe ecological groupings of species. According to Blondel (2003), "the guild concept refers primarily to the mechanisms of resource sharing by species in a competitive context whereas the functional groups concept is concerned with how a resource or any other ecological component is processed by different species to provide a specific ecosystem service or function" (Blondel 2003). Hooper et al. (2005) defined a functional group as "set of species that have either similar functional effect or similar response traits".

The main aim of the thesis was to characterize the functional traits of the soil organisms which are crucial for a balanced soil environment in the region of focus – termites and ants. I therefore studied the soil-arthropods' response to changing environmental parameters resulting from increasing human impact ('functional response traits') and quantified the ecological services they provide and which are playing a key role in the restoration of infertile, barren soils and the maintenance of a sustainable agricultural production ('functional effect traits').

In a baseline study, I therefore characterized the present state of the local termite and ant fauna (species inventory, species lists), I assessed the most important abiotic and biotic parameters characterizing the different land-use types and I studied the soil-arthropods' response to the changing environmental parameters resulting from increasing human impact. In the second and applied part of the thesis, I first rapidly assessed the relative importance of termite and ant structures for soil-turnover along the two disturbance gradients. The temporal cross-section of the traditional rehabilitation system Zaï in northern Burkina Faso was then chosen to determine the role of termites as ecosystem engineers in the process of soil restoration.

1.6. THE BIOTA PROJECT

The work presented here was part of the 'BIOTA West Africa' project ('BIOdiversity Monitoring Transect Analysis in Africa'), one of four big regional subprojects within a large interdisciplinary research programme called 'BIOTA AFRICA'[2]. The project belonged to the

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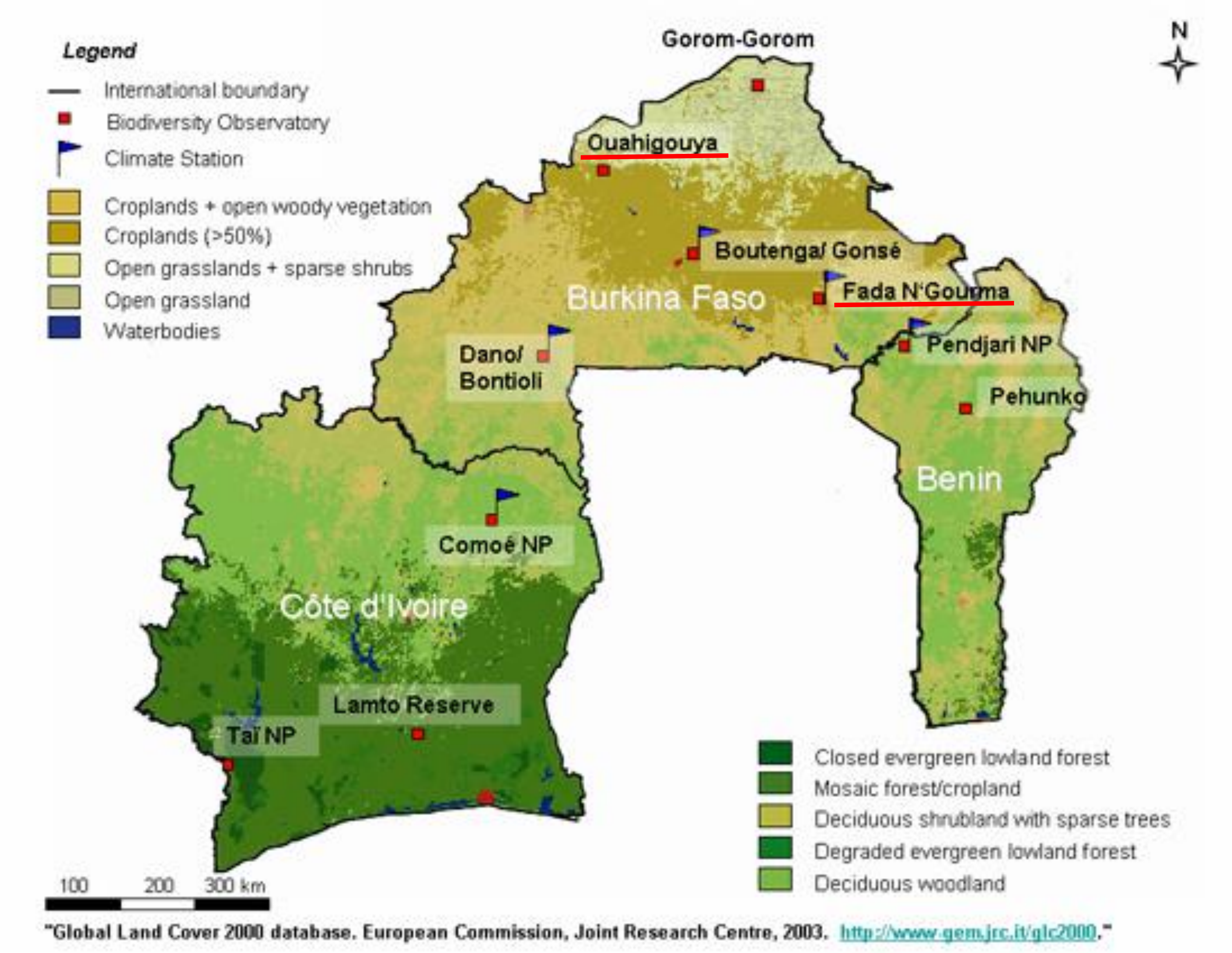
[2] The other regional subprojects were 'BIOTA Southern Africa', 'BIOTA East Africa', 'BIOTA Morocco'.

BIOLOG[3] framework programme of the German Federal Ministry of Education and Research (BMBF) and was funded from 2000 to 2010 (see also www.biota-africa.org).



"Global Land Cover 2000 database. European Commission, Joint Research Centre, 2003. http://www.gem.jrc.it/glc2000."

Fig. 1-1 Vegetation Map of Burkina Faso, Côte d'Ivoire and Benin (West Africa), showing the locations of the standardized sampling sites of 'BIOTA West', the so-called 'biodiversity observatories' located along a macro-transect which was following the climatic gradient from the Atlantic coast to the North. Termite and ant communities were assessed along two land-use intensification gradients (located at the underlined sites Ouahigouya and Fada N'Gourma). Each gradient represented a traditional agricultural system comprising four different habitat types.

The main objectives of 'BIOTA AFRICA' were to provide scientifically sound data on the actual status of biodiversity in the major biomes and ecosystems of the African continent, to monitor its changes in time and its responds to land use and climate change, and to understand the processes and mechanisms that are responsible for biotic change. Based on these findings, interventions schemes and decision making tools were developed for land users and policy makers aiming to provide suggestions for a sustainable land management that conserves biodiversity and its functions. BIOTA thus directly contributed to the

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[3] BIOLOG: 'Biologische Vielfalt und Globaler Wandel' – Biological Diversity and Global Change.

requirements of the intergovernmental agreement 'CBD' (Rio de Janeiro Declaration of 1992 on the 'Convention on Biological Diversity'), in particular the requirement of lending developing countries scientific support for the assessment, sustainable use and conservation of biodiversity. In 'BIOTA West', more than 150 researchers of 13 universities and institutes from Benin, Burkina Faso, Côte d´Ivoire and Germany collected data on various aspects of biodiversity covering different scientific disciplines (e.g. in remote sensing, climatology, soil sciences, botany, zoology, ethnology, etc.). Investigations were conducted on standardised sampling sites, the so-called 'biodiversity observatories', located along a macro-transect which was following the climatic gradient from the Atlantic coast to the North (see map in Fig. 1-1) and which was spanning rain forests, different types of savannas, the Sahel zone and the desert. The outcomes of BIOTA West Africa were published in a three-volume book 'Biodiversity Atlas of West Africa' (Konaté & Kampmann 2011; Sinsin & Kampmann 2011; Thiombiano & Kampmann 2010) – the three West African countries thereby fulfilled the CBD-requirement to make reliable and updated data on biodiversity available to the international community. 'BIOTA AFRICA' further met the obligations of the relevant UN conventions (UNCBD and UNCCD), to the Johannesburg Plan of Action of the World Summit on Sustainable Development (WSSD), the New Partnership for Africa's Development (NEPAD) and it was part of the international DIVERSITAS programme.

1.7. THESIS OUTLINE

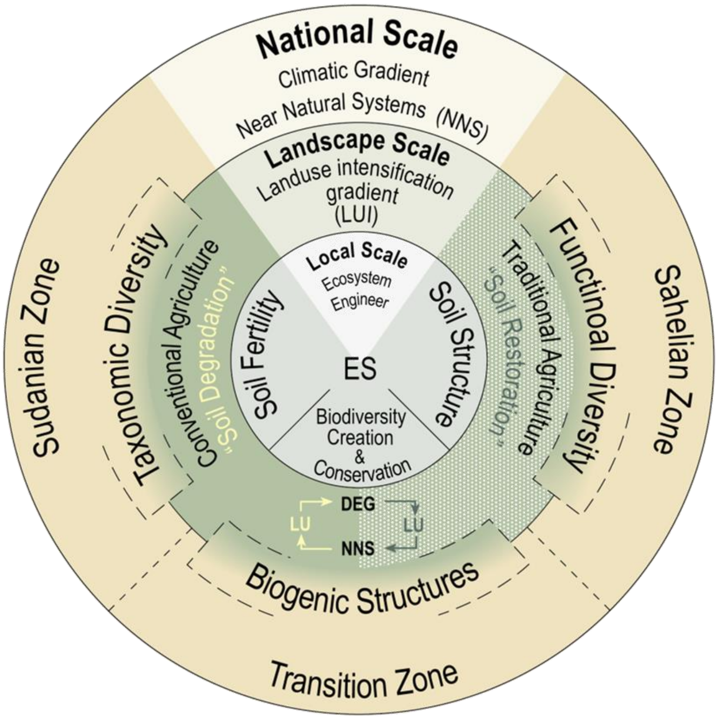

Fig. 1-2: Conceptual model of the present thesis. DEG: degraded land; NNS: near-natural system; LU: land-use; ES: ecosystem services, e.g. impact on soil structure, soil fertility and water holding capacity. Biogenic structures are, for instance, nests, mounds, subterranean galleries, soil-sheetings and foraging holes.

Chapter II of this thesis ('Study sites & study region') introduces general characteristics like the geography, the climate and the vegetation of the sub-Sahelian and the North-Sudanese regions in Burkina Faso. The traditional soil restoration technique Zaï applied by the small-scale farmer in the sub-Sahel zone is then explained. Furthermore, a general description and the site history are given for each habitat type selected along the two disturbance gradients.

Chapter III ('GENERAL METHODS') describes all methods combined in the standard transect protocol 'RAP' followed for the rapid assessment of termite and ant diversity. Included is further a description of the statistical methods used, for example the presence-absence approach recommended to analyze diversity data for social insects, the estimators used to obtain a reliable estimate of the habitats' total species richness, the diversity indices calculated and the procedure applied to identify environmental parameters which exert significant influence on variations in the composition of the ant and termite communities assessed along the disturbance gradients. The chapter ends with an introduction of the agricultural intensification index 'AI' calculated on the basis of the site history in order to rank the different land-use types according to the intensity of human interventions.

Chapter IV ('BIOTIC AND ABIOTIC HABITAT PARAMETERS') deals with environmental parameters measured either for the whole habitat or within each section (5 x 2 m) of the belt-transects conducted to rapidly assess the termite and ant fauna. The parameters comprised physico-chemical soil properties, vegetation features, precipitation, air and soil temperature, the quantity and composition of plant litter and other organic debris, and epigeal termite mounds. The aim was to characterize the study sites more thoroughly and to identify so-called 'predictor variables' for variations in the composition of the focal soil communities. In the four age stages of the Zaï system, additional soil samples were taken in the context of the experiment described in Chapter VIII. After introducing the methods used in the field and in the laboratory, I show all results – first for the sub-Sahelian, then for the North-Sudanese sites.

Chapter V ('DIVERSITY OF TERMITE AND ANT COMMUNITIES ALONG TWO LAND-USE INTENSIFICATION GRADIENTS IN SEMI-ARID BURKINA FASO') presents separately for each taxon and each disturbance gradient the taxonomic and functional group composition of the local termite and ant fauna, the species' relative abundance and distribution in the different habitats. The expected total species-richness calculated with different incidence-based estimators as well as the within-habitat diversity measured by means of two commonly used indices are indicated for each transect, each habitat and each region. The chapter ends with the variables predicting a significant share of variations in the composition of the focal soil communities: different ordination tri-plots resulting from a Canonical Correspondence Analysis are illustrating the replicate transects, common species and the three most influencing environmental parameters – again separately for each taxon and each disturbance gradient. I collected all specimens within belt-transects that were conducted according to a standard protocol which combined different sampling methods (described in Chapter III) – depending on the habitat, three or four replicate transects were conducted.

Chapter VI ('PHYSICAL ECOSYSTEM ENGINEERING – INTRODUCTION') introduces the second part of the present doctoral thesis, focusing on the physical ecosystem engineering aspect, the 'biogenic structures' built by the focal soil-arthropods. Biogenic structures comprise for example epigeal mounds, subterranean nests, galleries dug in the pedosphere (soil), foraging holes (macropores) and soil-sheetings constructed by foraging termites over the food source as protection against direct sun-radiation and predators.

Chapter VII ('RELATIVE IMPORTANCE OF TERMITE AND ANT STRUCTURES FOR SOIL TURN-OVER') illustrates the relative importance of the focal soil-dwelling arthropods for soil turn-over (bioturbation) in the different agro-ecosystems. The quantity of soil bioturbated by termites and ants to construct their epigeal biogenic structures was rapidly assessed during different years and seasons following a standard protocol.

Chapter VIII ('THE ROLE OF TERMITES IN THE PROCESS OF SOIL RESTORATION') demonstrates the role of fungus-growing termites (genera *Odontotermes* and *Macrotermes*) as ecosystem engineers in the process of soil restoration with the traditional Zaï technique. An experiment was conducted twice for a duration of four weeks (rainy season 2005, dry season 2006) in order to test the hypothesis, that termite-mediated processes can be induced and directed to restore soil quality in arid climates and to verify whether ecosystem services provided by termites represent a potential alternative to high priced inputs and to maintain agricultural sustainability in systems with low external input. A randomized complete block design was used to attract termites with different, locally available organic materials (compost, hay, wood) and to stimulate their foraging activity. While paying attention to potential influences of the season, the Zaï stage, the food type and the termite genus, the main aims were: i) to quantify soil turnover via their soil-sheetings, ii) to measure the effect of foraging holes on the water infiltration capacity and iii) to determine whether the termites significantly modify the soils' physico-chemical properties when constructing their protective soil-sheetings. To characterize the dynamics of foraging, soil-sheeting establishment was chronologically followed; all visible sheetings were mapped on millimeter paper and assigned to the respective termite genus.

Chapter IX ('SUMMARY AND CONCLUSIONS') summarizes the most important findings of this thesis and highlights the important role the focal soil-arthropods' play for ecosystem functioning in the arid and semi-arid regions of West Africa, thereby especially focusing on the ecological services provided by fungus-growing termites of the genera *Odontotermes* and *Macrotermes* for the restoration of degraded, barren and crusted soils.

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2. STUDY SITES & STUDY REGIONS

2.1. GENERAL CHARACTERISTICS OF THE STUDY REGION AND SITE SELECTION

Burkina Faso is a landlocked country in the semi-arid tropical zone in West Africa between the ninth and the fifteenth parallel in the northern latitudes (Fig. 2-1). Neighboring countries are Mali, Niger, Benin, Togo, Ghana and Côte d'Ivoire. The country has a total area of 274,190 square kilometer (km^2) with a population size of about 17,275,115 (CIA 2012; https://www.cia.gov). More than 48% of all Burkinabe are Mossi (language Mooré), the remaining belong to about 60 other ethnic groups (M.E.D. 2005). In Mooré and Dioula, the major native languages of the country, Burkina Faso means 'the land of upright people'. About 85% of the population is engaged in subsistence agriculture, which is vulnerable to periodic drought (Thiombiano & Kampmann 2010). Cotton is the main cash crop.

The country is subject to a high degree of climate variability and a population growth of about 2.3% per annum (Some et al. 2006). Main climatic features are a low level of rainfall with a high degree of spatiotemporal variability, high temperatures and a high level of evapotranspiration, particularly during the dry season. Overall, temperatures and temperature ranges increase from the south towards the north. According to a report of the 'Institut de l'Environnement et de Recherches Agricoles' (INERA) (Some et al. 2006), there is a latitudinal sliding of all isohyets towards the south, translating to a reduction of 100 mm in average rainfall. Between 1966 and 1973, the 400 mm isohyets rose up to the northern border of the country and the 1100 mm isohyets reappeared in the south (Marchal 1983; Some et al. 2006).

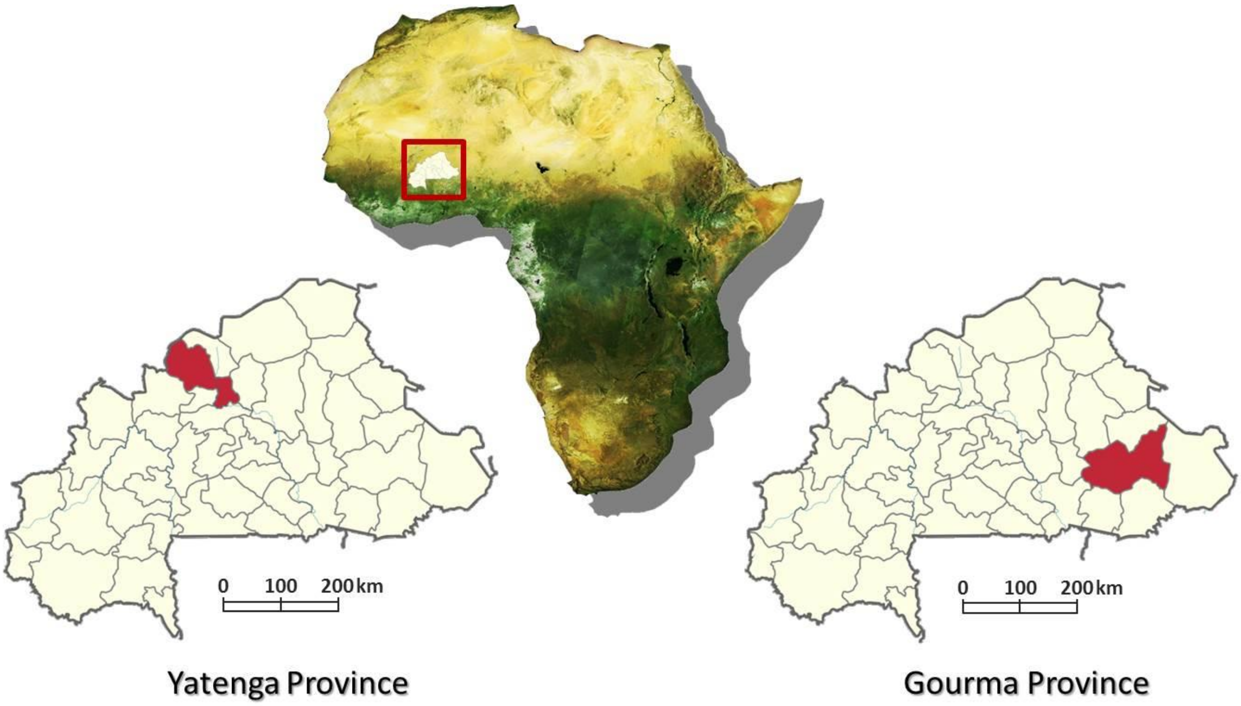


Fig. 2-1: Two agricultural systems were chosen in Burkina Faso, each representing a land-use intensification gradient (LUI) comprising four distinct habitats: LUI-1) a traditional soil restoration system in Ouahigouya (Yatenga Province, sub-Sahel region); LUI-2) a traditional agriculture type close to Fada N'Gourma (Gourma Province, North-Sudan region).

Major episodes of drought in the Sahel were 1972-74 and 1981-84 (http://go.worldbank.org/9H7HC6KZI0). These rainfall dynamics have serious consequences for crop production and food security in Burkina Faso (Some et al. 2006). In general, the soils' water-holding capacity is low in Burkina Faso. Soil and water conservation practices traditionally applied by farmers in Burkina Faso comprise various agronomic and biological as well as mechanical practices (Mazzucato & Niemeijer 2000). Agronomic and biological practices are for example crop rotation (growing a planned sequence of different crops on the same piece of land), fallowing, weeding, intercropping (growing two or more crops simultaneously in the same field), appropriate crop selection, adapted plant spacing, thinning, mulching, stubble grazing, weeding mounds, household refuse and manure application, compost pits. Mechanical are practices as perennial grass strips, stone lines, wood- or earth-barriers, half-moon, deep-plough, living hedges and Zaï (Mazzucato & Niemeijer 2000; Stroonsnijder & Hoogmoed 2002). Several examples of these practices are shown in Fig. A2-1 (Appendix 2).

Two agricultural systems were chosen in the two main phytogeographic regions of Burkina Faso. Each system represented a land-use intensification gradient (LUI) comprising four distinct habitats. The first intensification gradient (LUI-1), a traditional soil water conservation technique to restore fully degraded, heavily encrusted, barren lands named Zaï; meanwhile of widespread use in the Yatenga province in the North of the country (sub-Sahel zone) (13°32'N, 2°22'W) and, the second intensification gradient (LUI-2), a traditional agriculture type using crop rotation and fallow as nutrient management techniques, located about 52 km south of Fada N'Gourma in the Southeast of Burkina Faso (Gourma province, North-Sudan zone) (11°38'N, 0°31'E).

Table 2-1: Eight distinct land-use types belonging to two gradients of increasing land-use intensification (LUI) were studied in Burkina Faso. Indicated are the sites' abbreviation (Short), the number of plot replicates and the coordinates (Latitude / Longitude). The habitats representing the initial stage of the respective disturbance gradient are italicized.

Land-use types		Short	Plots	Latitude / Longitude
LUI-1: Land-use intensification gradient, Zaï system, sub-Sahel region, northern Burkina Faso				
Site 1	*Degraded, barren land*	ZDeg	2	13°32'36"N / 2°22'59"W
Site 2	Millet field (agricultural Zaï)	ZMil	2	13°32'29"N / 2°23'07"W
Site 3	Young Zaï forest, 20-yrs old	ZF20	1	13°32'34"N / 2°22'55"W
Site 4	Old Zaï forest, 30-yrs old	ZF30	1	13°32'25"N / 2°22'57"W
LUI-2: Land-use intensification gradient, North-Sudan region, south-eastern Burkina Faso				
Site 5	*Savanna in the reserve of Pama*	FRes	2	11°38'26"N / 0°31'45'E
Site 6	Pasture land	FPas	1	11°38'40"N / 0°30'03"E
Site 7	Short-term fallow	FFal	1	11°38'17"N / 0°30'09"E
Site 8	Cotton field	FCot	2	11°38'15"N / 0°30'27"E

The selection of sites aimed at covering both a) the land-use types typical for the respective region and b) a gradient formed by habitats with a known site history, now differing in the magnitude of human intervention but formerly having the same initial state. The latter assumption, i.e. comparable biotic and abiotic conditions and presumably similar soil arthropod communities in the beginning, was obligatory to allow conclusions about the arthropods' response to increasing human impact. The absence of more plot replicates for most sites reflect the absence of more than one or two plots in an homogeneous area in the vicinity of the study sites – especially regarding topographic position, soil type and hydrology (Table 2-1).

In each habitat, the vegetation was assessed once during the rainy season within an area of 900 m^2 (see methods and results in Chapter 4). Termites and ants were collected according to a standardized rapid assessment protocol (RAP) in three to four transects (see methods in

Chapter 3, results in Chapter 5). Samples of the habitats' topsoil were taken within and outside the transect-sections (see methods and results in Chapter 4).

2.1.1 First disturbance gradient, the agricultural system in the sub-Sahel region

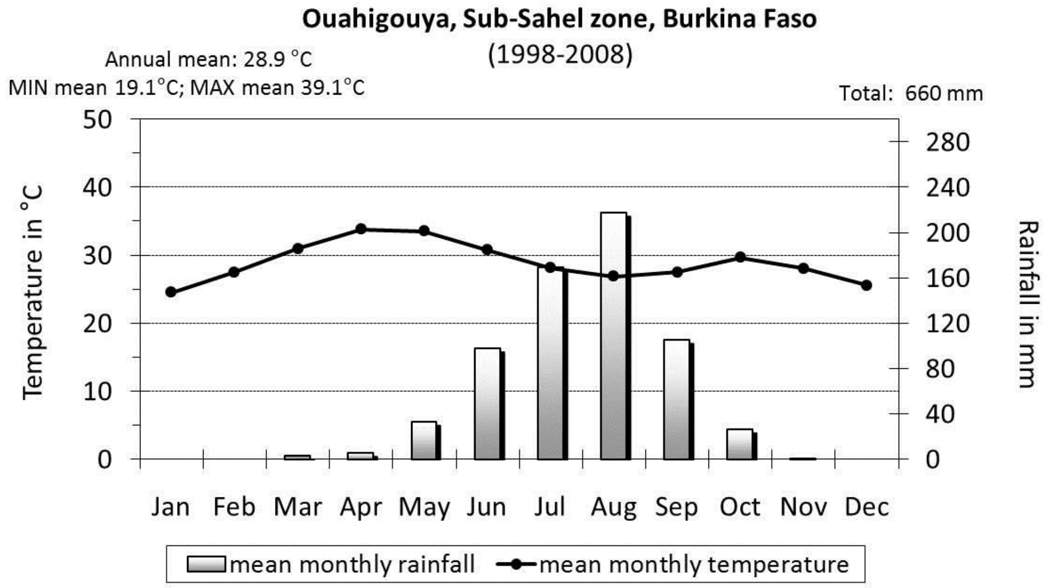
The first land-use intensification gradient (LUI-1) at an altitude of 336 m comprised four main succession stages, reflecting a temporal cross-section of the traditional soil restoration system Zaï in Ouahigouya, the administrative center of the Yatenga province in the sub-Sahel region of Burkina Faso (Fig. 2-1). The small-scale farmer Yacouba Sawadogo revived and optimized this ancient restoration method after the great Sahelian drought during the 1970s and 1980s, when the average annual rainfall was below 560 mm (Kaboré & Reij 2004).

2.1.1.1 Geography, climate, soil and vegetation

The Yatenga Province is situated in the northwestern region of Burkina Faso and has a total area of 6,799 km² (Some et al. 2006). The province has an undulating surface, dominated by hills and hardpan hillocks, steep blocks and cliffs and a gentle slope varying between 1 and 3% (Marchal 1983). The climate of the Sahel-Sudanese type (UNESCO 1977) is characterized by a short rainy season of four to five months and a long dry season of seven to eight months with high temperatures. The driest months are December to February, the hottest April to May with temperatures up to 42.7°C in April (Some et al. 2006).

Two types of wind alternate in this region, the Harmattan and the Monsoon. The regions' aridity is accentuated by the Harmattan, a dry wind which blows from the Sahara desert in a NNE-SSW direction and is the main force driving wind erosion (Some et al. 2006). The Monsoon blows from the Atlantic Ocean in a SW-NE direction, a cold wet wind which brings the rains (Some et al. 2006). The sub-Sahel zone typically has an annual rainfall between 400 and 700 mm. The rain falls in a unimodal pattern from end-May/June to mid-October; wettest months are July and August. However rainfall is irregular in time and space. The mean monthly temperature (°C) and the mean monthly rainfall (mm) which was prevailing in Ouahigouya between 1998 and 2008 are illustrated in Fig. 2-2. The numbers behind the figure are shown in the table below. The average monthly temperature ranged between 19.1°C and 39.1°C, the annual mean was 28.9°C (Fig. 2-2). Fig A2-2 in Appendix 2 additionally illustrates the mean monthly temperature in Ouahigouya calculated with data from 1973 to 2008 and the precipitation with data from 1940 to 2008. The tendency over the last 40 years has been for rainfall to decrease and temperatures to rise (Some et al. 2006).

The natural vegetation is of the steppe type according to UNESCO's classification, with large bare areas (UNESCO 1977). The phytogeographic zone, located between the 13th and 14th parallels of the northern latitude, is the area of interference for numerous generalist species from the Sahel and Sudanese regions.



Data source: Centre for Development Research (ZEF), Bonn, Germany; Direction régionale de l'Agriculture de l´Hydraulique et des Ressources halieutiques, Ouagadougou, Burkina Faso.

1998-2008 (LUI-1)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
mean temp (°C)	24.5	27.5	30.9	33.8	33.5	30.7	28.1	26.9	27.5	29.6	28.0	25.5
mean rainfall (mm)	0	0	3	6	33	98	170	218	106	27	0	0

Fig. 2-2: Mean monthly temperature (°C) and rainfall (mm) in Ouahigouya, Yatenga Province (sub-Sahel region, northern Burkina Faso), calculated with data measured between 1998 and 2008. Additionally, the means are shown in the table below the figure.

According to Guinko (1984), the elements Sahel and Saharan are typically dominating the flora. Comprehensive lists of the dominant vegetation are given in the literature (e.g. Guinko 1984; Ouedraogo 2006; Thiombiano & Kampmann 2010).

2.1.1.2 The traditional soil restoration technique Zaï

Two forms of Zaï exist today: the agricultural (Fig. 2-3) and the forestry Zaï (Fig. 2-4).

In the agricultural form, the farmer digs pits (micro-watersheds) in parallel rows. The dug-out soil is placed as small bund down-slope of each pit to produce mini-water catchments (Roose et al. 1993). In Ouahigouya, about 9,700 pits are dug per hectare (each about 20 cm deep and about 35–40 cm in diameter). Surrounding and traversing stone lines had been installed in all habitats except for the degraded area. Shortly before the onset of the rainy season, crop seeds and air-dried compost are put into these pits. Termites, attracted by the organic matter, dig underground galleries to reach the food source thereby enhancing the soil's aeration and its infiltration capacity. The compost is chopped up strongly by termites. As only a minor part is fully digested to mineralization, it increases soil fertility and represents an ideal breeding ground for microorganisms.

For the forestry Zaï, the crop fields lie fallow following four to five years of continuous agricultural Zaï cultivation. Shrub species germinating from the dung were already retained during the weeding (tillage) operations of the preceding cultivation years. Within 10 to 20 years, diverse woody and herbaceous vegetation develops which may then form a matrix for the introduction of e.g. medically or economically valuable species. For more information about the Zaï method see references in Appendix 2; for photos illustration the different stages of the agricultural Zaï technique see Fig. A2-5 (Appendix 2).

For each Zaï variant, two representative age stages were chosen (Fig. 2-3, Fig. 2-4). A degraded, barren area (ZDeg) was chosen to represent the initial habitat form. Millet fields (ZMil) were chosen for the agricultural variant. For the silvopastoral or forestry Zaï variant, a young forest with an age of about 20 years (ZF20) and an old one with about 30 years (ZF30) were selected. The two Zaï forests will often simply be referred to as young and old forest. Each site had an area of about one hectare (ha) and laid within a radius of 300 to 400 m to the other habitats.

2.1.1.3 Description of the study sites

Site 1 (Fig. 2-3): Degraded land (ZDeg), representing the initial stage of all Zaï sites; a completely barren area of reddish, infertile soil with about 70% gravel in the soil samples and with a crusted, impermeable surface devoid of any vegetation or organic matter – except for a few blades of grasses and occasionally some droppings of cattle that were passing through. The degraded site adjoined Site 3, the young Zaï forest. More habitat photos are shown in Fig. A2-6 (Appendix 2).

Site 2 (Fig. 2-3): Two neighboring agricultural fields cultivated with the Zaï technique (ZMil): Sorghum (*Sorghum bicolor*) or millet (*Pennisetum glaucum*) combined with nitrogen-fixing Leguminosae like green beans. During the last decade, the small-scale farmer Yacouba Sawadogo started to cultivate his fields longer than he did before. In contrast to the Zaï forests which laid fallow after four cultivation years, he continued to cultivate his millet fields without fallowing. In 2009, both fields were about 11 years old (age since the initial degraded stage)**.** At the time of sampling the focal soil-arthropods, the fields were in the 5th, 7th and 8th cultivation year. The shallowest spot encountered was about 30 cm deep. Due to regular tilling, almost no grass was covering the ground. Few trees up to 2 m high were growing within the fields. However, a lot of saplings, young trees and shrubs that had been growing from the compost of the preceding years were left by the farmer. Before the harvest, only very little litter was on the ground – except for the compost and some decaying tree stumps. After the harvest, animal droppings and a lot of millet-stubs cut about 20 cm above ground were left in the fields. Most of the millet-straw was collected to feed the cattle during the dry months. After the harvest, grazing was allowed to the farmer’s own cattle. More habitat photos are shown in Fig. A2-7 (Appendix 2).

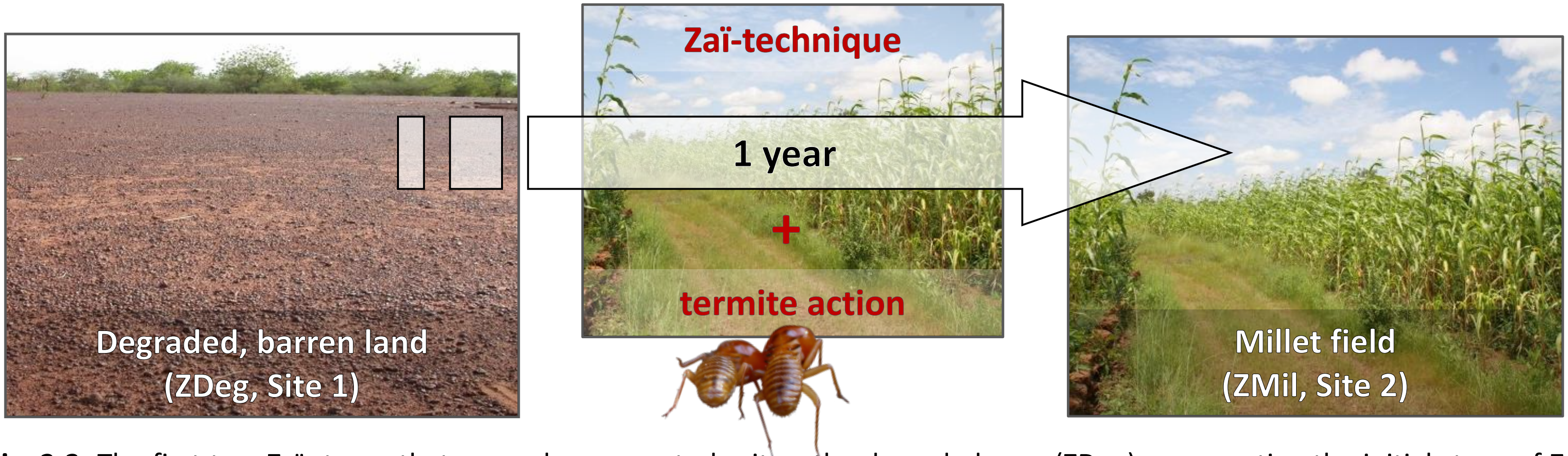


Fig. 2-3: The first two Zaï stages that were chosen as study sites: the degraded area (ZDeg) representing the initial stage of Zaï restoration; and, the millet fields (ZMil) representing the agricultural Zaï variant resulting from the Zaï cultivation method and termite actions during the first year.

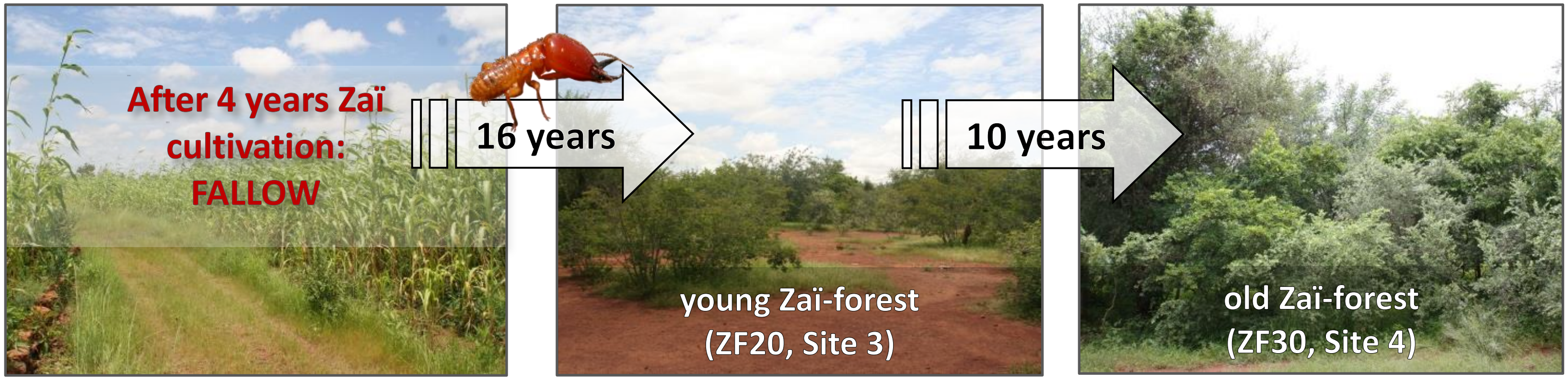


Fig. 2-4: For the forestry Zaï, the crop fields lie fallow following 4–5 years of continuous agricultural Zaï cultivation. Within 10–20 years, diverse vegetation develops. Two stages were chosen as representatives: a young Zaï forest (ZF20) and an old Zaï forest (ZF30). About ten years of succession separated the two forests: Both were first cultivated with the Zaï method for the duration of four years and were then left as fallow, the young forest for the last 16 years, the old one for the last 26 years.

More habitat photos are shown in Appendix 2 (Fig. A2-6 to Fig. A2-10).

Site 3 (Fig. 2-4): Young Zaï forest (ZF20), in 2009 about 20 years since the initial, degraded stage. During the first four years, the land had been cultivated with the Zaï method and was then left fallow for the last 16 years. Stone lines were still present. In the rainy seasons of 2004, 2006 and 2007 when the focal soil-arthropods had been sampled, the young forest was around 15 years, 17 years and 18 years old. Diverse woody and herbaceous vegetation started to grow, however still patchily distributed; trees were up to 4 m high. Few zones had a thin but more or less closed canopy; areas comprising dense grass sods with shrubs and isolated trees existed equally as did degraded, still barren spots and areas with thin grass cover and isolated trees. The soil between the grass swards was mostly still bare and hard. Dead wood and leaf litter available in reasonable quantities was irregularly distributed. During the dry season, grazing was allowed to the farmers own livestock and the women collected wood for cooking. Soil-sheetings of foraging termites were distributed on the ground and on tree trunks. Epigeal mounds of fungus-growing termites (genus *Macrotermes*) and the smaller mounds of soil-feeders were mostly located at the base of trees. More habitat photos are shown in Fig. A2-8 (Appendix 2).

Site 4 (Fig. 2-4): Old Zaï forest (ZF30), in 2009 about 30 years since the initial, degraded stage. In the rainy seasons of 2004, 2006 and 2007, when soil-arthropods had been sampled, the forest was thus around 25 years, 27 years and 28 years old. The first four years, the land had been cultivated with the Zaï method and was then left fallow ever since; about 26 years during which a diverse woody and herbaceous vegetation developed (Fig. 2-4). Several medically valuable tree species were additionally planted by the farmer. Almost everywhere thin but closed canopy of up to 8 m height. Dense grass sods existed mostly in the areas with open canopy. Traversing stone lines were still present and, during the last two study years, lines of dead branches were placed by the farmer at the sites' borders where the last barren spots were located. No wood collection or grazing was allowed during the last 10 years – before, wood collection and grazing during the dry season as in ZF20. Large amount of litter could be found on the ground or still attached to trees. Soil-sheetings of foraging termites were visible everywhere, during the dry season most tree trunks were also covered. The farmer planned to introduce more medicinal plant species. A fence to surround the forested land and a well were financed by the ministry BMBF in the last project year. Several mounds of *Macrotermes* and of soil-feeders were built mostly at the base of trees. More habitat photos are shown in Fig. A2-9 (Appendix 2).

More detailed information about the biotic and abiotic parameters assessed in each habitat (physico-chemical soil properties, vegetation, etc.) is given in Chapter 4. The relative position of the Zaï stages to one another is shown in Fig. A2-10 (Appendix 2).

2.1.2 Second disturbance gradient, the agricultural system in the North-Sudan region

The second land-use intensification gradient (LUI-2) at an altitude of 253 m comprised four land-use types about 52 km south of Fada N'Gourma, the capital of the Gourma province in the North-Sudan region, south-eastern Burkina Faso (Fig. 2-1). Unlike the first gradient which was beginning its succession with a degraded, barren and crusted soil, the second gradient was starting from the 'opposite end of the succession', a protected woody grass savanna in the Pama reserve. Increasing human impact was leading to increasing habitat degradation.

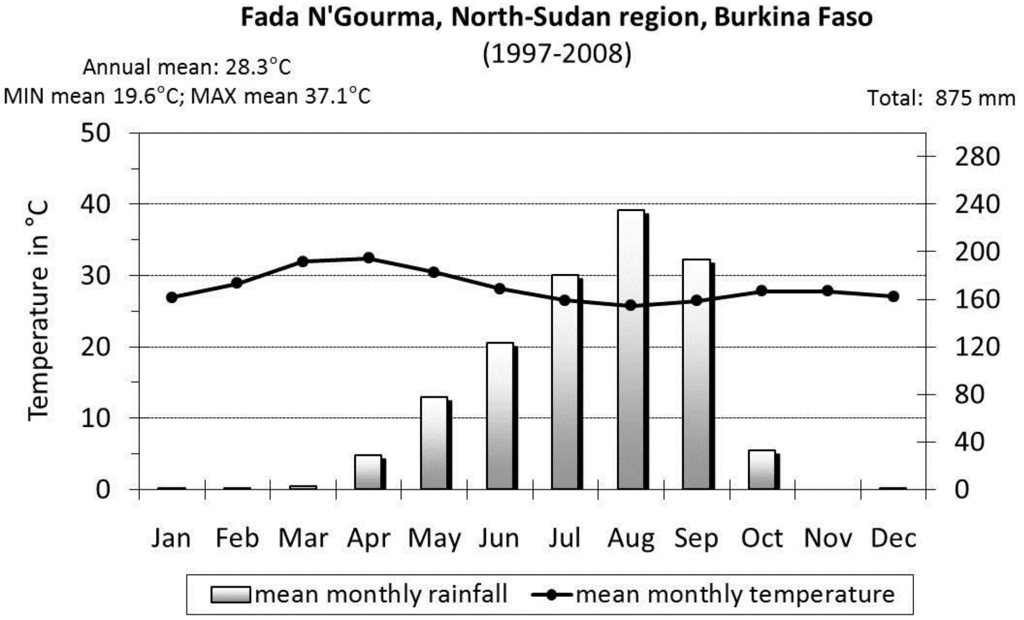
2.1.2.1 Geography, climate, soil and vegetation

The Gourma Province is located in the eastern and southeastern part of Burkina Faso. It is located between longitudes 0°7'W and 1°25'E and latitudes 13°7'N and 11°55'N and has a total area 11,217 km² (Some et al. 2006).

The North-Sudanese climate type typically has an annual rainfall between 750 and 1,000 mm. The rainy season starts with the onset of the monsoon winds around mid-April and lasts till mid-September/October (Some et al. 2006). The wettest months are July to September, the driest and coldest December and January. The hottest months are March to May. Inter-annual variability in rainfall is significant and a declining trend in rainfall was experienced during the 1980s, with annual rainfalls ranging between 709 mm and 612 mm (Some et al. 2006). The mean monthly temperature (°C) and the mean monthly rainfall (mm) which was prevailing in Fada N'Gourma and PK52 between 1997 and 2008 are illustrated in Fig. 2-5. The numbers behind the figure are shown in the table below. The average monthly temperature ranged between 19.6°C and 37.1°C, the annual mean was 28.3°C (Fig. 2-5). The mean total annual rainfall summed up to 875 mm (Fig. 2-5). Fig A2-11 in the Appendix of Chapter-2 additionally illustrates the mean monthly temperature (°C) in Fada N'Gourma calculated with data from 1980 to 2008 and the precipitation (mm) with data from 1940 to 2008.

Lixisols, Leptosols, Arenosols, Regosol and Acrisols were reported as the commonest soil types in the area (Niemeijer & Mazzucato 2003). INERA identified four main soil types in the area: ferruginous soils, gravelly soils, Vertisols and brown soils (INERA 1995). The leached ferruginous soils, sometimes associated with other types of soils, cover most of the province (Some et al. 2006). They are moderately deep to deep, sandy on the surface and sandy/clayey at greater depth and have low fertility levels (Some et al. 2006). Soils generally have a low chemical fertility, low levels of organic matter, a limited availability of exchangeable cations, poor water retention, low permeability and porosity and also suffer from sealing, crusting and hard-setting (Niemeijer & Mazzucato 2003; Some et al. 2006).

The natural vegetation of the Sudanese domain in general appears denser than the northern one and is of the savanna type according to UNESCO's classification (UNESCO 1977). Typical tree species occurring throughout the region are mahogany tree (*Khaya senegalensis*), shea tree (*Vitellaria paradoxa*), locust tree (*Parkia biglobosa*), baobab (*Adansonia digitata*) and various acacia species (Niemeijer & Mazzucato 2003). Comprehensive lists of the dominant vegetation are given in the literature (e.g. Guinko 1984; Ouedraogo 2006; Thiombiano 1996; Thiombiano 2005; Thiombiano & Kampmann 2010). The main crops, ordered according their importance, are sorghum, millet, groundnuts, maize, cowpea and sesame. Minor crops include rice, Bambara groundnuts, yams, sweet potatoes, cassava, cotton and soya (Mazzucato & Niemeijer 2000).



Sources: BIOTA West climatology group (2005-2008); Centre for Development Research (ZEF), Germany; Direction régionale de l'Agriculture de l´Hydraulique et des Ressources halieutiques, Burkina Faso.

1997-2008 (LUI-2)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
mean temp (°C)	26.9	28.9	31.9	32.4	30.4	28.2	26.5	25.8	26.4	27.8	27.8	27.1
mean rainfall (mm)	0	1	3	28	78	123	180	235	194	33	0	0

Fig. 2-5: Mean monthly temperature (°C) and rainfall (mm) in Fada N'Gourma and PK52, Gourma province, south-eastern Burkina Faso, calculated with data measured between 1997 and 2008. The data basis used is given in the table below the figure.

2.1.2.2 Description of the study sites

In 2000 botanists of the BIOTA project installed ten 'biodiversity observatories' (BOs, each with an area of 1 km^2) for vegetation long-term monitoring in the protected savannas of the Pama reserve. They proposed two BOs as characteristic near-natural habitat for the region. These two plots were chosen as Site 5, representing the initial habitat stage of this second land-use intensification gradient (LUI-2) (Fig. 2-6). Separated from the park border by a street was the farmer community called 'PK52', a rural area comprising habitats differing in the magnitude of human impact. A pasture, a field left fallow (henceforth referred to as 'fallow') and two cotton fields were chosen as Sites 6, 7 and 8 (Fig. 2-7 to Fig. 2-9).

Fig. 2-6: Two plots with protected savanna in the Pama reserve (FRes; Site 5), representing the initial habitat stage of the second land-use intensification gradient located about 52 km south-east of Fada N'Gourma.

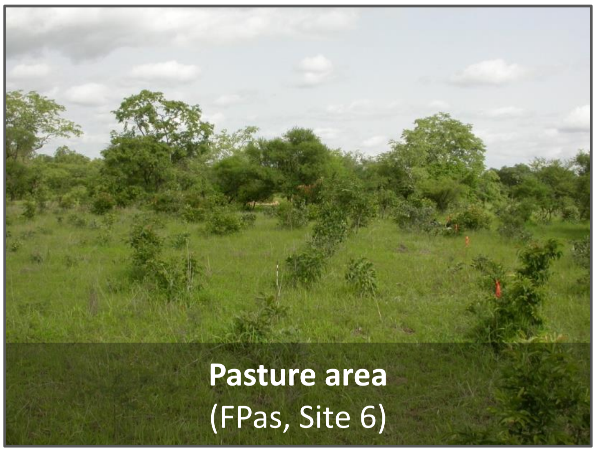


Fig. 2-7: Pasture land since 20 years exclusively used for grazing cattle (FPas; Site 6). The pasture is located in a rural area, the farmer community 'PK52' which is separated from the reserve-border by a street.

Fig. 2-8: Short-term fallow (FFal; Site 7). The area was the last fallow in the community; when sampling in the 2nd and 4th year fallow. Crop rotation was practiced every 3rd year (see text). Adjoined the cotton field sampled in 2004.

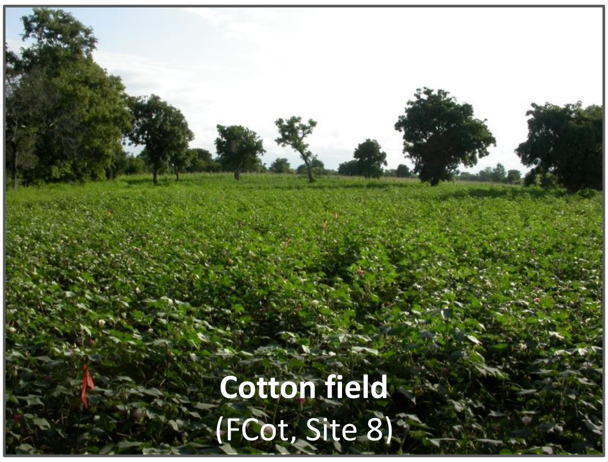


Fig. 2-9: Two fields of the cash-crop cotton (FCot; Site 8), when sampling both in the 2nd year of cotton cultivation; most disturbed habitat although crop rotation was practiced every 3rd year. Seven different insecticides and pesticides were applied in one season.

More photos of the study sites are shown in Appendix 2 (Fig. A2-12 to Fig. A2-15). The relative location of the four study sites to one another in Fig. A2-16 (Appendix 2)

Each plot had a size of about one hectare. The linear distance between the two savanna-plots and the agricultural sites was 1.5 km and 2.5 km, respectively. The small-scale farmer Ousmane Loualy was practicing crop-rotation since 20 years to help the soil recover from the pesticides and insecticides applied during the years of cotton cultivation. Every third year the crop was changed from cotton (*Gosypium barbadense*) to maize (*Zea mays*) to millet (*Pennisetum typhoides*) or sorghum (*Sorghum bicolor*) and again to cotton to maize to millet or sorghum and so on. Every tenth year, he planned to leave the fields lie fallow for two or three consecutive years. However, due to space limitations he abandoned the latter procedure in recent years. Minor variations of this practice were noted during the study period – see site history of the two cotton fields.

Site 5 (Fig. 2-6): Protected near-natural arboreous and shrubby savanna in the Pama reserve (FRes), representing the initial stage of all sites belonging to the second disturbance gradient (LUI-2). Most areas had dense grass sods, bushes and 8–9 m high trees with open canopy (assemblages of *Combretum* spp., *Anogeisus leiocarpus*, *Vitellaria paradoxa* according to data source of Adjima Thiombiano, see also Thiombiano and Kampmann (2010). As the reserves' true age was unknown, the age of the oldest site (20-years old pasture) was assumed for the reserve in order to calculate an agricultural intensification index (method see Chapter 3.5; results see Chapter 5). Wood collection and grazing was strictly forbidden in the whole park. Foresters managed the reserve traditionally by burning the vegetation during each dry season. Large amount of litter and decaying wood could be found on the ground and still attached to trees. Traces of active soil fauna, especially termites and earthworms, were noticeable all-over the ground. More habitat photos are shown in Fig. A2-12 (Appendix 2).

Site 6 (Fig. 2-7): Pasture land (FPas) of the farmer community which was exclusively used for grazing cattle since about 20 years (in 2009). The pasture comprised few areas with thin but closed canopy of up to 9 m in height, others with grass and some bushes and those with bushes and open canopy but more than just a few isolated trees. Most areas had more or less dense grass cover; the soil between the grass swards was mostly very hard. In the few degraded, barren spots, gullies were formed by water-runoff during rainfalls. The pasture had a light incline towards the fallow located south of the pasture. A lot of dead wood, leaf litter and animals droppings were irregularly distributed. More habitat photos are shown in Fig. A2-13 (Appendix 2).

Site 7 (Fig. 2-8): Agricultural field fallowed for 4 years (2003–2006) (FFal); the area represented the last fallow in the farmer community (subsequently referred to as 'short-term fallow' or 'fallow'). In 2009, the field was about 19 years old (since the initial stage). When sampling soil-arthropods in 2004 and 2006, the field was 14 years and 16 years old and in the 2nd and the 4th year fallow, respectively. Before fallowing, crop rotation was practiced every third year (crop-sequence see below), including 4 years cotton cultivation with extensive use of pesticides. The fallow adjoined one of the two cotton fields (cotton field-1, sampled in 2004). All trees originally growing within the area had been felled, only four 3–4 m high trees were left at the sites' margin: two individuals of *Vitellaria paradoxa* and two grazing-resistant *Balanites aegyptiaca* – both highly valuable species. Within the field, only some smaller bushes of the fallow-typical species *Pyliostigma thonningii* and *Acacia gourmaensis* were left by the farmer. Most areas had dense grass cover; the soil between the grass swards was mostly very hard. Litter, dead wood or dung was present in reasonable quantities, however irregularly distributed. The site had an exceptionally high number of nests of the granivorous ant species *Messor galla*: in 2004, about 85 nest-entrances were counted within the whole hectare plot. More habitat photos are shown in Fig. A2-14 (Appendix 2).

Crop sequence:
1991-1992: Sorghum / millet
1993-1994: Cotton
1995-1996: Maize
1997-1998: Sorghum / millet
1999-2000: Cotton
2001-2002: Maize
2003-2006: Fallow
2007-2008: Maize

Site 8 (Fig. 2-9): Two fields of the cash-crop cotton (FCot), about 300–400 m apart. In 2009, both fields were cultivated for about 13 years. In the rainy seasons of 2004 and 2006, when soil-arthropods had been sampled, both fields were in the 2nd year of cotton cultivation. Site 8 represented the most disturbed habitat although crop rotation was practiced every third year (crop-sequence see below). During one season of cotton cultivation, seven different insecticides and pesticides were applied (9.3 kg ha^{-1} yr^{-1}). One 4.5 m high *V. paradoxa* tree was left at the margin of cotton field-1. After the harvest, decaying leaves, dung and stumps of cotton plants were spread on the ground while only little organic matter was noticed during the rainy season. Except for some soil-sheetings constructed by foraging termites at the fields' margin, almost no traces of active soil fauna were found within the fields. More habitat photos are shown in Fig. A2-15 (Appendix 2).

Crop sequence cotton field-1:	Cotton field-2:
1997–1998: Cotton	1997–1998: Sorghum / millet
1999–2000: Maize	1999–2000: Cotton
2001–2002: Sorghum / millet	2001–2002: Maize
2003–2005: Cotton (3 years)	2003–2004: Sorghum / millet
2006–2007: Maize	2005–2007: Cotton (3 years)
2008–2009: Sorghum / millet	2008–2009: Maize

More detailed information about the characteristics of each habitat (physico-chemical soil properties, vegetation, etc.) is given in Chapter 4.2.2. The relative position of the land-use types to one another is shown in Fig. A2-16 (Appendix 2), a screenshot made in Google Earth.

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3. GENERAL METHODS

3.1. TRANSECT PROTOCOL FOR THE RAPID ASSESSMENT OF TERMITE AND ANT DIVERSITY

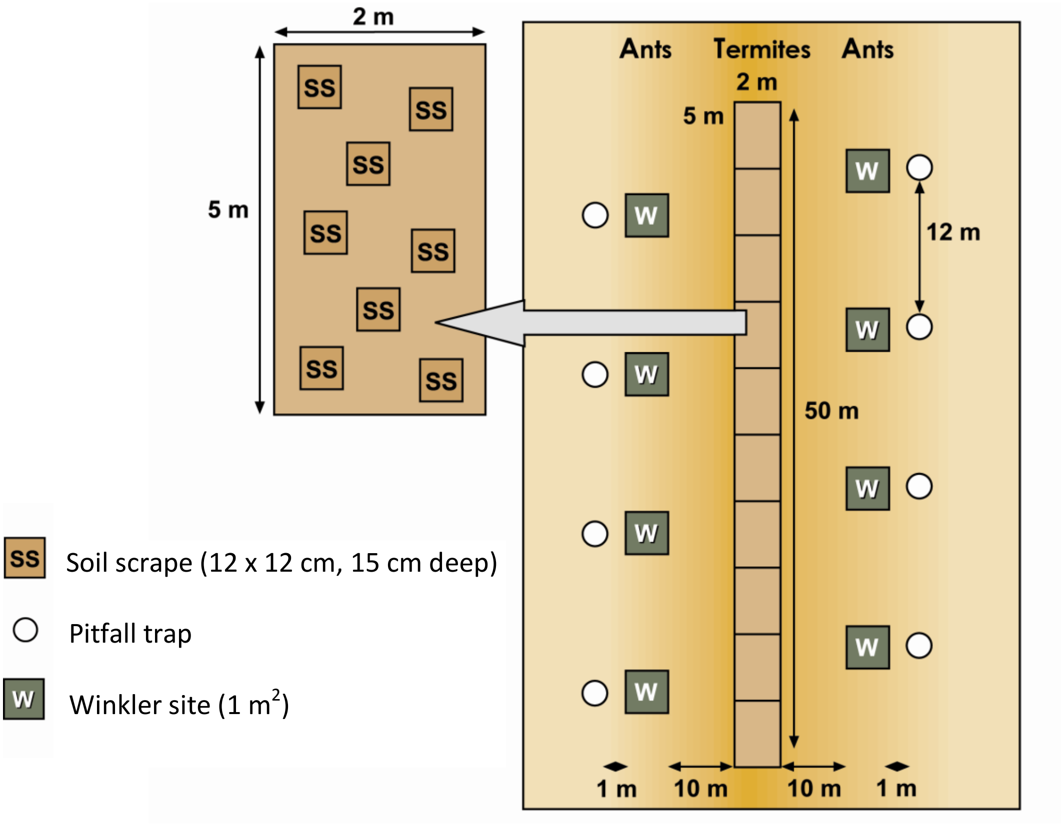

Fig. 3-1: Relative position of sampling sites according to the combined and standardized rapid assessment protocol (RAP), followed to assess termite and ant communities.

By following the standard protocol, sampling was conducted aiming to determine the taxonomic and functional group composition of the local termite and ant fauna, their relative abundance and distribution in the different habitats. It was also intended to provide reliable estimates of the asymptotic species richness. All data used in the analysis originate from standardized transects which were run in the rainy seasons between 2004 and 2008. Whenever logistically feasible, all sampling was done during the cooler morning hours (06:00 a.m. – 12:00 a.m.) since termite activity in the savanna was observed to decrease markedly later during the day.

3.1.1. Termite communities

As described by Jones and Eggleton (2000) for termites in tropical forests, the baseline transect protocol was a 100 m long and 2 m wide belt-transect. The belt-transect was divided into 20 contiguous sections of 10 m^2 (each 5 x 2 m) which were numbered sequentially. Due to the limited size of most habitats that were studied in Burkina Faso, the transect-length had to be shortened to 50 m resulting in 10 contiguous sections (Fig. 3-1). In all sites too small for placing transect-replicates randomly, care was taken that the same area was not sampled twice. Since transects represented the sample in statistical analyses (*N* = 4 means four transects were conducted), they had to cover all the heterogeneity within a respective habitats: e.g. they were placed along the topography in case of an existing slope.

Sampling termites in the transect-sections involved two parts: microhabitats and soil scrapes. One section had to be completed in one man-hour, resulting in 30 min sampling-time for each of the two parts (see Fig. 3-1 and Fig. 3-2).

3.1.1.1. Microhabitats

Part 1: microhabitats (MH). In each section, the following micro-sites were searched for termites (Fig. 3-1, Fig. 3-2): humus-rich soil and accumulations of litter or fallen leaves at the base of tree trunks; between grass tufts; the inside of dead wood, broken twigs or branches; dry grass; millet or cotton stems; under the bark and in dead wood attached to trees up to a height of 2 m; soil inside and under rotten logs; termite-made structures like soil sheetings and runways on vegetation, epigeal mounds and subterranean nests. Soil-sheetings are constructed by termites during their foraging activity over the food source as protection against desiccation and predators (Fig. 3-2). More examples of microhabitats searched for termites are shown in Appendix 3 (Fig. A3-1). Care was taken that the available sampling-time of 30 min was distributed across as many of these microhabitats as possible, so that not all the time was spent for looking in one type only. That means for example, when termites had been collected under soil-sheetings for the duration of 5–10 min already, they were next sampled in rotten wood, under the bark or at the base of trees – whichever microhabitat was present in the section as well – even if more soil-sheetings were left unsearched. Epigeal termite mounds were sampled destructively to allow for sampling of the inquiline species (Eggleton & Bignell 1997).

3.1.1.2. Soil scrapes

Part 2: soil scrapes (SS). Eight samples of surface soil (so-called ‘soil scrapes’) with the dimensions of 12 x 12 cm and about 15 cm deep were dug with a machete at random locations distributed over the whole section-area (Fig. 3-1, Fig. 3-2). The dug-out soil was hand-sorted on a tray *in situ* to collect a representative sample of the termites (workers, soldiers if present). The original protocol was slightly changed since (Jones & Eggleton, 2000) dug 12 scrapes of the same area but to a depth of 10 cm only. More examples are shown in Appendix 3 (Fig. A3-1).

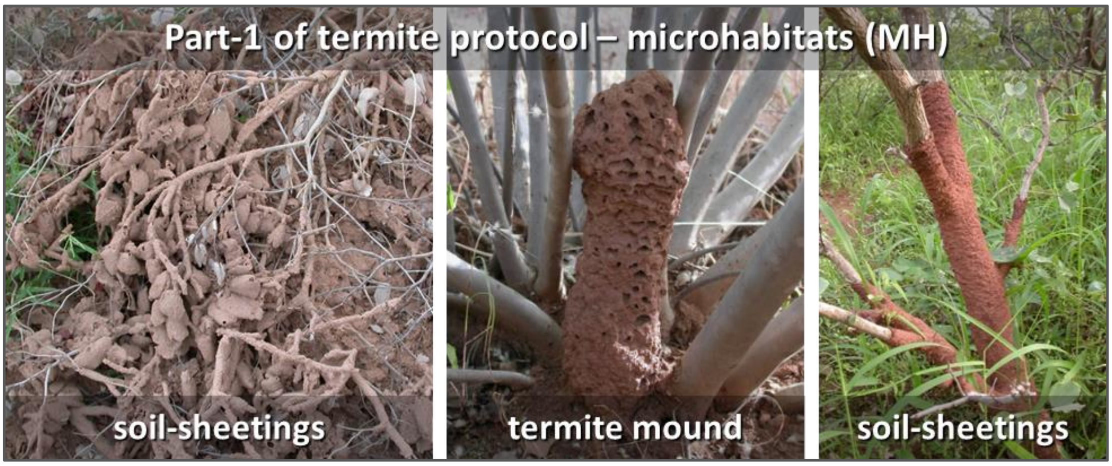

Fig. 3-2: Sampling methods to rapidly assess termite communities following the combined and standardized assessment protocol (RAP). Above examples for the first part, the microhabitats searched for termites; below the second part, the soil scrapes. More photos are shown in Appendix 3 (Fig. A3-1).

3.1.1.3. Timing and stopping-rule

Previous experience suggested that the search time of one man-hour per section applied in tropical forests can often be reduced in savannas without loosing accuracy. Savannas and agro-ecosystems are structurally less diverse and have fewer termite inhabited microhabitats than tropical forests. Therefore, stopping rules apply if no or only very few microhabitats can be found (e.g. in cotton fields or degraded soil) – thus resulting in a shorter sampling time per transect.

3.1.1.4. Specimen selection

Since species can only be reliably identified with a microscope, collectors were trained to sample specimens from every termite population encountered. Priority was given to finding soldiers, as these are the easiest to identify; workers were always collected.

3.1.1.5. Additional sampling methods hand-collection and baiting

The results of the standardized sampling protocol were supplemented with species records collected during approximately equal time spent sampling casually (hand-collections) in the area around the belt-transects (radius about 50 m). Furthermore, termites were actively attracted to different bait types which were placed in a standardized pattern all over the habitats.

For termites, two bait types each replicated 10 times, toilet paper rolls and soft wood blocks, were alternately placed on the soil surface in a distance of about 5–10 meter to each other, depending on the size of the study site. The 20 baits were regularly checked for up to 10 days. For photos illustrating baiting, please refer to Appendix 3 (Fig. A3-2).

3.1.2. Ant communities

Ants were collected on parallel transects in a distance of 10 m along both sides of the termite transect – at a total of eight sampling stations (16 stations for 100 m transect length), four stations at an interval of about 12 m on either side (Fig. 3-1).

As prescribed by the ALL (Ants of the Leaf Litter) protocol (Agosti & Alonso 2000), each sampling station or site comprised one pitfall trap and 1 m apart a Winkler quadrate, both methods especially suited to characterize the leaf litter ant community. However, the limited size of our habitats led to the reduction of the 20 originally prescribed sampling stations. Following our combined assessment protocol (Kaiser et al. 2011), three parts were involved in sampling ants: Pitfall traps, Winkler sites and termite transect (Fig. 3-1, Fig. 3-3). More photos are shown in Appendix 3 (Fig. A3-3).

3.1.2.1. Pitfall traps

Part 1: Pitfall traps. As pitfall trap, we used the lower halves of 1 ½ l plastic water bottles (Laafi, Ø 10 cm) which can be found everywhere in Burkina Faso. Each trap was dug 1 m apart of the Winkler site with as little disturbance of the surrounding ground as possible. Its upper border was on a level with the soil surface (Fig. 3-1, Fig. 3-3, and Fig. A3-3). Ants, walking on the ground, simply fall into these traps. The traps were closed for 24 hours before the start of sampling to reduce the digging-in effect (Greenslade 1973). A longer time period was not feasible due to tight schedules in other regions. The next day, all traps were filled with 45% alcohol. A transparent roof was fixed at a height of about 5 cm by three to four thin metal rods to protect the trap against rain or litter falls. Pitfall traps were then left open for 48 hrs.

3.1.2.2. Winkler sites

Part 2: Winkler sites. The original Winkler method described for forest habitats where litter covers the soil surface was applied in all land-use types for one year (see photos in Fig. A3-3; Appendix 3). Since comparable litter layers were virtually missing in our land-use types studied in BF, a modified version was applied henceforth: in an area of 1 m^2 (so-called 'Winkler sites') the vegetation was at first searched for ants and thereupon totally removed, and all ants were collected for the duration of 5 minutes (Fig. 3-1, Fig. 3-3)

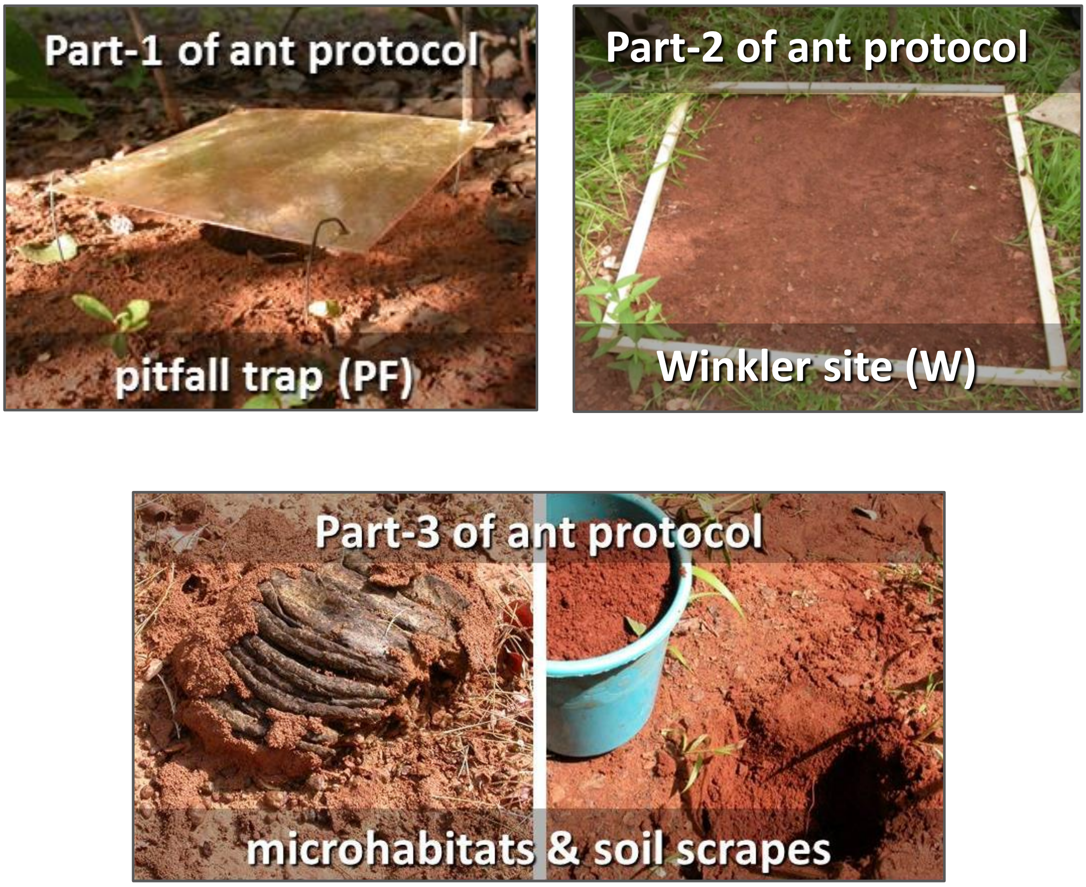

Fig. 3-3: Sampling methods to rapidly assess ant communities following the combined and standardized assessment protocol (RAP). Above examples for the first and second part, pitfall traps and Winkler sites; below the third part, microhabitats and soil scrapes of the termite transect. More photos are shown in Appendix 3 (Fig. A3-3).

3.1.2.3. Microhabitats and soil scrapes

Part 3: Termite transects. According to our new combined protocol, ants were additionally collected whenever encountered within the termite transect. Microhabitats and soil scrapes thereby increase the standard methods used to collect ants which can be compared between the different land-use types (Fig. 3-1, Fig. 3-3).

For a detailed description of the working steps see also Kaiser et al. (2011). More photos are shown in Appendix 3 (Fig. A3-3).

3.1.2.4. Additional sampling methods hand-collection and baiting

The results of the standardized sampling protocol were supplemented with species records collected during approximately equal time spent sampling casually (hand-collections) in the area around the belt-transects (radius of about 50 m). Furthermore, ants were actively attracted to different bait types. Four bait types following two protocols were used to attract ants actively. For photos illustrating all of these bait types please refer to Appendix 3 (Fig. A3-4).

Sieve buckets. For subterranean army ants, palm oil was mixed with soil and filled in the lower halves of 1 ½ liter plastic water bottles (Laafi). A soldering iron was used to perforate all sides. These ‘sieve buckets’ (Berghoff et al. 2003) were then burrowed below the soil surface so that its upper border was on a level with the soil surface. They were checked regularly for the duration of 14 days. A handle made from wire were used to lift the sieve buckets out of the soil.

Cookies, tuna and sugar water. Crumbs of cookies, tuna and sugar water, each replicated 10 times, were placed on plastic bags and alternately distributed across the habitat. The distance between the thirty baits was about 5 to 10 m, depending on the size of the study site. Two hours, mostly additionally four hours after placement, all baits were checked for ants.

3.2. IDENTIFICATION OF COLLECTED SPECIMEN

All collected specimens were placed in vials filled with 90% ethanol and stored for later identification. Termites have been identified by Tra-Bi Crouland (Université de Cocody-Abidjan UCA, Station d´Écologie Tropicale de Lamto, Côte d’Ivoire), ants by Dr. Yéo Kolo (Université d’Abobo Adjamé, Centre de Recherche en Écologie, Côte d’Ivoire). Specimens of both taxa were identified to named species by using the taxonomic works of e.g. Bolton et al. (2007), Bolton (1995) and Bolton (1994) for ants, and e.g. Webb (1961), Emerson (1928), Sands (1998), Sands (1965b) and Sands (1965a) for termites. Whenever that was not possible, they were identified to genus level and based on external morphological characters assigned to morphospecies which were numbered in ascending order (sp. 1, sp. 2, etc.) according to their occurrence in the taxonomic identification. Additionally to taxonomic identification keys species were identified with reference to the collections of West African termites and West African ants, both held in the research station in Lamto (see above). For termite and ant species collected in Burkina Faso, own reference collections were assembled. They will be stored in the University of Ouagadougou (Burkina Faso), as well as in the University of Abidjan (Côte d’Ivoire) in order to serve as training material for students and as reference for later biodiversity assessments.

3.3. CLASSIFICATION OF TERMITES IN FUNCTIONAL GROUPS

It has been widely recognized that termites show different ecological responses according to their feeding habit, e.g. to habitat disturbance or natural and human induced successions (e.g. Eggleton et al. 2002; Eggleton et al. 1995; Eggleton et al. 1997; Hemachandra et al. 2010; Jouquet et al. 2006). In order to understand processes mediated by termites or to predict consequences for ecosystem functioning resulting from the loss of termite diversity due to habitat disturbances, it therefore is important to be able to recognize termite feeding groups. A recently developed feeding group classification (Donovan et al. 2001), based on morphological characters (e.g. molar plate ridges) and gut dissection to assign termite species according to their position along the humification gradient, has been applied by several authors (e.g. Deblauwe et al. 2008; Eggleton et al. 2002; Eggleton & Tayasu 2001; Hemachandra et al. 2010; Jones et al. 2003). However, due to the lacking potential for sophisticated and time-consuming gut dissections and the focus of our applied studies on the role of fungus-growing termites in the process of soil restoration, termites were assigned according to their food spectrum (Josens 1972), their mandible morphology (Deligne 1966) and following Tano (1993), Grassé (1986), and Kouassi (1999) to one of the following four functional/feeding groups (FG): soil feeder, wood feeder, grass feeder and fungus grower.

Soil feeder (sf):	feed on humus, mineral soil or on extremely decayed wood that has lost its structure and became soil-like;
Wood feeder (wf):	consume wood;
Grass feeder (gf):	also known as harvester termites, subsist on grass (Poaceae);
Fungus-grower (fg):	collect a whole range of plant material and animal excrements to cultivate a fungus (genus *Termitomyces,* Basidiomycotina) responsible for the decomposition of the organic matter.

The same classification was applied in all termite studies conducted in the framework of BIOTA West Africa (Ivory Coast, Benin, Burkina Faso), thereby resulting in fully comparable data sets (e.g. Dosso et al. 2010).

3.4. STATISTICAL METHODS

Only those species collected following the protocol for the combined and rapid assessment of termite and ant communities have been considered in the statistical analyses. Species collected by means of the additional sampling methods baiting and hand-collection were exclusively used to complete the consolidated species lists of termites and ants.

3.4.1. The presence-absence approach

Due to the social habits of termites and ants, only nest-counts could count as true abundance data. These nest counts, however, are practically impossible to perform since many species have inconspicuous, belowground nests (Chung & Maryati 1996; Fisher 1999). For social insects, the presence-absence approach is recommended (Folgarait 1998; Longino 2000) which, however, gives no measure of the absolute abundance per unit area. Instead, a semi-quantitative measure of the relative abundance is provided via the number of encounters per transect even if autocorrelation among sections might confound results (Jones 2000; Jones et al. 2003). One encounter is defined as the recorded presence of a species in one transect-section (Jones & Eggleton 2000). The species' frequencies of occurrence, which are more independent of identical sampling efforts behind, might be easier to handle – especially for comparisons among habitats. The frequency of a species can be calculated by dividing the sum of encounters with the respective species through the total number of sampled sections and multiplying the result with 100. With frequencies, habitats can also be compared if slight differences exist between the section-number sampled per site (i.e. the sampling-effort).

3.4.2. Species richness estimators and the use of accumulation and rarefaction curves

Community species richness is one of the most important criteria used to assess the conservation value of an ecosystem. To obtain a reliable estimate of species richness is an important goal (Chichilnisky 1996; Kremen et al. 1993)**.** Colwell and Coddington (1994) treat communities as though they were discrete and propose that biodiversity is partitioned into two parts, the species richness of the local community and the complementarity among these communities. With this assumption, species accumulation or rarefaction curves rise owing to increasingly accurate sampling and species richness is considered a finite community parameter (Longino 2000). Whenever sampling effort differed between the habitats to be compared, the rarefaction method was used to calculate the number of species expected in a subsample randomly selected from multiple samples (Chiarucci et al. 2008; Koellner et al. 2004; Sinclair & Byrom 2006). However, irrespective of the method used, estimators only yield reliable estimates of the total species richness of a community, when the species accumulation or rarefaction curve is close to reaching an asymptote (Soberon & Llorente 1993). To visualize the general trend more clearly, smoothed curves were produced by randomizing the data 500 times. Randomizing averages the data and removes chance effects of the sample order. The slopes of species accumulation and rarefaction curves illustrate the rate at which new species were added with increasing sampling effort. However, unless sampling has been exhaustive, they do not directly reveal total species richness. Increasing sampling effort was equivalent with increasing number of a) transect sections for termites, and b) sampling units, each comprising one transect section, one pitfall trap and one Winkler quadrate (1 m^2) in the case of ants. However, only eight ant sampling stations (each comprising one pitfall trap and one 'Winkler-site') were installed per 50 m transect; two sampling units for ants consequently correspond to one transect section only.

A rarefaction curve can be regarded as statistical expectation of the corresponding accumulation curve, with lower species numbers. While accumulation curves are viewed from left to right, rarefaction curves are viewed from right to left. According to Magurran (2004), rarefaction curves are used to graphically compare the species richness of two or more communities at a smaller common sampling effort. Rarefaction curves represent the mean of repeated re-sampling of all pooled samples. Thus, comparable to species accumulation curves, samples are added randomly to the curve and this procedure is repeated 500 times, thereby producing smoothed – or randomized – curves. According to Colwell and Coddington (1994), extrapolations to estimate the species richness are logically possible when "a uniform sampling process for reasonably stable universe" is represented by the accumulation curves. In other words, extrapolations should only be made when samples were taken in a systematic way and from a reasonably homogenous habitat (i.e. neither *ad hoc*-sampling nor large-scale biogeographic zones).

For incidence data, the most common non-parametric estimators used to calculate the species richness per transect or per habitat are Chao-2, the incidence-based coverage estimator or short ICE, Jackknife-1, Jackknife-2, and bootstrap. They are termed 'non-parametric' methods because they are not based on the parameter of a species abundance model; their performance depends on the underlying distribution (as in other diversity measurements). Moreover, the asymptotic estimator Michaelis-Menten Mean was calculated. The software EstimateS Version 7.51 for Windows (Colwell 2005) was used to calculate the species accumulation and rarefaction curves as well as the estimators. Brose et al. (2003) used simulated systems to study the accuracy and bias of different richness estimators. They concluded that the accuracy of the different methods was influenced by the sampling intensity, the actual species number and the species evenness i.e. the pattern of relative abundance. The formulas used to calculate the estimators are shown in Appendix 3. For a more detailed description of their mathematical background please refer to the literature (e.g. Chao et al. 2006; Colwell et al. 2012; Magurran 2004).

The performance of the estimators can be evaluated by calculating the mean deviation (MD), the mean square deviation (MSD), and the mean square proportional deviation (MSPD) (Palmer 1990). Additionally, Pearson's correlation coefficient (r^2) between estimators and true values measures the adequacy of estimators for comparison purposes. The formulas used to calculate these measures are shown in Appendix 3.

3.4.3. Diversity indices

Diversity indices are mathematical functions that combine species richness and evenness of a community in a single measure (Colwell 2009). Whittaker (1960) introduced the terms alpha-diversity (α), beta-diversity (β) and gamma-diversity (γ) in 2006. His classification refined in 1972 was adopted here (Whittaker 1972): *Alpha-(α)-diversity*, the diversity of species within a community or habitat. *Beta–(*β*)–diversity*, a measure of the rate and extent of change in species along a gradient, from one habitat to another. Alpha–diversity is a quality that just has a magnitude and could theoretically be described by a single number, a scalar. Beta-diversity, in contrast, is analogous to a vector which has a magnitude and direction. Although there are many others, the most commonly used alpha-diversity indices in ecology are Shannon diversity and Simpson diversity (Colwell 2009). These widely used indices Simpsons' D and Shannons H' were thus applied to compare the α–diversity of separate transects and by combining all replicates of land-use types. The use of these indices is especially practical for a comparison with the literature, i.e. for other ant (Delgado et al. 2008; Delsinne 2007; Delsinne et al. 2010; Leponce et al. 2004; Sakchoowong et al. 2008) or termite community studies (Birang 2004; Dosso et al. 2010; Tripathi et al. 2007). The results are displayed as boxplots, showing the variations of the different replicate transects. Additionally the numbers are given in tables since these are easier to compare with the literature. The software EstimateS Version 7.51 for Windows (Colwell 2005) was used to calculate the indices; Simpson diversity is computed in its inverse form, a higher number therefore means higher diversity. The formulas used to calculate them are shown in Appendix 3. For a more detailed description of their mathematical background please refer to the literature (e.g. Colwell 2009; Hill 1973; Magurran 2004).

3.4.4. Comparisons among study sites

The Windows version of SPSS 15.0 (SPSS Inc. 2006) was used for comparisons between the different habitats concerning their species composition, the number of species observed (or expected at the common sampling effort), the various species richness estimators as well as the α-diversity indices. Friedman's ANOVA was used to compare species composition and the number of species observed (or expected at the common sampling effort) between land-use types belonging to the same gradient, i.e. between related land-use types as for example the four Zaï stages. The non-parametric equivalent to the dependent t-test, the Wilcoxon sign-rank Test, was used for pairwise comparisons between related land-use types. In order to correct for family-wise error inflation, the Bonferroni correction was applied afterwards to adjust the level of significance.

We performed a Wilcoxon rank-sum Test as well as the Mann-Whitney U Test when comparing two independent samples as e.g. the comparison of communities on a regional level. SPSS automatically produces both statistics – since they are related they always say the same. The effect size 'r' was calculated from the difference (Z-score) with the formula: $\mathrm{r} = \frac{\mathrm{Z}}{\sqrt{\mathrm{n}}}$

3.4.5. Parameters correlating with variations in community composition

The existence of the horseshoe effect has been used to argue that Principal Components Analysis (PCA) is inappropriate for ecological or environmental studies and should not be used to study organization along gradients. Instead, 'Correspondence Analysis' (CA) or 'Detrended Correspondence Analysis' (DECORANA) should be considered to study the organization along gradients (Henderson & Seaby 2008). In this study, 'Canonical Correspondence Analysis' (CCA) was used to find possible causal factors explaining variations in community composition and the relative abundance of termites and ants along the intensification gradients. CCA is an ordination method derived from CA which was modified to incorporate environmental data into the analysis. The analysis was carried out using the 'Environmental Community Analysis 2.1.3' software (ECOM-2; Pisces Conservation Ltd. 2007) (Henderson & Seaby 2007b) with ant and termite frequencies at the lowest taxonomic level possible. The result is a plot showing the relationship between the RAP-transects ('samples'), the species or functional groups (FG) within each transect ('dependent variables') and the environmental parameters ('explanatory variables'). CCA is called a constrained analysis method as the ordination is constrained by the environmental variables. For a detailed explanation of the method please refer to Henderson and Seaby (2008). ECOM offers the choice between two ways of scaling the CCA-plot: 'sites at species centroids' and 'species at site centroids', the first is emphasizing the difference between the species, the latter between the samples (here: transects) – the former was taken to scale the plots shown in the result-section.

The environmental parameters used in the analysis were: 1) parameters assessed during sampling to characterize the different transect-sections (estimated crown cover percentage, soil temperature, litter density, etc.); 2) results of laboratory analyses of soil samples taken within the RAP-transect sections (soil organic matter content, pH, CN-ratio, etc.); 3) parameters describing the vegetation of the different habitats that were assessed once per land-use type in an area of 900 m^2. Parameter as the latter, taken to characterize the whole habitat, were then used for all replicate transects. As all environmental parameters were needed for the whole transects rather than separate sections, the medians (*Md*) of the parameters were calculated for each transect and then used in the analysis. Please refer to Chapter 4 (biotic and abiotic habitat parameters) for the methods and a description of the parameters assessed to describe the soil, the vegetation and the transect-sections.

The statistical significance of the environmental variables (indicated by the analysis) in explaining the variation in the data was tested by a Monte-Carlo test based on 10,000 random permutations.

3.4.6. The adjustment of environmental and species data before the analysis

The environmental variables used varied greatly in magnitude, with the area covered by tree trunks ranging from 0 to 12,528, the soil organic matter content from 0.4 to 1.9 or the litter-density ranging on a scale 0 to 4. To address the numerical dominance of e.g. the total tree trunk area which might have dominated the analysis simply because of the unit of measurement used, all parameters were standardized by dividing the values by their respective (row) maximum value. As a result all parameters covered the same order of magnitude and were ranging from 0 to 1. Furthermore, since rare species seldom add to the analysis only causing confusion in the graphical presentation, they were removed before carrying out the CCA analysis.

3.4.7. Significance of replicate-transects to differentiate land-use types

The significance of groups formed by transects that were run in the same land-use type (the replicate-transects) was tested using the '*Analysis of Similarities*' (ANOSIM) and the '*Similarity Percentages*' analysis (SIMPER). The idea behind: if the groups are meaningful, samples within groups – the replicate-transects – should be more similar in their composition than samples from different groups (here: transects run in different land-use types) (Henderson & Seaby 2008). The CAP4 software (Community Analysis Package, Pisces Conservation Ltd.) (Henderson & Seaby 2007a) was used to perform both analyses.

3.4.7.1. Analysis of similarities (ANOSIM)

The 'Analysis of Similarities' (ANOSIM), a method first developed by Clarke (1988), was used to test if replicate-transects were more similar in their composition than transects from different land-use types. The null hypothesis tested was that there were no differences between transects of the different habitats. Hence, the null hypothesis was rejected if replicate-transects were more similar in their composition than transects from different land-uses. The test statistic 'R' measures in ANOSIM the difference between the mean of the ranked similarity between and within groups by using the Bray-Curtis measure of similarity (Henderson & Seaby 2008). R ranges from +1 to -1; with R = +1 indicating that the most similar samples are all within the same groups, and R = -1 that they are never in the same group; R = 0 thus indicates that high and low similarities are perfectly mixed and are never related to groups (Henderson & Seaby 2008). Samples are randomly assigned to groups 1,000 times and R is calculated for each permutation. The observed value of R is then compared with the one calculated for random distribution. According to Henderson and Seaby (2008), it can be concluded that transects of the same habitat are more similar than would be expected by chance if the R-value is significant.

3.4.7.2. Similarity percentages (SIMPER)

The '*Similarity Percentages*' (SIMPER) analysis breaks down the contribution of each species to the observed similarity or dissimilarity between individual samples – in our case the RAP-transects. It allows the identification of those species that are most important in creating the observed pattern of similarity (Henderson & Seaby 2008). To undertake the SIMPER test, the group membership of the replicate-transects had to be defined first. The method uses the Bray-Curtis measure of similarity, comparing in turn, each sample in group 1 (land-use type 1) with each sample in group 2 (land-use type 2). The Bray-Curtis method operates at the species level and therefore the mean similarity between land-use type 1 and 2 can be obtained for each species (Henderson & Seaby 2008). SIMPER results are presented in WITHIN- and BETWEEN-tables of groups, both types on the level of species. The within-group tables show the within-group similarities while the between-group dissimilarities for each pairwise group combination are shown in the between-group tables (Henderson & Seaby 2008).

3.4.8. Species characterizing the different land-use types

Additionally, the '*Two-Way Indicator Species Analysis*' (TWINSPAN) (Hill 1979) was used to examine similarities in species composition among the 16 transects belonging to the first intensification gradient (LUI-1) and among the 13 transects belonging to the second (LUI-2). The CAP4 software (Henderson & Seaby 2007a) which was used to perform TWINSPAN displays the classification as a dendrogram. TWINSPAN identifies those species (so-called 'preferentials') that are influential in determining which transects are separated at each node, thus helping to define the dissimilarity between communities at that level of the dendrogram (Henderson & Seaby 2008).

3.5. Calculation of the agricultural intensification index (AI)

To rank the different land-use systems along their respective intensification gradient from the least to the most intensive ones, we quantitatively assessed parameters that reflect the frequency and intensity of human interventions. Parameters like the duration of cropping periods, the mean tillage frequency or the mean fertilisation rate were then used to calculate an agricultural intensification index (AI). This AI-index which was modified from Decaëns and Jimenez (2002) and Giller et al. (1997) is given by the following equation:

$$\mathrm{AI} = \frac{\mathrm{CI} + \mathrm{PCR} + \mathrm{GP} + \mathrm{FR} + \mathrm{TF}}{\mathrm{N}}$$

Where 'AI' is the agricultural intensification index, 'CI' is in this context the mean cultivation-intensity (land-use intensity), i.e. the proportion of the year the system is cropped, 'PCR' the mean pest control rate (kg of chemicals used annually per ha), 'GP' the mean grazing-pressure per year (in %), 'FR' the mean fertilisation rate (kg of compost used annually per ha), 'TF' the mean tillage frequency per year and 'N' the number of parameters or 'sub-indices' used for the calculation of the AI-index. The annual stocking rate (International Animal Units ha^{-1}) could not be determined with the information given by the farmers. Therefore, the mean grazing-pressure was used instead, indicated as the annual mean when grazing was allowed (in %). For the calculation of the AI-index, each sub-index is calculated as an annual mean use of a given agricultural practice, which takes into account all the years since the establishment of the system (age of the site). The sub-indices' respective maximum values are brought back to 1 by dividing each individual value by the corresponding highest value. As a consequence, all sub-indices are weighted equally and range from 0 to 1 for all systems. Low AI-values (close to 0) reflect the least intensified systems, e.g. the near-natural savanna of the Pama Reserve. High AI-values (close to 1) on the other hand reflect the most intensified ones, e.g. the cotton fields with pesticide application.

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4. BIOTIC AND ABIOTIC HABITAT PARAMETERS

Several key environmental factors were measured in order to characterize the study sites more thoroughly and to identify so-called 'predictor variables' for variations in the focal soil communities. Predictor variables are biotic and abiotic habitat parameters which exert significant or causal influence on variations in the taxonomic richness, the functional diversity or the composition of termite and ant communities. Some of these biotic and abiotic parameters were measured for the whole study site, while others were especially noted for each section of the belt-transects that were conducted to rapidly assess the termite and ant fauna. Please refer to Chapter 3 for a detailed description of the standard protocol 'RAP' followed to sample the focal soil-dwelling arthropods.

4.1. METHODS

4.1.1. General site characteristics

The general characteristics of the two study regions in Burkina Faso, as well as the general characteristics of the studied land-use types including their site history are described in Chapter 2. A summary is given in Chapter 5 (Table 5-1 and Table 5-2).

4.1.2. Physico-chemical soil properties

In each of the land-use types studied in the sub-Sahelian (LUI-1) and North-Sudanese (LUI-2) region in Burkina Faso, numerous topsoil samples (0–10 cm) were taken in the sections of the transects conducted to collect termites and ants. In the four Zaï stages (LUI-1), additional topsoil samples were taken at locations that were predetermined by the design of the experiment described in Chapter 8, among other things conducted to study the effect of foraging termites on soil turn-over – topsoil samples were taken in the control-plots.

For habitat characterization, additional samples were taken every 10 cm along soil profiles that were dug at randomly chosen locations – in the sub-Sahelian sites up to 1 m depths (N = 5 in ZF20, N = 13 in ZDeg, ZMil and ZF30), in the North-Sudanese sites up to 30 cm depths (N = 3). In the Zaï stages, only the profile-locations in the millet field and the young Zaï-forest were randomly chosen; those in the degraded land and the old forest were predetermined by the design of another experiment, conducted to study the effect of the foraging activity of termites on the soil water content (not yet analyzed).

Sample pre-treatment procedure

All samples were sun-dried, weighed with an electronic scale (0.01 g sensitivity), then crushed and passed through a 2 mm sieve to separate coarse fragments and gravel from the fine earth fraction (so-called 'matrix soil'). To account for the small-scale heterogeneity of most tropical soils, the fine earth fraction (about 150 g) was mixed subsequently with three to four comparable samples (same horizon, same transect) to form a composite soil sample. Duplicate samples were stored for both, separated and composite soil samples.

Table 4-1: Physico-chemical parameters analyzed in the pedological laboratory (University of Frankfurt, Germany) including their abbreviations (short), units and the methods used.

Soil parameters	short	Unit	Laboratory methods
Soil-pH	pH_{KCL}	–	In suspension of deionized water and 0,1 n potassium chloride (KCl) pursuant DIN 19684-1
Electrical conductivity	EC	mS cm^{-1}	In filtrate from suspension of ultrapure water and 0,01 m $CaCl_2$; DIN 19684-1
Soil organic carbon	SOC	g kg^{-1} or mg kg^{-1}	LECO EC-12 for mineral soil; DIN ISO 10694 (1996)
Soil organic matter	SOM		Calorimetrically
Total soil nitrogen	N_{total}		Kjeldahl-method (Kjeldahl 1883) as described by (Anderson & Ingram 1993), DIN 19684-4
Total soil phosphorous	P_{total}		Inductively coupled plasma optical emission spectrometry (ICP-OES); DIN EN ISO 11885
Exchangeable cations	Na^+, K^+, Mg^{2+},Ca^{2+}	$mmol_c$ kg^{-1}	Mehlich-procedure set out in DIN 19684-8 and DIN ISO 13536 (1997); exchangeable cations: sodium (Na), potassium (K), magnesium (Mg), calcium (Ca)
Cation exchange capacity	CEC		
Base saturation	BS	%	
Plant-available phosphorous	P_CAL	mg kg^{-1}	CAL-method as described by (Schüller 1969)
Plant-available potassium	K_CAL		
Soil water content	SWC	%	Gravimetrically
Bulk density	BD	µS cm^{-1}; mS cm^{-1}	In the Zaï stages: 'sand replacement method' as in DIN 18125-2; in the sites near Fada N'Gourma: core method as in (Blake 1965)
Grain size distribution, soil texture	clay%, silt%, sand%,	%	Köhn-method (Köhn 1928) set out in DIN 19683-1,2; Measured were the seven fractions clay, coarse- (gU), middle- (mU) and fine silt (fU), coarse- (gS), middle- (mS) and fine sand (fS); the totals of the three main fractions were used in the analysis

All soil samples were transported to the pedological laboratory of the University of Frankfurt (Germany) for the analysis of the physical and chemical soil parameters assumed to be important for soil-dwelling arthropods. In Table 4-1, the parameters, their abbreviations and units as well as the methods used in the laboratory to analyze the samples are listed.

Chemical soil parameters (Table 4-1)

Soil-pH (pH_{H2O}); electrical conductivity (EC); soil organic carbon (SOC), soil organic matter content (SOM); total soil nitrogen (N_{total}); total soil phosphorous (P_{total}); exchangeable cations sodium (Na^+), potassium (K^+), magnesium (Mg^{2+}) and calcium (Ca^{2+}); potential cation exchange capacity (CEC) and base saturation (BS). Selected soil samples were additionally analyzed for the plant-available nutrients phosphorous (P_CAL) and potassium (K_CAL).

Physical soil parameters (Table 4-1)

For the soil texture which is the grain size distribution seven size fractions were analyzed (coarse, middle, fine sand; coarse, middle, fine silt; clay) and are illustrated for each horizon along the soil profile. However, only the totals of the main fractions (sand%, silt%, clay%) were used in the analysis and the formulation of the soil type.

The soil textural triangle used to determine the soil type is illustrated in Fig. A4-1 (Appendix 4). For the samples taken every 10 cm along soil profiles dug in the four Zaï stages, bulk density (BD) and soil water content (SWC) were determined. SWC was immediately determined gravimetrically. Due to the high proportion of stones and gravel in the soil of the Zaï stages, bulk density could not be determined following the standard core method. Alternatively, the ‘sand replacement method’ (Sandersatzmethode) was used for each horizon to determine the volume of soil samples (pursuant DIN 18125-2). To account for the small scale heterogeneity of soils in general, BD was measured along five soil profiles per Zaï stage.

4.1.3. Vegetation characteristics

The prominent vegetation features were assessed once per site during the rainy season – in 2006 and 2007 in the North-Sudan and sub-Sahel zone, respectively. A square-cut survey plot with an area of 900 m^2 was installed in the center of each site and sub-divided into plots of 2 x 2 m, yielding a total of 225 contiguous subplots per land-use type.

In each subplot, the following measures were taken (Table 4-2): The vascular plant species richness, the number of individuals and the number of seedlings per species. The crown-cover percentage which is the area shaded by tree crowns when the sun is straight above and the grass-cover percentage were visually estimated. The height and the circumference at the base of the main stem were measured for all trees exceeding 100 cm height. Calculated from these circumferences was the woody plant basal area, which is the total soil-surface, covered by tree trunks; however, values are very conservative since only the main trunk was measured per tree. Specimens of all encountered plant species were collected to create a reference collection for later studies. In the different Zaï-stages, the assessment and the identification of plant species was supported by Zan Idrissa, a technician from the IRD ('Institut de recherche pour le développement') in Ouagadougou, and in the North-Sudanese sites, by botany students of BIOTA West Africa (Amadé Ouédraogo, Oumarou Ouédraogo, Sylvestre Da) and technicians (Yacouba Guinko and Cyrille Sinare) of the University of Ouagadougou.

Table 4-2: Vegetation features assessed either once per site in a square-cut plot of 900 m^2 during the rainy season (2006 North-Sudan, 2007 sub-Sahel), or within each transect-section.

Vegetation parameters assessed within a square-cut plot of 900 m^2 area (225 sub-plots)	
Vascular plant species richness	
Number of individuals per species	
Number of seedlings per species	
Grass cover percentage (1)	visually estimated proportion of each sub-plot (100% = 4 m^2)
Crown cover percentage	
Height of the main stem per tree	of all trees ≥ 100 cm height
Circumference at the base of the main stem	
Woody plant basal area	calculated with the circumferences
Vegetation parameters assessed within each transect section (2 x 5 m)	
Grass cover percentage (1)	visually estimated proportion of each transect section (100% = 10 m^2)
Crown cover percentage	
Degraded area percentage	
Litter availability	semi-quantitative estimates on an ordinal scale from 0 to 4
Gravel in the topsoil in percent	gravimetrically

(1) Maximum value possible for grass cover was 85% (Prof. A. Thiombiano, pers. comm.)

Measurements on the level of transect-sections (Table 4-2): To characterize each section of the termite transects, grass cover percentage, crown cover percentage and the degraded area were visually estimated and are given as a proportion of the total surface area of one section (100% = 10 m^2). The maximum value possible for grass cover percentage was 85% (Prof. Adjima Thiombiano, pers. comm.).

4.1.4. Air temperature and precipitation

In cooperation with the climatology group of BIOTA-West, climatic stations were installed in both agricultural systems. For the North-Sudanese sites, a station was installed in 2005 between the reserve and the three intensified habitats close to the house of Ousmane Loualy, the farmer who cultivated the fields. And in 2007, a climatic station was installed in the degraded site of the Zaï system in the sub-Sahelian region (Fig. A4-2 in Appendix 4). This location was already chosen in 2005 to install a tipping-bucket rain gauge and a temperature sensor (both HOBO) (Fig. A4-2). Among other parameters, the two climatic stations of the climatology group were measuring the air temperature, the relative humidity, wind speed, wind direction and the air pressure every ten minutes.

For the years before the start of BIOTA, daily temperature and rainfall data were provided by the 'Centre for Development Research' (ZEF) affiliated to the University of Bonn (Germany) and by the 'Direction régionale de l'Agriculture de l´Hydraulique et des Ressources halieutiques' in Ouagadougou (Burkina Faso). For the sub-Sahelian sites, these data were recorded in Ouahigouya about 3 km west of the study sites. The data provided for the North-Sudanese sites were measured in Fada N'Gourma, about 54 km north of the studied agro-ecosystems.

During the periods in which transects were conducted to rapidly assess the diversity of termites and ants, additionally Thermochron^{TM} iButton thermologgers (DS1921, Dallas Semiconductor) were used to monitor the air temperature in the respective habitat. IButtons are coin cell shaped data loggers that record up to 2048 temperature values (resolution of 0.5°C), taken at user-defined equidistant intervals (from 1 to 255 min). They are often used to monitor the temperature during the transport of sensitive material like frozen or fresh food, blood products or drug reagents. The air temperature was measured hourly with iButtons attached two meters above the ground to a tree.

4.1.5. Soil temperature

Thermochron^{TM} iButton thermologgers (DS1921, Dallas Semiconductor) were used to monitor the soil temperature when transects were run to rapidly assess termite and ant communities. The iButtons, programmed to record the temperature every 10 to 30 minutes, were buried in different soil-depths. Before burying the iButtons, they were wrapped in orange plastic tape to protect the device during heavy rainfalls and to facilitate re-finding them. The signal tape was also used as label to note the iButtons location, the starting date, sample rate and soil-depth.

The disadvantage of these otherwise low priced, self-sufficient systems was a relatively high failure rate. Up to 10% of the iButtons could not be programmed and had to be discarded from the start. About 10% to 20% of the iButtons used in the field showed malfunctions afterwards and the data could not be read out. Therefore, as well as to cover for any data losses due to iButtons that had been swept away during heavy rainfalls, soil temperature was measured at several locations in the respective habitat whenever spare iButtons were available.

4.1.6. Plant litter and other organic debris

In each study site, the quantity and main composition of food resources available to termites during the dry season was assessed in a standardized way. In 5–10 m intervals, 10–20 quadrats with an area of 1 m^2 area were placed along a line transect. Within each quadrat, all plant litter (dead plant material like dry grass, leaves and twigs that had fallen to the ground) and other organic matter (e.g. animal feces, crop residues) was collected and sorted according to its type. Samples were sun-dried and weighed with an electronic scale (0.01 g sensitivity). The term **'**litter**'** is used henceforth when referring to plant litter, animal feces and crop residues.

To account for annual climate variations, litter collection was replicated during several years. In the sub-Sahelian sites, litter was collected during four consecutive years (2006–2009), in the North-Sudanese sites during two (2006, 2007).

Measurements on the level of transect-sections (Table 4-2): To have a comparable measure for the amount of litter present in each transect-section, semi-quantitative estimates were made on an ordinal scale from 0 to 4, with:

'0'	No litter,
'1'	little,
'2'	some,
'3'	much,
'4'	plenty of litter.

4.1.7. Epigeal termite mounds

In each land-use type, epigeal mounds were assessed once during the rainy season; in the sub-Sahelian sites they were assessed within the whole hectare-plot, in the North-Sudanese sites they were assessed together with the vegetation within an area of 900 m^2. For the methods and the results of the mound assessment, please refer to the end of Appendix 4.

4.2. RESULTS

4.2.1. Disturbance gradient in the sub-Sahel region of Burkina Faso (LUI-1)

In the four succession stages of the Zaï system, the habitats that were forming the first land-use intensification gradient (LUI-1) studied in the sub-Sahelian zone of Burkina Faso, several biotic and abiotic parameters were assessed to characterize the habitat and the transects that were run within each habitat.

4.2.1.1. Physico-chemical soil properties

For each of the sub-Sahelian sites, between 18 and 22 composite samples were analyzed from the habitats' topsoil (0–10 cm). The most important parameters, including the sample number *N*, are listed in Table 4-3. Additionally, the topsoils' plant available nutrients, its cations, the potential cation exchange capacity and its base saturation are shown in Appendix 4 (Table A4-2). These latter parameters were analyzed for a reduced sample number only (*N* = 15 in the degraded soil and the young Zaï forest, *N* = 8 in the millet field, *N* = 10 in the old forest) (Table A4-2).

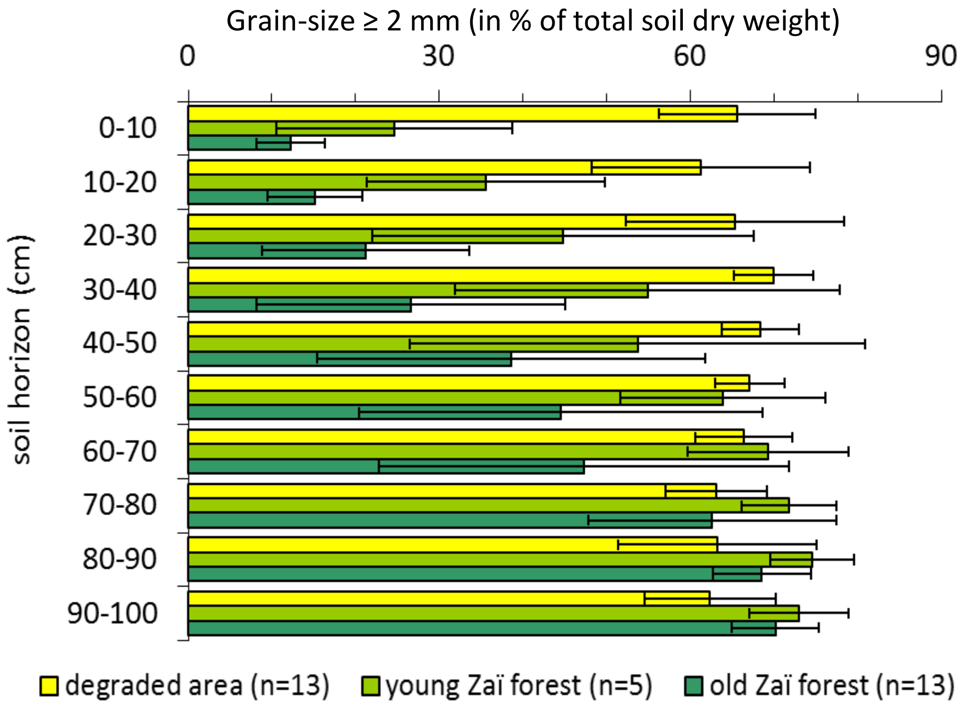


Fig. 4-1: The mean gravel content (in %), that is grain-size ≥ 2 mm, shown for each Zaï stage and each horizon along the soil profile. The means, calculated of all replicate profiles dug per habitat (*N* = 5 in the young forest, *N* = 13 in the other sites), are shown as share of the total soil dry weight. The standard deviations are indicated by the horizontal bars.

For habitat characterization, additional soil samples were taken every 10 cm along soil profiles which were dug up to a depth of one meter – five profiles in the young forest and 13 in the other three Zaï stages. The physico-chemical soil properties which characterize these profile samples, namely the soils' texture, its content in organic matter (SOM), total nitrogen (N_{total}), total phosphorous (P_{total}) and the pH-value are shown for each land-use type and each horizon (Fig. 4-2, Fig. 4-3, Fig. 4-4, Fig. 4-5). Fig. 4-1 illustrates for each horizon of the soil profiles dug in the degraded land, the young and the old Zaï forest, the resulting mean values for the gravel content (grain-size ≥ 2 mm) in percent of the total soil dry weight. The gravel content in the millet fields was discarded in this figure due to the limited maximal profile depth of 60 cm. The corresponding figure including the millet field is shown in Fig. A4-

3a (Appendix 4). For the profiles dug in the degraded area and the old Zaï forest, additionally the mean soil water content in percent of the total soil dry weight is shown in Fig. A4-3b (Appendix 4).

Between the four sites, differences could be noted with regard to the physico-chemical soil properties of both, the topsoil samples and the samples taken along the soil profiles (Fig. 4-1, Fig. 4-2, Fig. 4-3, Fig. 4-4, Fig. 4-5 and Table 4-3).

The topsoil of all Zaï stages was very acidic with a median pH value of below 5.6 (Table 4-3). Only two samples in the millet field were slightly acid. Four samples in the young forest were slightly acid to moderately alkaline (pH between 6.1 and 7.4); and four samples of the old forest were moderately to slightly acid. However, pH values measured in potassium chloride (KCl) solutions were reported to be often 1 unit lower than pH's taken in soil by water solution. All Zaï sites had a narrow CN-ratio with a median below 12 (Table 4-3). However, every succession stage had some samples with medium (12-15) and wide CN-ratios (15-20). The sand content was relatively high in all four habitats (Table 4-3). Electrical conductivity (EC), the parameter that estimates the amount of total dissolved salts or ions in the water, was very low in the four Zaï sites. The median and the maximum values of the EC indicated that saline effects were negligible to the crops; soils in the Zaï system were classified non-saline (Table 4-3).

The cation exchange capacity (CEC) is a measure of the soil's ability to retain the cation nutrients, including calcium (Ca^+), magnesium (Mg^+), potassium (K^+), and nitrogen in the ammonium form (NH_4^+). The negatively charged surfaces of clay and humus particles attract these positively charged elements. Once the cations are bound to these sites, they are protected from leaching away in water, while being still available for uptake by plant roots.

As plants absorb the cations, their roots release positively charged hydrogen ions (H^+), which then attach to the negatively charged sites previously occupied by the cation nutrients. As plants continue to take up the cation nutrients, there are more H^+ ions on clay and humus particles and in the soil water surrounding the particles, the acidity increases. More cation nutrients need to be added to assure an adequate future supply. The median-values of the potential CEC were very low in the young Zaï forest and low in the other three age stages (Table A4-2, Appendix 4). Base saturation (BS) represents the percentage of soil cation exchange sites occupied by the basic ions Ca^{2+}, Mg^{2+}, Na^+ and K^+. The difference between this value and 100% is the percentage of cation exchange sites occupied by acidic cations Al and H. Values over 60%, which are desirable under most conditions, were seldom obtained in the Zaï sites – once in the degraded soil and the millet field, twice in the young and four times in the old Zaï forest. Plant-available nutrients varied strongly in all Zaï stages (Table A4-2). Median-values of plant-available potassium are very low, especially in the degraded area and the young Zaï forest (Table A4-2). However low to medium values were also measured, especially in the millet field and the older Zaï forest. Plant available phosphorus, measured with the content in phosphorus pentoxide, was similarly low in all Zaï stages (Table A4-2).

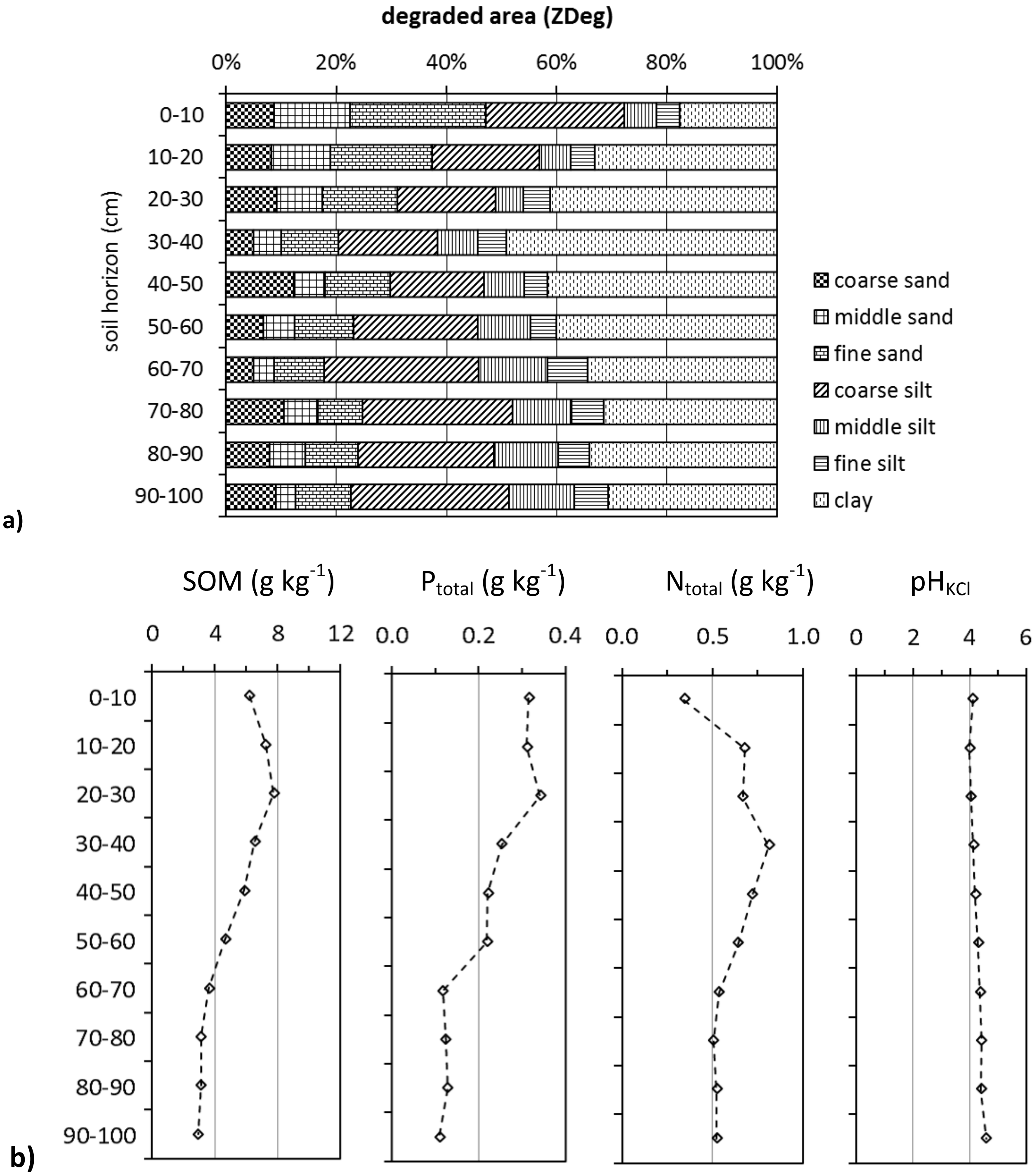
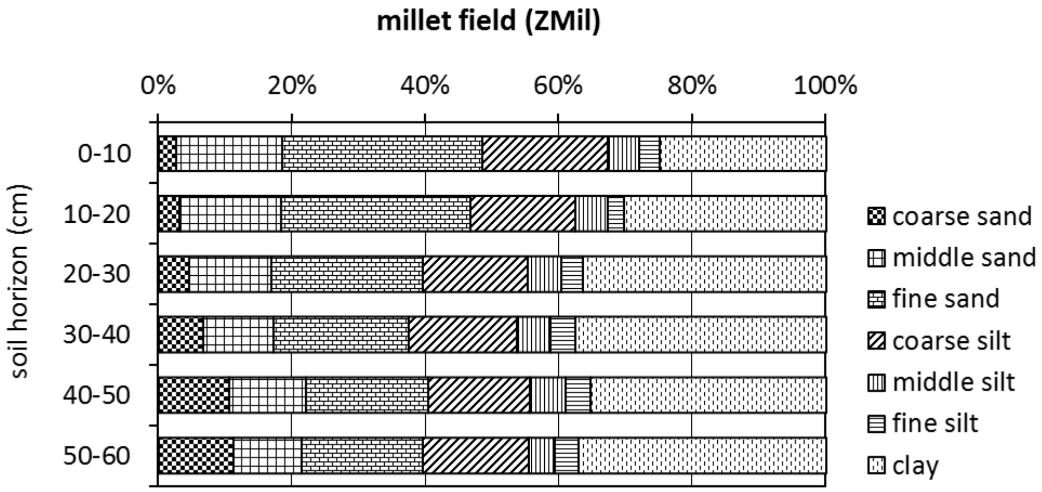
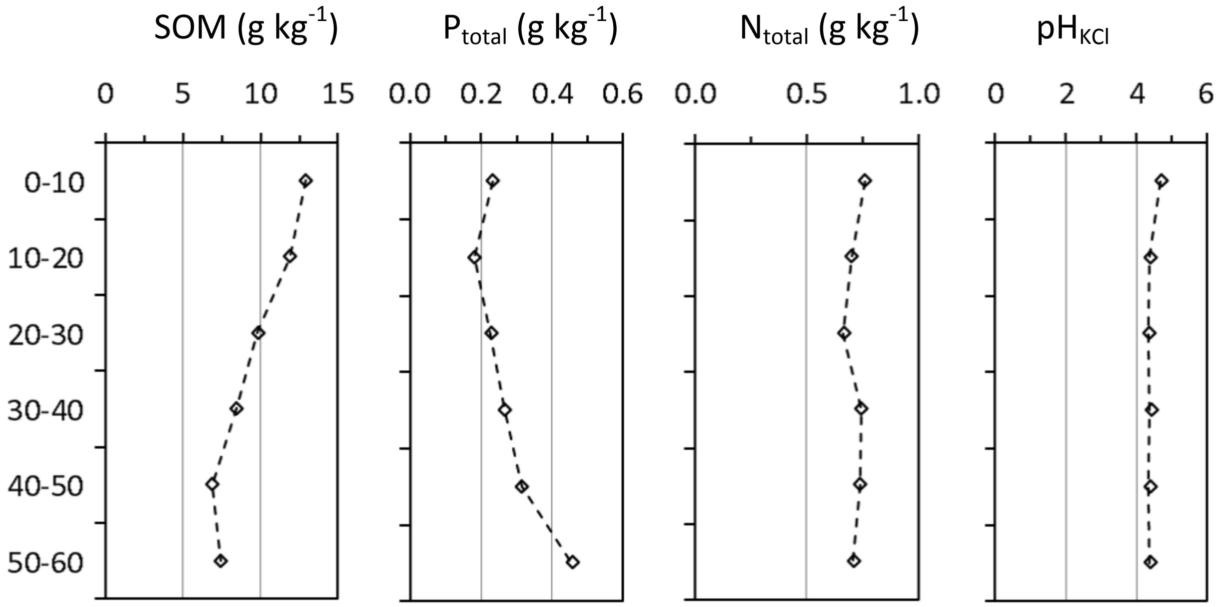


Fig. 4-2: For each horizon along the soil profile in the degraded area (ZDeg, Site 1) a) the soils' texture or grain size distribution of the fine earth fraction, and b) the soils' content in total nitrogen, total phosphorous and organic matter and the pH-value are shown. Analyzed were composite samples of the respective horizons of four profiles.



a)



b)

Fig. 4-3: For each horizon along the soil profile in the millet field (ZMil, Site 2) a) the soils' texture or grain size distribution of the fine earth fraction, and b) the soils' content in total nitrogen, total phosphorous and organic matter and the pH-value are shown. Analyzed were composite samples of the respective horizons of four profiles.

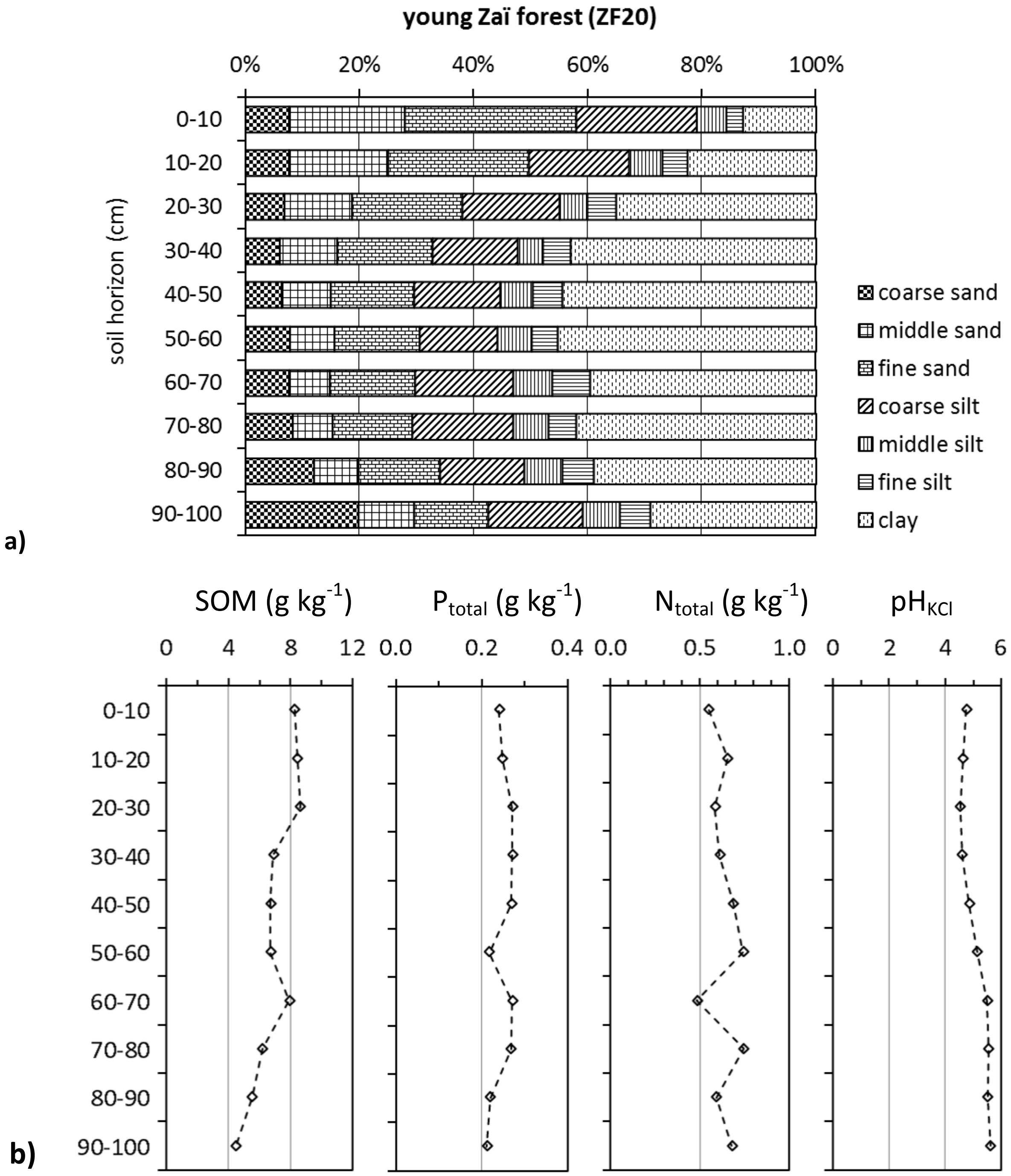
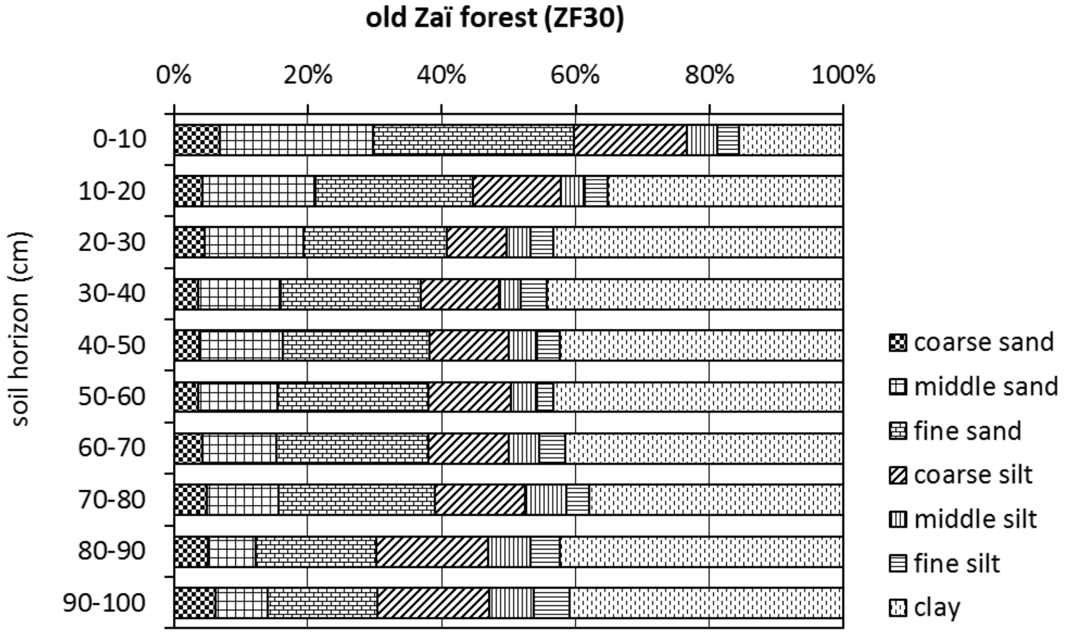
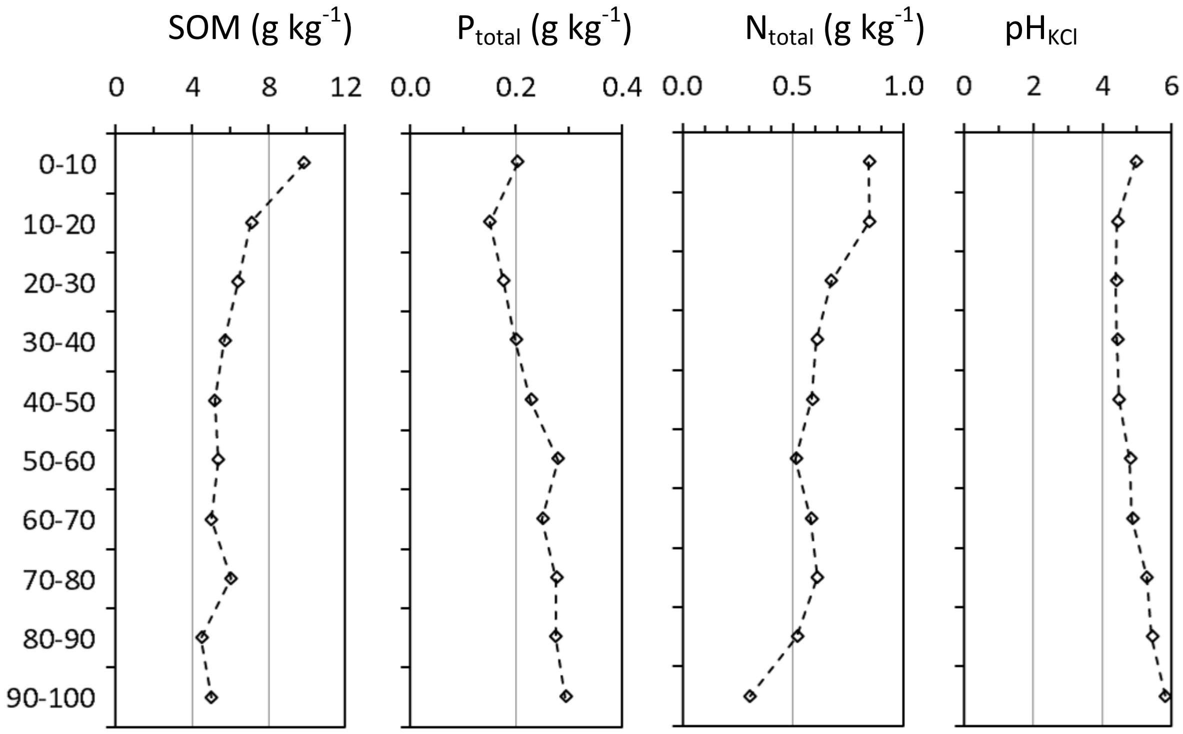


Fig. 4-4: For each horizon along the soil profile in the young Zaï forest (ZF20, Site 3) a) the soils' texture or grain size distribution of the fine earth fraction, and b) the soils' content in total nitrogen, total phosphorous and organic matter and the pH-value are shown. Analyzed were composite samples of the respective horizons of four profiles.



a)



b)

Fig. 4-5: For each horizon along the soil profile in the old Zaï forest (ZF30, Site 4) a) the soils' texture or grain size distribution of the fine earth fraction, and b) the soils' content in total nitrogen, total phosphorous and organic matter and the pH-value are shown. Analyzed were composite samples of the respective horizons of four profiles.

Table 4-3: Physico-chemical parameters of the topsoil samples (0–10 cm), taken in the succession stages of the Zaï system in Ouahigouya (sub-Sahel zone, Burkina Faso). For each parameter, first the median ± standard deviation, then minimum / maximum values are shown.

Study sites of the sub-Sahel zone	Characteristics of the habitats' upper soil horizon (0–10 cm)			
	degraded area ZDeg	millet field ZMil	young Zaï forest ZF20	old Zaï forest ZF30
N	18	22	20	21
Soil type	sandy loam	loam	loam	sandy loam
Sand (%)	57.9 ± 6.2	45.7 ± 9.4	51.9 ± 6.8	60.7 ± 9.5
	47.2 / 66.7	30.9 / 64.6	36.7 / 63.2	44.8 / 78.4
Silt (%)	25.0 ± 3.8	37.8 ± 6.6	37.2 ± 6.6	24.8 ± 7.0
	20.9 / 35.1	25.9 / 47.5	25.8 / 49.1	16.0 / 37.9
Clay (%)	15.2 ± 4.2	13.0 ± 6.2	10.9 ± 4.5	12.9 ± 5.1
	10.4 / 28.3	9.4 / 31.6	7.8 / 28.7	5.3 / 25.7
EC (µS cm^{-1}) *	50 ± 22	64 ± 16	45 ± 131	51 ± 41
	14 / 96	39 / 87	30 / 450	15 / 209
SOC (g kg^{-1})	3.3 ± 0.6	9.3 ± 2.2	6.2 ± 3.3	5.7 ± 2.3
	2.5 / 4.8	4.5 / 12.4	4.3 / 16.3	2.7 / 10.3
SOM (g kg^{-1})	5.7 ± 1.1	16.0 ± 3.8	10.7 ± 5.7	9.8 ± 4.0
	4.3 / 8.3	7.8 / 21.4	7.4 / 28.1	4.7 / 17.8
pH_{KCl}	4.3 ± 0.4	5.3 ± 0.5	5.2 ± 0.8	5.3 ± 0.5
	3.8 / 5.6	4.2 / 6.4	4.5 / 7.4	4.5 / 6.2
N_{total} (g kg^{-1})	0.40 ± 0.21	0.98 ± 0.18	0.61 ± 0.26	0.60 ± 0.24
	0.18 / 0.94	0.67 / 1.30	0.33 / 1.36	0.22 / 0.95
P_{total} (g kg^{-1})	0.26 ± 0.04	0.33 ± 0.14	0.27 ± 0.06	0.22 ± 0.08
	0.19 / 0.35	0.21 / 0.76	0.16 / 0.43	0.09 / 0.46
CN-ratio	7.6 ± 4.1	9.3 ± 2.2	10.8 ± 5.0	11.0 ± 2.5
	4.1 / 18.8	5.9 / 12.1	6.3 / 29.0	6.7 / 15.3

* EC-values (electrical conductivity): *N* = 16 for ZDeg, *N* = 12 for ZMil, *N* = 18 for ZF20, *N* = 19 for ZF30. Abbreviated parameters left are: *N* = sample number; the grain sizes = sand, silt, clay; SOC = soil organic carbon; SOM = soil organic matter; N_{total} = total soil nitrogen; P_{total} = total soil phosphorous; CN-ratio = carbon-nitrogen ratio.

4.2.1.2. Vegetation characteristics

The prominent vegetation features characterizing the Zaï stages were assessed once during the rainy season 2007 in a square-cut plot of 900 m^2 area. The assessment plot was divided into 225 contiguous subplots of 4 m^2. A summary of the parameters assessed is given in Table 4-4.

Table 4-4: Vegetation features characterizing the land-use types in Ouahigouya (sub-Sahel zone, Burkina Faso). In each habitat, the vegetation was assessed once during the rainy season 2007 within an area of 900 m^2 (divided into 225 contiguous sub-plots of 4 m^2 area).

	Vegetation characteristics (plot-area 900 m^2)			
Study sites of the sub-Sahel zone (LUI-1) (number of subplots x area)	Degraded area ZDeg (225 x 4 m^2)	Millet field ZMil (225 x 4 m^2)	Young forest ZF20 (225 x 4 m^2)	Old forest ZF30 (225 x 4 m^2)
Vascular plant species richness	0	12	21	24
Number of tree individuals	0	47	301	422
Mean height of main tree stem (cm)	–	116	170	284
Min / Max	–	50 / 270	50 / 390	93 / 825
Woody plant basal area (cm^2)	–	675	7,437	12,530
Number of seedling species	0	20	28	31
Number of seedlings	0	644	8064	15124
Dominant grass species	2	3	12	10
Mean crown cover per sub-plot (in %)	0	1	49	80
Min / Max	0 / 0	0 / 30	0 / 97	0 / 100
Mean grass cover per sub-plot (in %)	0	50 millet stalk 5 grasses	30	35
Min / Max	0 / 3	30 / 50 millet 0 / 10 grasses	0 / 80	0 / 80

The species lists of all vascular plants are shown in Table A4-3 in Appendix 4. The species are ranked in descending order depending on their abundance in a) the combined area of the four vegetation assessment plots (3,600 m^2), and b) in each habitat separately. The species names, which are abbreviated in Table A4-3, are listed in Table A4-1 (Appendix 4) – including the family and the order each species belongs to. Ten species represented 91% of all tree individuals that were assessed in the four habitats (total area of 3,600 m^2) (Table A4-3).

Vascular plant species richness and the number of tree individuals increased with increasing habitat restoration (Table 4-4). While neither trees nor seedlings were found in the degraded site, 47 trees belonging to 12 species were found in the millet field and 301 trees from 21 species in the young forest. The old forest was most diverse with 24 species and 422 tree individuals (Table 4-4). A comparable tendency was observed with regard to the number of seedlings, the number of species to which the seedlings belonged, the mean and the maximum tree height and the total area that was covered by tree trunks (Table 4-4).

4.2.1.3. Plant litter and other organic debris

The quantity and main composition of food resources available to termites during the dry season was assessed once per year (2006–2009). In 10–20 quadrates of 1 m^2 area which were placed along a line transect, all organic matter was collected and sorted according to its type (dead wood, leaves, dry grass etc.). The term 'litter' is used henceforth when referring to plant litter, animal feces and crop residues.

The total litter dry weight in gram per square meter and month within dry season is illustrated per Zaï stage in Fig. 4-6. With increasing habitat restoration or habitat complexity more food resources were available to termites (Fig. 4-6). In Fig. 4-7, Fig. 4-8, Fig. 4-9 and Fig. 4-10, the quantity is illustrated separately for each litter type. Leaf litter and dry grass comprised most of the collected litter – the amount increased with increasing habitat restoration (Fig. 4-7).

Additional remark: In 2006, the litter quantity was assessed in 36 quadrates in each of the four Zaï stages. However, the collected litter was not separated according to its type. The sample number (*n*) in Fig. 4-6 illustrating the total litter dry weight therefore differs from the sample number indicated in Fig. 4-7, Fig. 4-8, Fig. 4-9 and Fig. 4-10.

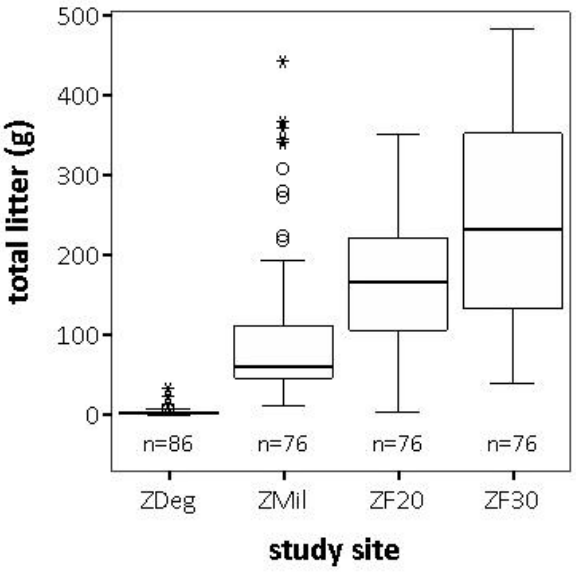


Fig. 4-6: Total litter dry weight (g) per square meter and month dry season. Litter was assessed during four consecutive years (2006–2009) in a standardized way. The difference between the sample number (*n*) in the figure and the number in the following four figures is due to the year 2006, when 36 quadrates were assessed per habitat but not separated according to the litter type.

Study sites are ZDeg: degraded land, ZMil: millet field, ZF20: young Zaï forest; ZF30: old Zaï forest.

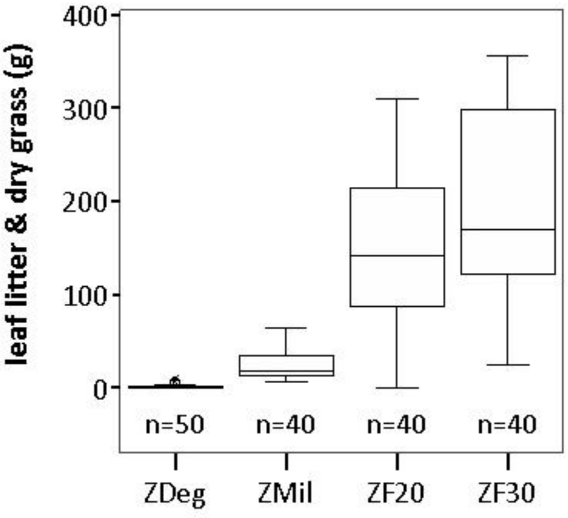


Fig. 4-7: Total amount of leaf litter and dry grass (g) assessed during three consecutive years (2007–2009) is shown per square meter and month dry season.

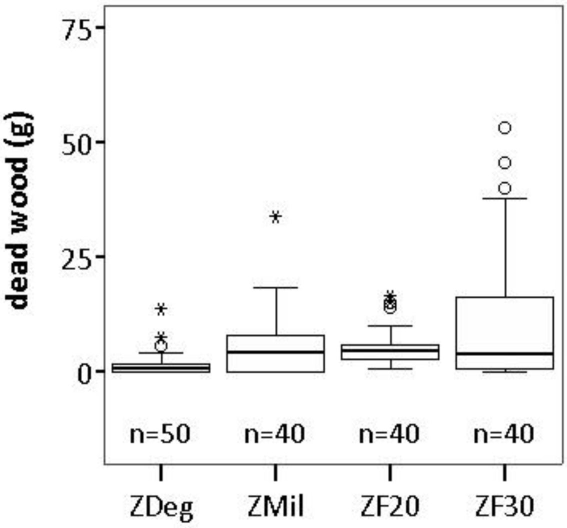


Fig. 4-8: Total amount of dead wood (g) assessed during three consecutive years (2007–2009) is shown per square meter and month dry season.

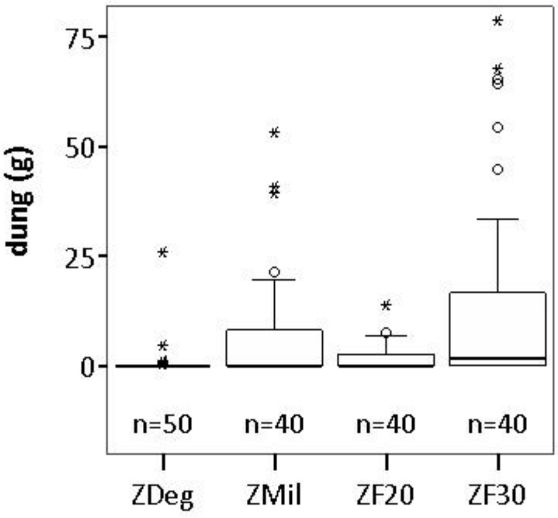


Fig. 4-9: Total amount of dung (g) per square meter and month dry season. Litter was assessed during three consecutive years (2007–2009) in a standardized way.

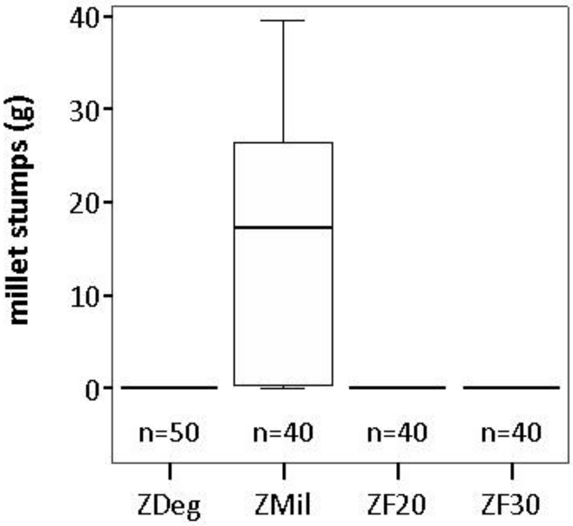


Fig. 4-10: Total amount of millet stumps (g) per square meter and month dry season. Litter was assessed during three consecutive years (2007–2009) in a standardized way.

Study sites are ZDeg: degraded land, ZMil: millet field, ZF20 / ZF30: young / old Zaï forest.

4.2.2. Disturbance gradient in the North-Sudan region of Burkina Faso (LUI-2)

In the four land-use types, that were forming the second land-use intensification gradient (LUI-2) studied in the North-Sudanese zone of Burkina Faso, several biotic and abiotic parameters were assessed to characterize the habitat and the transects that were run within each habitat.

4.2.2.1. Physico-chemical soil properties

For each of the North-Sudanese sites, between 6 and 13 composite samples were analyzed from the habitats' topsoil (0–10 cm); the samples were taken within sections of transects conducted to rapidly assess the termite and ant fauna. The most important parameters for these topsoil samples, including the sample number *N*, are shown in Table 4-5. The topsoils' potential cation exchange capacity (CEC) and base saturation (BS), analyzed for one composite sample per land-use type, are shown in Table A4-4 in Appendix 4.

For habitat characterization, four additional samples were taken from 0–30 cm soil depth, separated into the horizons 0–10 cm, 11–20 cm and 21–30 cm. The characteristics of these latter samples, namely the soils' texture, its content in organic matter (SOM), total nitrogen (N_{total}), total phosphorous (P_{total}), and the pH-value are shown for each habitat and each horizon (Fig. 4-11, Fig. 4-12, Fig. 4-13, Fig. 4-14).

Between the four habitats, differences could be noted with regard to the physico-chemical soil properties of the topsoil samples and those taken along the soil profiles (Fig. 4-11 to Fig. 4-14, Table 4-5). The combined content of coarse, middle and fine sand was very high in the reserve and the pasture area; both sites had values of about 60% although the variation over the three horizons varied in the pasture (Fig. 4-11, Fig. 4-12). The clay content was low in these two sites; about 10% in the reserve and between 10% and 20% in the pasture. The opposite was observed and in the cotton field and the fallow: clay contents were ranging from 30–40%, and combined sand-contents were varying between 20% and 30% in the upper two horizons and between 30% and 40% in the third horizon (Fig. 4-13, Fig. 4-14).

The topsoil of the four habitats was moderately acidic with the median pH value ranging between 5.6 and 6.0 (Table 4-5). Maximum pH values fell into the range slightly acid to neutral. The reserve, the pasture and the cotton field had a narrow CN-ratio with a median value between 8 and 10.5 – only one sample of the reserve had a medium ratio (9.5) (Table 4-5). The fallow had a medium CN-ratio (median of 13.3) although 5 of the 11 samples taken had a narrow CN-ratio between 6.9 and 9.5. The median and the maximum values of the electrical conductivity (EC) indicate that saline effects were negligible to the crops – all sites had values below 100 microSiemens (µS) or 0.1 millimhos (mmhos) per centimeter (Table 4-5). The soil in the sites near Fada N'Gourma was thus classified non-saline.

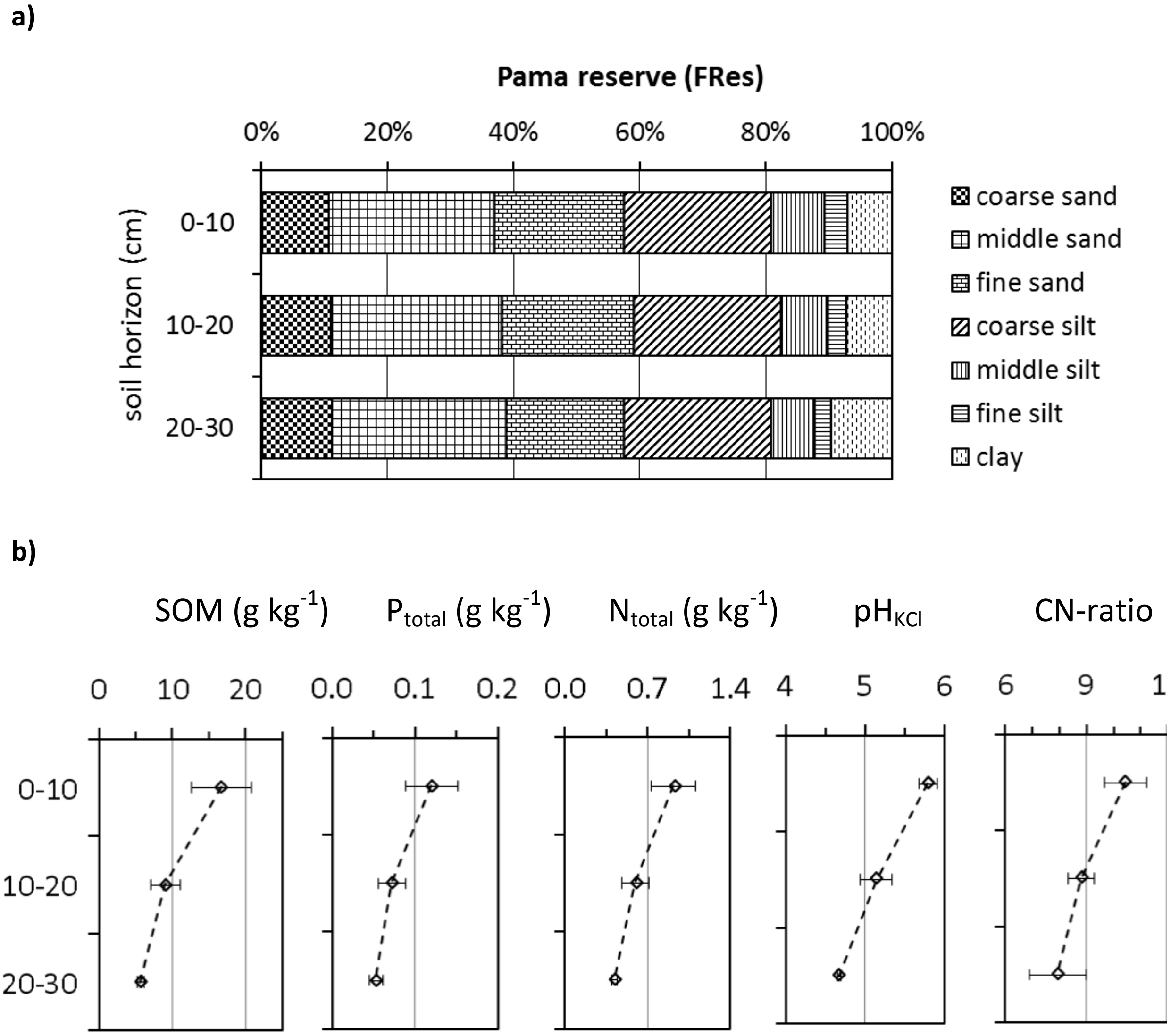


Fig. 4-11: For the upper 30 cm along the soil profile in the Pama reserve (FRes, Site 5) a) the soils' texture or grain size distribution of the fine earth fraction and b) the soils' content in total organic matter, total phosphorous, total nitrogen, its pH-value and the CN-ratio are shown. For each horizon, the means were calculated from four samples – one composite sample of four profiles plus samples of three separate profiles. The standard deviations are indicated by the horizontal bars.

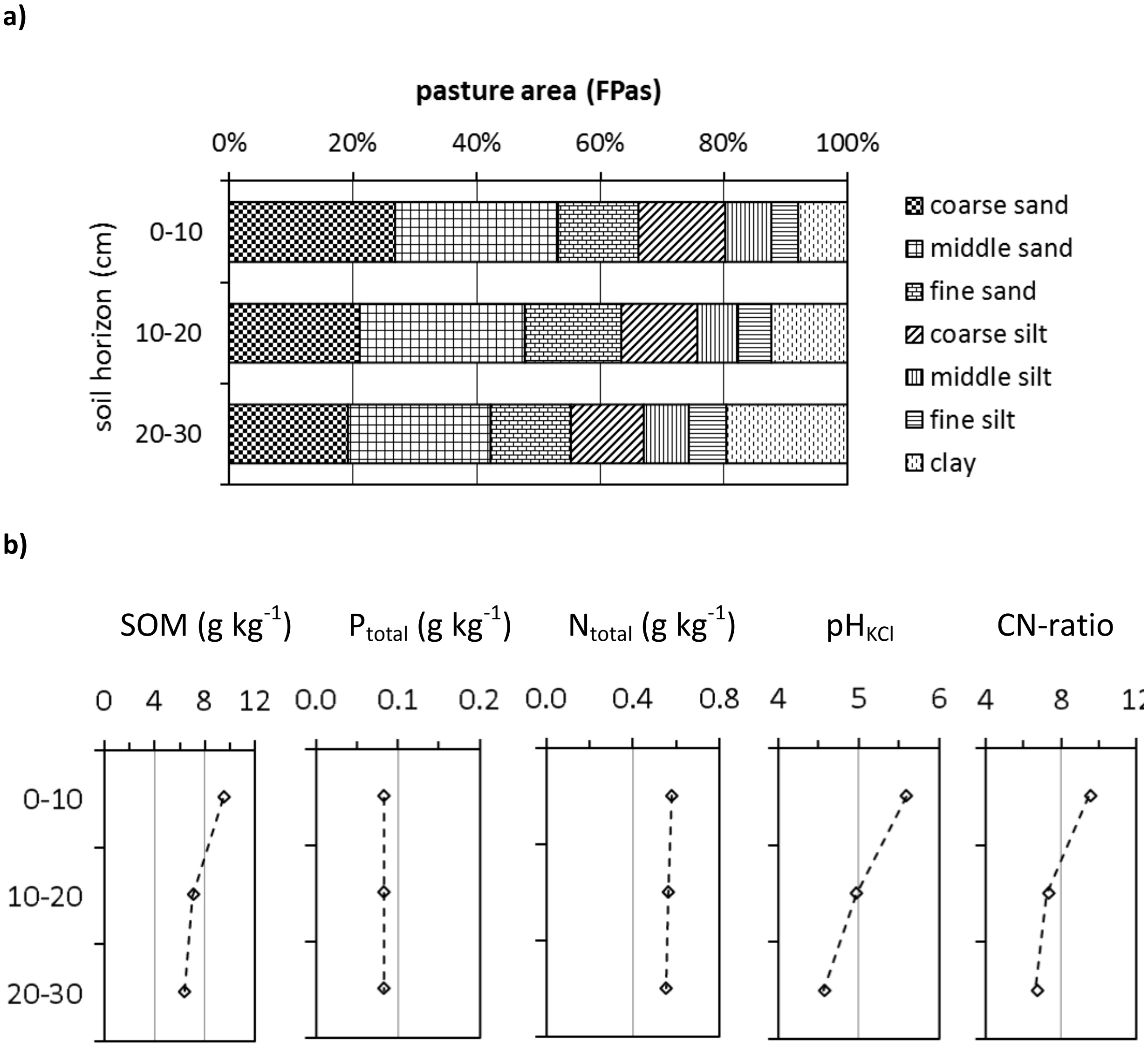


Fig. 4-12: For the upper 30 cm along the soil profile in the pasture area (FPas, Site 6) a) the soils' texture or grain size distribution of the fine earth fraction and b) the soils' content in total phosphorous, total nitrogen and organic matter, the pH-value and the CN-ratio are shown. The means were calculated from composite samples of the respective horizons of four profiles.

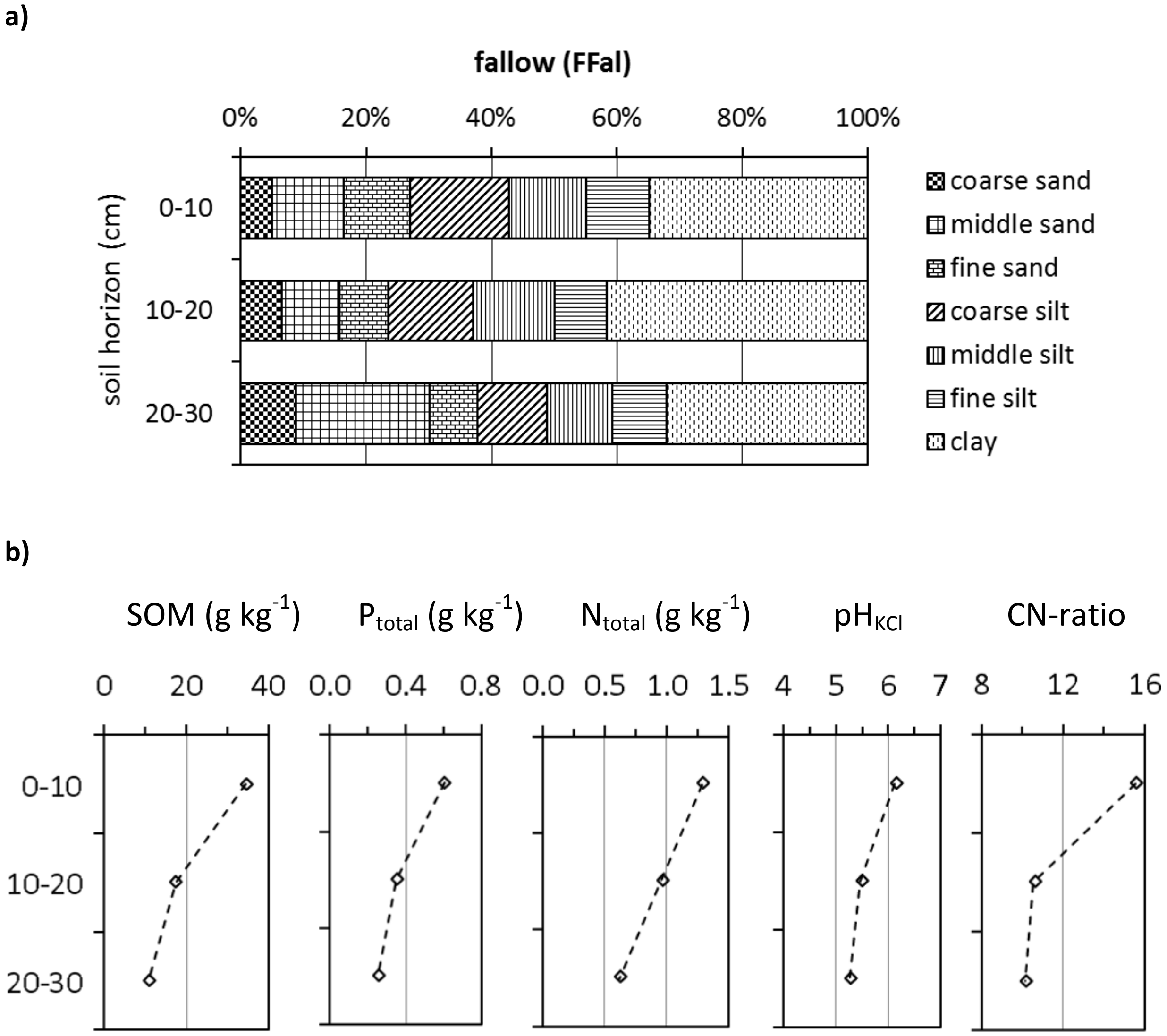


Fig. 4-13: For the upper 30 cm along the soil profile in the short-term fallow (third year fallow) (FFal, Site 7) a) the soils' texture or grain size distribution of the fine earth fraction and b) the soils' content in total phosphorous, total nitrogen and organic matter, the pH-value and the CN-ratio are shown. The means were calculated from composite samples of the respective horizons of four profiles.

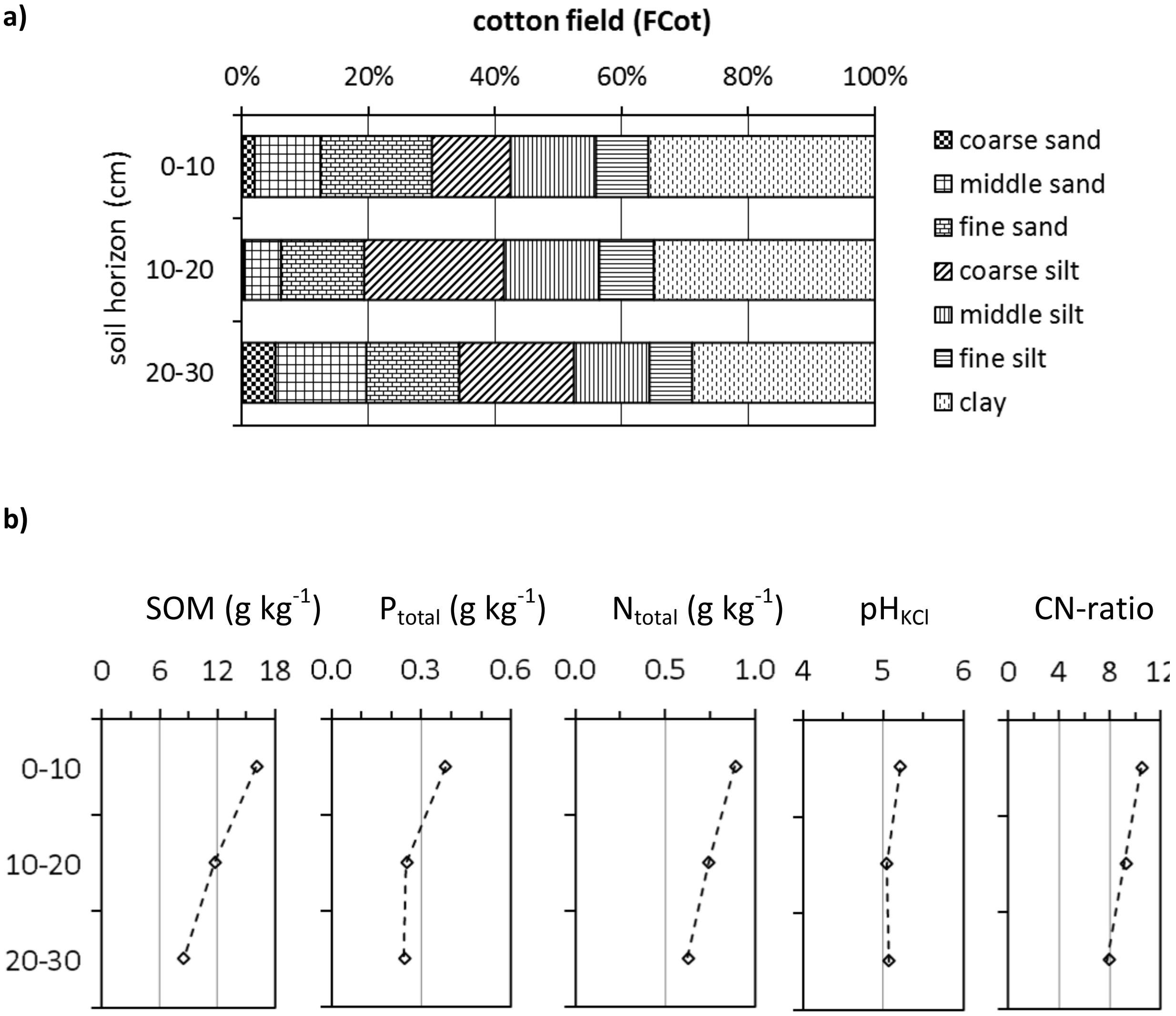


Fig. 4-14: For the upper 30 cm along the soil profile in the field cultivated with cotton in the second year (FCot, Site 8) a) the soils' texture or grain size distribution of the fine earth fraction and b) the soils' content in total phosphorous, total nitrogen and organic matter, the pH-value and the CN-ratio are shown. The means were calculated from composite samples of the respective horizons of four profiles.

Table 4-5: Physico-chemical properties of the topsoil (0–10 cm) in the land-use types near Fada N'Gourma (North-Sudan zone, Burkina Faso). For each parameter, first the median ± standard deviation, then minimum / maximum values are given.

	Characteristics of the habitats' topsoil (0–10 cm)			
Study sites in the North-Sudan zone, Burkina Faso (LUI-2)	Savanna in the Pama reserve FRes	Pasture area FPas	Fallowed field (2nd and 4th year) FFal	Cotton field FCot
N	9	13	11	6
Soil type	sandy loam	sandy loam	clay loam	loam
Sand (%)	61 ± 8 51 / 74	59 ± 6 45 / 69	28 ± 17 13 / 66	37 ± 12 19 / 47
Silt (%)	31 ± 8 19 / 43	26 ± 3 24 / 33	38 ± 8 18 / 43	34 ± 3 32 / 39
Clay (%)	7 ± 1 6 / 9	12 ± 6 6 / 26	34 ± 10 16 / 44	28 ± 9 20 / 43
EC (µS cm^{-1}) *	35.8 ± 9.5 27 / 49.6	49.1 ± 42.2 4.49 / 105	58.8 ± 7.5 45.8 / 64	32.2 ± 18.3 3.8 / 54.9
SOC (g kg^{-1})	8.3 ± 2.2 6.5 / 14.1	5.7 ± 1.9 4.6 / 10.9	20 ± 8.0 5 / 26.7	8.9 ± 2.4 5.1 / 12.5
SOM (g kg^{-1})	14.1 ± 3.8 11.2 / 24.3	9.8 ± 3.3 7.9 / 18.8	34.5 ± 13.8 8.6 / 46	15.3 ± 4.1 8.8 / 21.6
pH$_{KCl}$	5.8 ± 0.3 5.6 / 6.4	5.6 ± 0.6 4.9 / 6.7	5.9 ± 0.3 5.5 / 6.4	5.7 ± 0.3 5.2 / 6.1
N$_{total}$ (g kg^{-1})	0.84 ± 0.17 0.6 / 1.2	0.76 ± 0.15 0.6 / 1.1	1.29 ± 0.40 0.6 / 1.7	0.95 ± 0.22 0.8 / 1.3
P$_{total}$ (g kg^{-1})	0.16 ± 0.08 0.1 / 0.4	0.10 ± 0.13 0.1 / 0.5	0.61 ± 0.41 0.3 / 1.4	0.39 ± 0.08 0.2 / 0.4
CN-ratio	10.5 ± 1.5 7.7 / 12.8	8.0 ± 1.1 6.2 / 10.2	13.3 ± 3.5 6.9 / 15.7	8.9 ± 1.3 6.6 / 10.5

* EC-values (electrical conductivity): *N* = 5 for FCot and FPas, *N* = 7 for FFal, *N* = 4 for FRes.

Abbreviated parameters left are: *N* = sample number; grain sizes = sand, silt, clay; SOC = soil organic carbon; SOM = soil organic matter; N$_{total}$ = total soil nitrogen; P$_{total}$ = total soil phosphorous; CN-ratio = carbon-nitrogen ratio.

Soil organic nitrogen exists in many complex forms but test procedures do not discriminate among these forms (whether estimated by Kjeldahl digestion or a combustion technique). Hence, they cannot be used to directly estimate the nitrogen-mineralization potential, the ability of the soil to convert organic nitrogen to mineral nitrogen that is available for plant uptake. However, some generalizations can be drawn: Soils with less than 0.07%, that is 0.7 gram total nitrogen per kilogram soil (N$_{total}$) have limited nitrogen-mineralization potential, while soils with over 0.15% (or >1.5 g kg^{-1}) total nitrogen would be expected to mineralize a significant amount of nitrogen during the following crop cycle. Accordingly, a moderate nitrogen mineralization potential was assumed for the North-Sudanese sites (Table 4-5).

As already noted for the samples taken in the sub-Sahelian sites (Chapter 4.2.1.1), the cation exchange capacity (CEC) is a measure of a soil's capacity to retain and release the cation nutrients such as potassium (K^+), calcium (Ca^+) and ammonium (NH_4^+). Soils with high clay or organic matter content tend to have a high CEC – sandy soils a low CEC. This tendency can also be seen in the four North-Sudanese sites (Table A4-4, Appendix 4). The reserve and the pasture, both having a high sand-content, had a CEC between 50–55 mmol$_c$ per kilogram of soil (equals 5–5.5 mEq 100 g-^{1}). The fallow and the cotton field, both having relatively high clay- and low sand-contents, had a CEC between 260–323 mmol$_c$ per kilogram of soil. At CEC levels above 200–250 mmol$_c$ per kg of soil, the soil can hold many more nutrients than a plant would normally need in a year. All four habitats had relatively high base saturation (BS) values, with 60% in the pasture and between 77% and 85% in the other three sites (Table A4-4). As the difference between the BS-value and 100% represents the percentage of cation exchange sites that are occupied by acidic cations (Al, H), high values (> 60%) are desirable under most condition.

4.2.2.2. Vegetation characteristics

The prominent vegetation features characterizing the land-use types in the North-Sudanese region were assessed once during the rainy season 2006 in a plot of 900 m^2 area. In the reserve and the pasture, the plot was divided into 225 contiguous subplots of 4 m^2. In the cotton field and the young fallow (assessed when the site was in the 4th year fallow), the plot was divided into 36 contiguous subplots of 25 m^2. A summary of the parameters assessed is given in Table 4-6.

The species lists of all vascular plants are shown in Table A4-5 in Appendix 4. The species are ranked in descending order depending on their abundance in a) the combined area of all four vegetation assessment plots (3600 m^2) and b) in each habitat separately. The species names in Table A4-5 are abbreviated; the corresponding full species names including the family and order they belong to are listed in Table A4-1 (Appendix 4). Ten species represented 83% of all tree individuals that were assessed in the four habitats (total area of 3,600 m^2) (Table A4-5).

Vascular plant species richness and the number of tree individuals decreased with increasing anthropogenic intensification (Table 4-6). In the cotton field, only one old Shea tree (*Vitellaria paradoxa*), a traditional African food plant that grows naturally in the dry savanna belt of West Africa, had been left by the farmer (Table 4-6).

Table 4-6: Vegetation features characterizing the land-use types studied near Fada N'Gourma (North-Sudanese zone, Burkina Faso). The vegetation was assessed once during the rainy season 2006 in a plot of 900 m^2 area. The plot was either divided into 225 contiguous sub-plots of 4 m^2 (reserve and pasture) or into 36 contiguous sub-plots of 25 m^2 (short-term fallow and cotton field).

Study sites of the North-Sudan zone (LUI-2) (subplot-no x subplot area)	Vegetation characteristics (plot area 900 m^2)			
	Pama reserve FRes (225 x 4 m^2)	Pasture area FPas (225 x 4 m^2)	Fallow (4^{th} year) FFal (36 x 25 m^2)	Cotton field FCot (36 x 25 m^2)
Vascular plant species richness	12	9	7	1
Number of tree individuals	79	52	18	1
Mean height of main tree stem (cm)	374	355	194	450
Min / Max	100 / 800	70 / 900	80 / 400	–
Woody plant basal area (cm^2)	11,392	10,073	2,298	390
Number of seedling species	28	24	7	6
Number of seedlings (all species)	1,883	1,626	47	38
Number of dominant grass species	11	12	3	0
Mean crown cover (in %) per sub-plot (per m^2)	18.9 (4.7)	36.9 (9.2)	6.9 (0.3)	1.0 (0)
Min / Max	0 / 90	0 / 98	0 / 35	0 / 16
Mean grass cover per sub-plot (in %)	66.4	54.4	24.7	0
Min / Max	2 / 85	4 / 85	15 / 35	0 / 0

* Please refer to Tab. A4-5 (Appendix 4) for the species lists of all vascular plants (names abbreviated), ranked according to their relative abundance. For the corresponding species names, including the family and order the species belong to please refer to Tab. A4-1 (Appendix 4).

18 trees belonging to 7 species were found in the fallow and 52 trees from 9 species in the pasture. The Pama reserve was most diverse with 79 trees from 12 species (Table 4-6). A comparable tendency was observed with regard to the number of seedlings, the number of species to which the seedlings belonged, the grass cover and the total area that was covered by tree trunks (Table 4-6). The percentage crown cover was higher in the pasture than in the reserve (Table 4-6).

4.2.2.3. Plant litter and other organic debris

The quantity and main composition of food resources available to termites during the dry season was assessed in a standardized way – once in 2006 and once in 2007. In 10–20 quadrates of 1 m^2 area which were placed along a line transect, all organic matter was collected and sorted according to its type (dead wood, leaves, dry grass etc.). The term 'litter' is used henceforth when referring to plant litter, animal feces and crop residues. The total litter dry weight in gram per square meter and month within dry season is illustrated per land-use type in Fig. 4-15. With increasing habitat intensification or increasing habitat simplification, a decreasing litter quantity was collected (Fig. 4-15).

In Fig. 4-16, Fig. 4-17, Fig. 4-18 and Fig. 4-19, the dry weight is illustrated separately for each litter type. Leaf litter and dry grass comprised most of the collected litter. Again, a decreasing litter dry weight could be observed with increasing habitat intensification or with increasing habitat simplification (Fig. 4-16). The same tendency could be observed for the amount of dead wood and of dung (Fig. 4-17, Fig. 4-18). However, almost no dung was collected in the protected savanna in the Pama reserve where grazing was prohibited (Fig. 4-18).

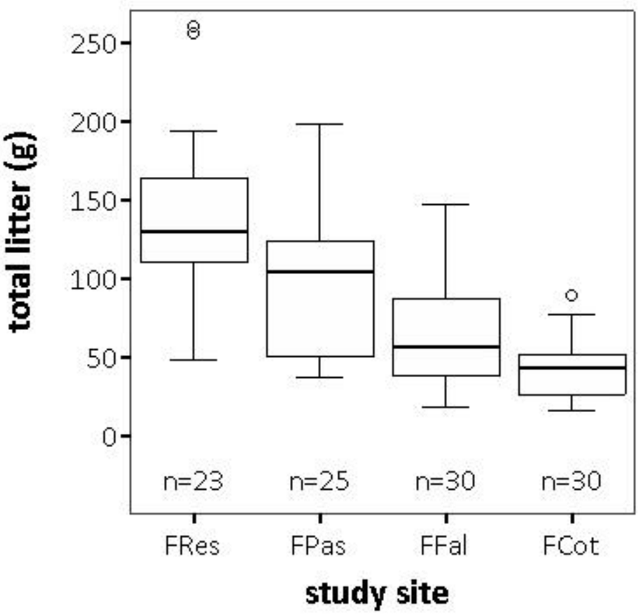


Fig. 4-15: Total litter dry weight (g) per square meter and month dry season. Litter was assessed end of the dry season of 2006 and 2007 in a standardized way.

Study sites are FRes: near-natural woody savanna in the Pama reserve (National Park), FPas: pasture area, FFal: short-term fallow (field was cultivated for 15 years, and was then left fallow during 4 years), FCot: cotton fields.

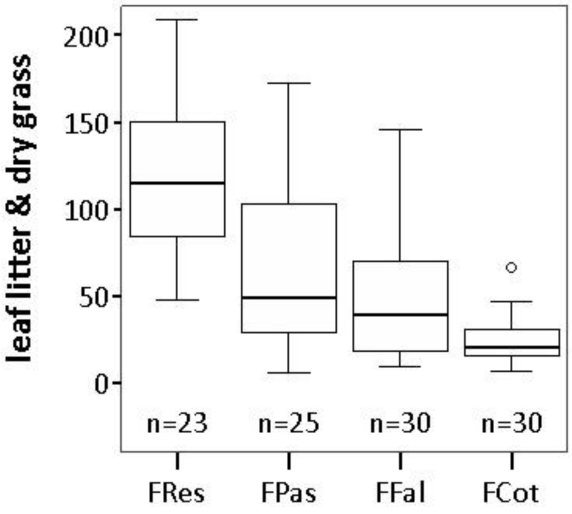


Fig. 4-16: Total amount of leaf litter and dry grass (g) per square meter and month dry season. Litter was assessed end of the dry season of 2006 and 2007 in a standardized way.

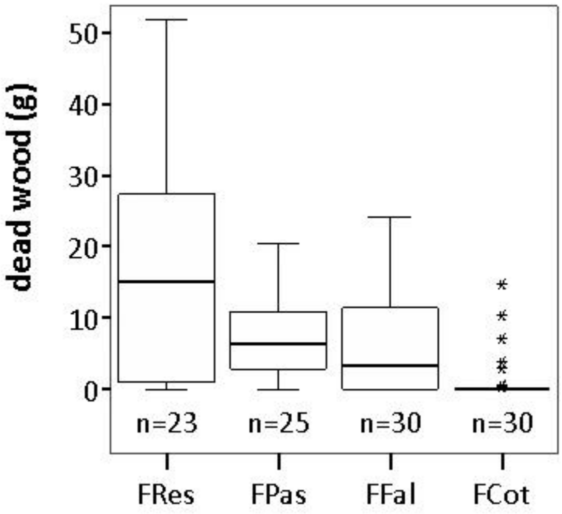


Fig. 4-17: Total amount of dead wood (g) per square meter and month dry season. Litter was assessed end of the dry season of 2006 and 2007 in a standardized way.

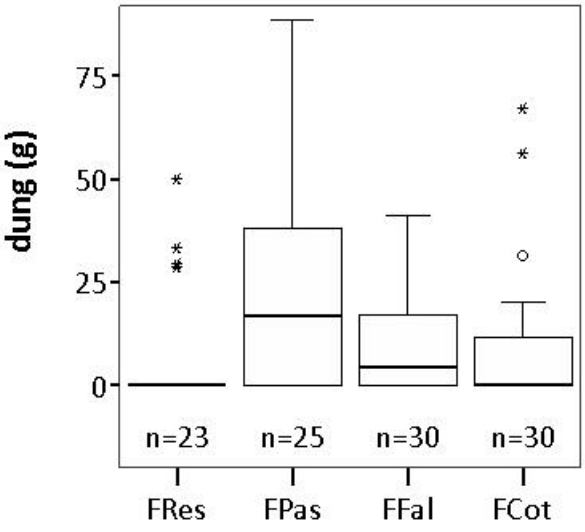


Fig. 4-18: Total amount of dung (g) per square meter and month dry season. Litter was assessed end of the dry season of 2006 and 2007 in a standardized way.

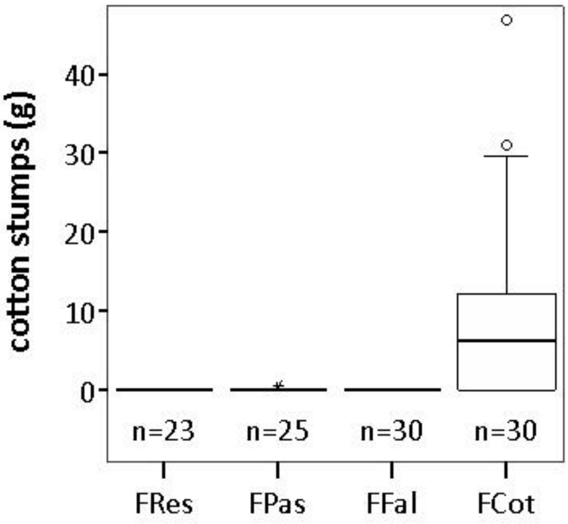


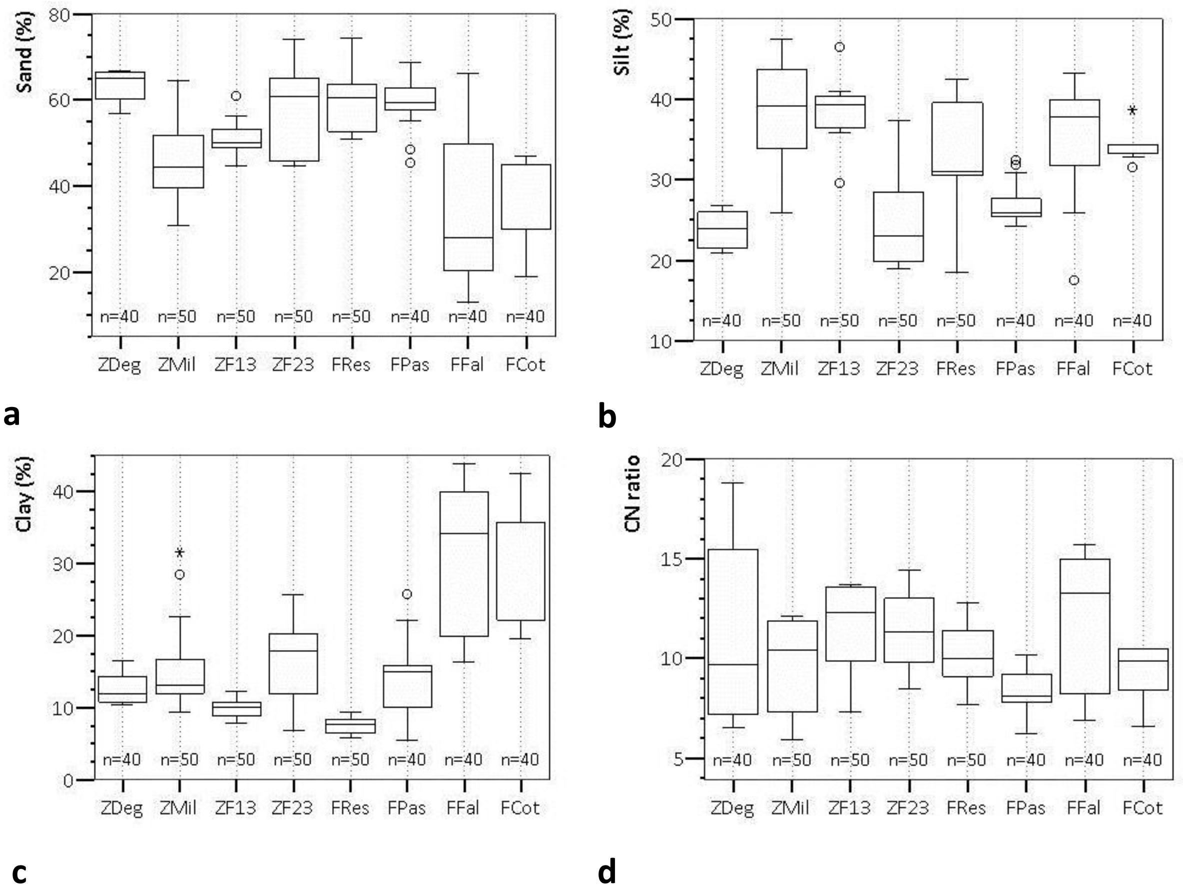
Fig. 4-19: Total amount of cotton stumps (g) per square meter and month dry season. Litter was assessed end of the dry season of 2006 and 2007 in a standardized way.

Study sites are FRes: near-natural woody savanna in the Pama reserve (National Park), FPas: pasture area, FFal: short-term fallow (field was cultivated for 15 years, and was then left fallow during 4 years), FCot: cotton fields.

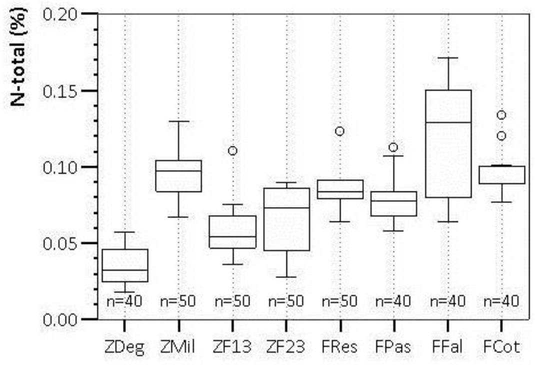
4.2.3. Summary of the biotic and abiotic parameters in both regions

A summary of all environmental parameters that were measured in the land-use types near Fada N'Gourma (North-Sudan) and the succession stages of the Zaï system in Ouahigouya (sub-Sahel) are shown in Fig. 4-20 a-u). Illustrated are physical and chemical soil parameters (a-k); parameters characterizing the RAP transect sections (l-o); vegetation parameters (p-s), assessed once per site during the rainy season in an area of 900 m^2; and the quantity of food resources available to termites during the dry season (t-u) – the weights are the calculated means of 40 to 50 quadrates (each 1 m^2) and are shown per square meter and month dry season (Fig. 4-20).

In each land-use type, epigeal mounds were assessed once during the rainy season; in the sub-Sahelian sites they were assessed within the whole hectare-plot, in the North-Sudanese sites they were assessed together with the vegetation within an area of 900 m^2. For the results of the mound assessment, please refer to the end of Appendix 4.



Land-use types ZDeg: degraded land, ZMil: millet fields, ZF20 / ZF30: young / old Zaï forest; FRes: near-natural woody savanna in the Pama reserve (National Park), FPas: pasture area, FFal: short-term fallow (in the 2nd and 4th year fallow), FCot: cotton fields.



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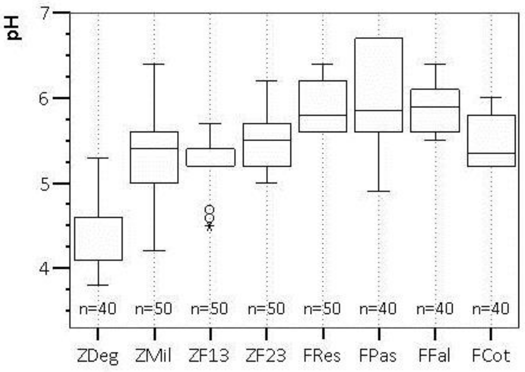

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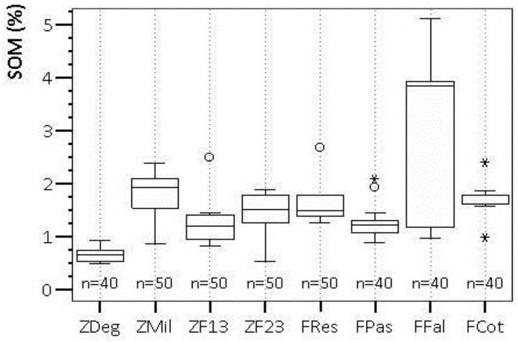

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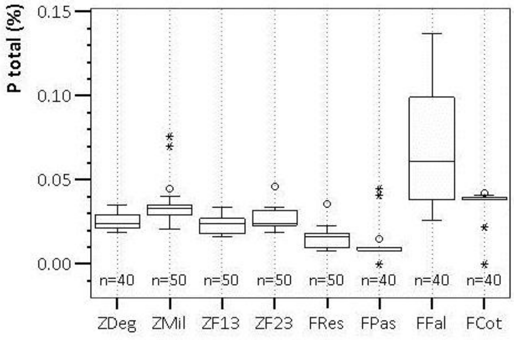

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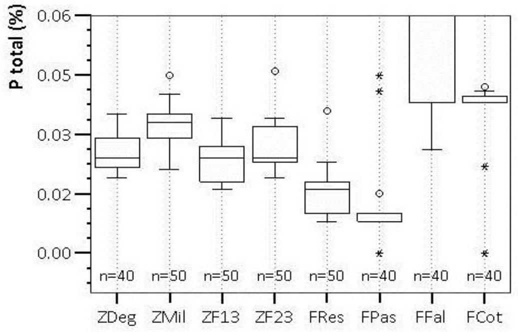

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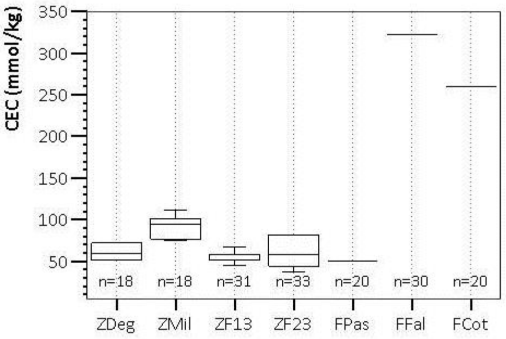

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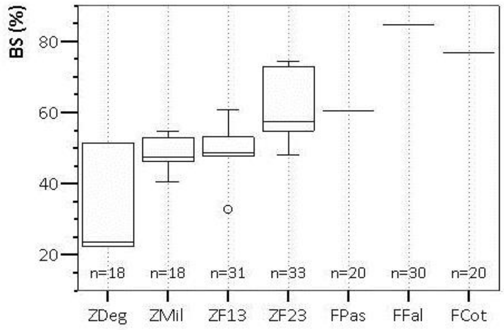
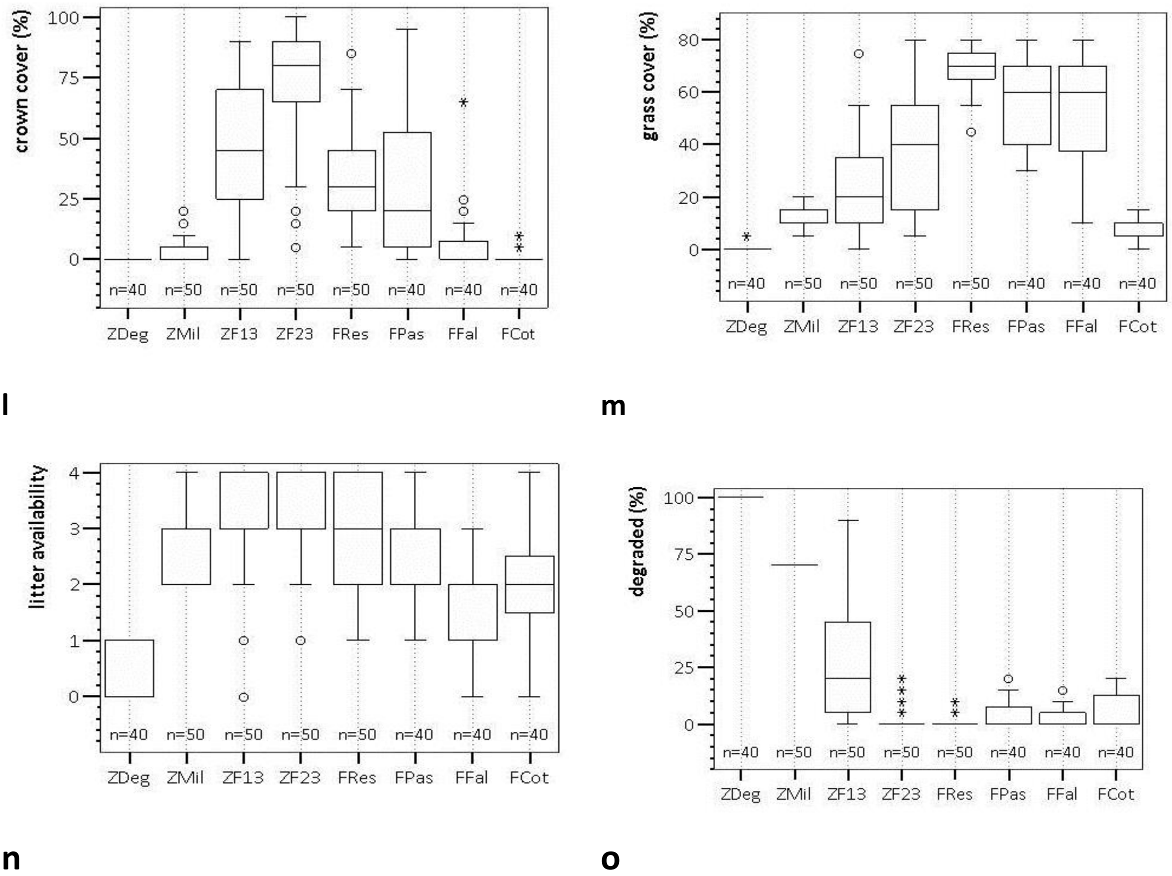


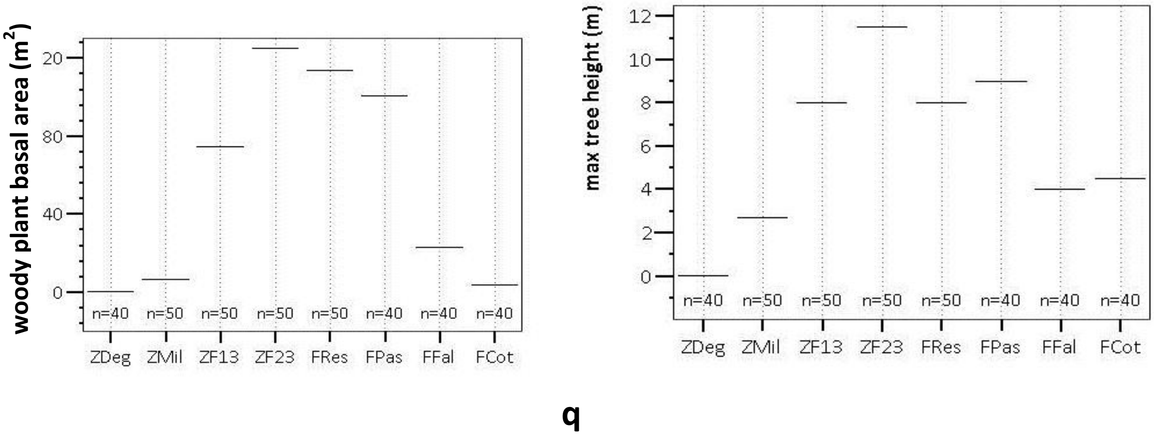
k

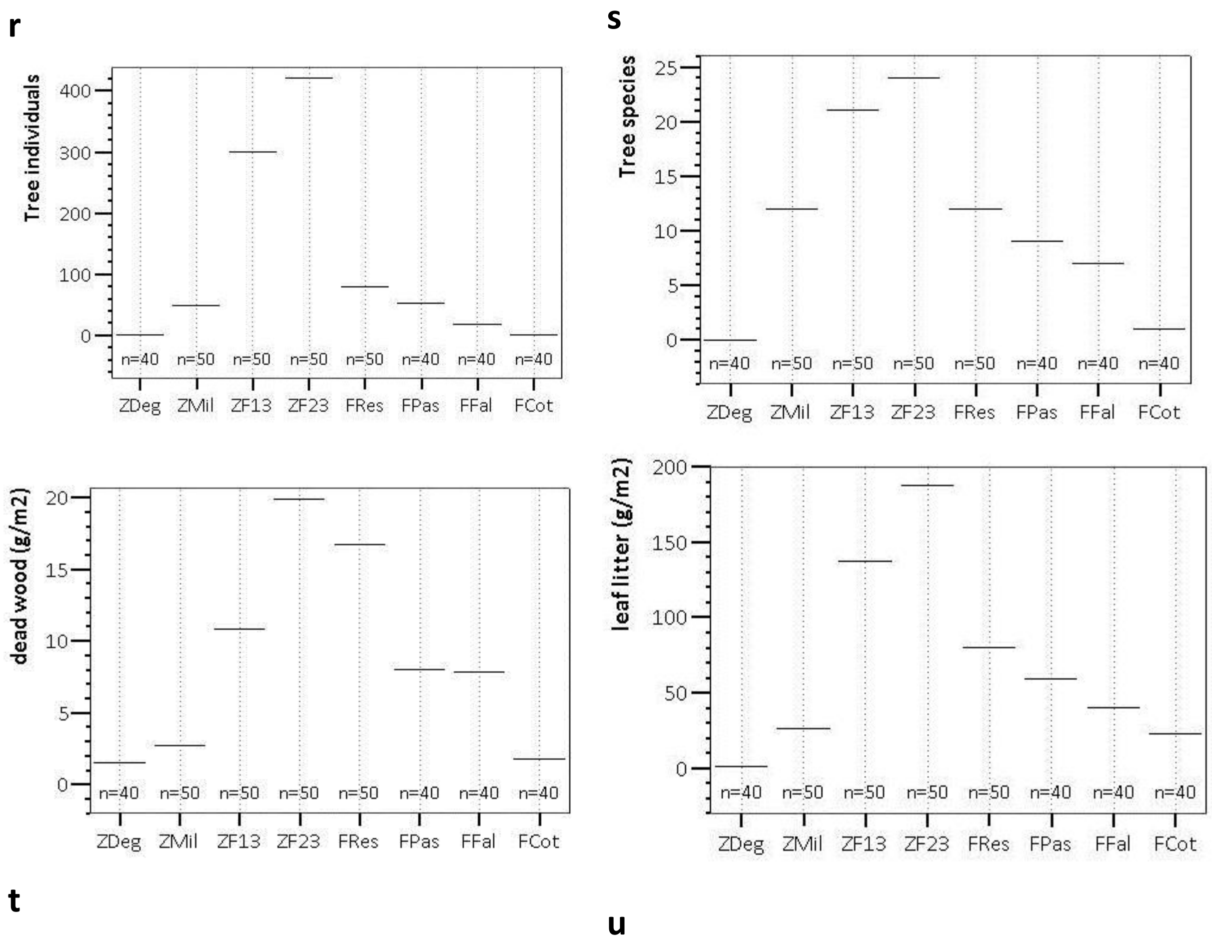
a-k) Physico-chemical parameters measured in composite soil-samples: a) Sand (%); b) silt (%); c) clay (%); d) CN-ratio; e) N-total (%); f) pH; g) SOM (%); h) P-total (%); i) close-up P-total (%); j) CEC (mmol kg^{-1}); k) base saturation (%). Habitats are ZDeg: degraded land, ZMil: millet fields, ZF20 / ZF30: young / old Zaï forest; FRes: near-natural woody savanna in the Pama reserve (National Park), FPas: pasture area, FFal: short-term fallow (in the 2nd and 4th year fallow), FCot: cotton fields.



l-o) Habitat parameters measured during the standardized and rapid assessment of termites and ants within the sections of the replicate transects run during the rainy season (between 2004 and 2008): l) crown cover (%); m) grass cover (%); n) litter availability; o) degraded (%).

Habitats are ZDeg: degraded land, ZMil: millet fields, ZF20 / ZF30: young / old Zaï forest; FRes: near-natural woody savanna in the Pama reserve (National Park), FPas: pasture area, FFal: short-term fallow (in the 2nd and 4th year fallow), FCot: cotton fields.





p-u) Vegetation parameters, assessed once per site in an area of 900 m^2 (rainy season): p) woody plant basal area (m^2), q) maximum tree height (m); r) number of tree individuals; s) number of tree species; t) mean dry weight of dead wood (g m^{-2}); u) mean dry weight of leaf litter (g m^{-2}).

Fig. 4-20: a-u) Boxplots showing environmental parameters for each of the four Zaï sites located in the sub-Sahel zone, and the four Fada N'Gourma sites located in the North-Soudane zone of Burkina Faso.

Habitats are ZDeg: degraded land, ZMil: millet fields, ZF20 / ZF30: young / old Zaï forest; FRes: near-natural woody savanna in the Pama reserve (National Park), FPas: pasture area, FFal: short-term fallow (in the 2nd and 4th year fallow), FCot: cotton fields.

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5. DIVERSITY OF TERMITE AND ANT COMMUNITIES ALONG TWO LAND-USE INTENSIFICATION GRADIENTS IN SEMI-ARID BURKINA FASO

5.1 INTRODUCTION

5.1.1 Interdependency of ecosystem properties and biodiversity

Ecosystem properties depend greatly on the functional characteristics as well as the spatial-temporal distribution and abundance of the organisms present in the habitat (Hooper et al. 2005; Scherer-Lorenzen 2005). The effects that species have in influencing ecosystem properties interact with the effects of climate, resource availability and disturbance regimes (Hooper et al. 2005).

The *hypothesis* that the sustainability and stability of ecosystems rely on their biological diversity has been in the focus of numerous ecological studies (e.g. see Hooper et al. 2005; Lee & Wood 1971; Lobry de Bruyn & Conacher 1990; Malézieux 2011; Wood et al. 1983). Species richness and abundance of flora and fauna however, may be severely affected by disturbances caused by land-use practices (Lavelle et al. 1997). Land-use practices convert natural ecosystems for human use or change management practices in human-dominated habitats. The outcome of the great variety of different practices existing world-wide is always the provision of humans with their daily needs (e.g. food, water, shelter, fiber), often at the expense of degrading environmental conditions (Foley et al. 2005). As plants and animals originally present in the habitat may fail to adjust to the new ecological setting in the modified or degraded environment, the drivers that accelerate the further decline of biodiversity most severely are i) habitat loss or change through expansion of agriculture, mining and forestry, and ii) the degradation or desertification of arable and grazing lands (Bai et al. 2008; Darkoh 2003; Green et al. 2005). Agricultural processes are particularly affecting ecosystems and have been a leading cause of global biodiversity loss (Green et al. 2005) and land degradation (Bai et al. 2008; Darkoh 2003).

Evidence is growing that species extinctions are altering key processes which are crucial for the productivity and sustainability of the Earth’s ecosystems (Hooper et al. 2012; Hooper et al. 2005; Loreau et al. 2001; Tilman 1999; Wardle et al. 2011). This is especially true for so-called ‘ecosystem engineer’ species (sensu Jones et al. 1994). Ecosystem engineers are “organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials” (Jones et al. 1994; Jones et al. 1997). Important ecosystem engineers expand the distributional limits for numerous species by alleviating limiting abiotic and biotic stresses, and they often form the foundation for community development (Crain & Bertness 2006; Jones et al. 1994; Jones et al. 1997).

5.1.2 Termites and ants

Termites (Isoptera) and ants (Hymenoptera: Formicidae) are among the most important soil ecosystem engineers in arid and semi-arid drylands (Evans et al. 2011; Lee & Foster 1991). They play a central role in the dynamics of ecosystem functioning (e.g. nutrient and carbon fluxes, soil turn-over, etc.) in many natural and anthropogenically modified habitats, particularly amid arid and infertile environments (e.g. see Bignell & Eggleton 2000; Evans et al. 2011; Hölldobler & Wilson 1990; Holt & Lepage 2000).

In sub-Saharan Africa, these two invertebrate taxa represent the only active soil macrofauna during the dry season (Rouland et al. 2003; Schuurman 2006). By creating so-called ‘biogenic structures’ of varying size and nature (mounds, subterranean nest chambers, galleries, macropores and soil-sheetings) they differently affect important processes such as e.g. soil turn-over, water infiltration and water retention in the soil or the dynamics and relocation of organic matter (Evans et al. 2011; Hölldobler & Wilson 1990; Holt & Lepage 2000; Lavelle et al. 1997; Wood 1996; Wood & Sands 1978). In the savannas and dry forests of West-Africa**,** where fungus-growing termites are a common and often dominant component of the community (Bignell & Eggleton 2000), termites are the major agents of the first steps of plant litter decomposition (e.g. Wood & Sands 1978) and in the sub-Sahel zone of Burkina Faso, they even represent the only active decomposers all year round (Mando & Brussaard 1999). Please refer to Chapter 1.4 for more detailed information about the important role of termites and ants as ecosystem engineers and the effect of the different biogenic structures on physico-chemical soil properties.

Communities of ecosystem engineers generally have relatively low species richness (Lavelle et al. 1997). For example termites: Species numbers of the most diverse termite communities in lowland tropical forests are ranging between 50 and 80 species per hectare – the numbers in savannas and agro-ecosystems, however, are generally much lower (Bignell & Eggleton 2000; Eggleton 2000; Eggleton & Bignell 1995). The overall function of these invertebrates may therefore be dramaticly affected by species losses (Lavelle et al. 1997). Generalizations about the effect of species extinctions on ecosystem processes, however, are difficult since the identity of the species lost largely determines the resulting changes (Hooper et al. 2012).

Therefore and because of their important role for soil fertility and ecosystem functioning, monitoring of termites and ants is of crucial importance in order to assess changes in their diversity, distribution and abundance triggered by direct and indirect human impact and global climate change. Please refer to Chapter 1.5 for more detailed information about their value as biological indicators as well as global distribution patterns and species numbers of these important soil-arthropods.

5.1.3 Modifications in the composition of termite and ant communities

Modifications of termite and ant communities may be studied from a taxonomic and/or a functional point of view (see also Chapter 1.5). In the present study, taxonomic changes are described by characterizing the number of species, genera and families in the habitat, their relative abundance and by calculating different species richness estimators or diversity indices. For changes in the functional composition on the other hand, different ecological or functional groups are described (Fragoso et al. 1997). For example, most termite communities represent a mosaic of different functional groups, each with another physical feeding style (Donovan et al. 2001; Lavelle et al. 1997). The classification used in the present study separates soil feeders (humivorous), wood feeders (xylophagous), grass feeders (harvesters) and fungus-growers.

According to their feeding habit, termites have different functional effect traits and different functional response traits (Hooper et al. 2005) (see also Chapter 1.3); that means, functional groups may differently impact soil processes such as pedoturbation (effect traits), and they may, for example, differently respond to habitat disturbance or in ecological successions (response traits) (e.g. Davies et al. 1999; Donovan et al. 2001; Dosso et al. 2010a; Eggleton et al. 2002; Eggleton et al. 1996; Eggleton et al. 1995; Eggleton et al. 1997). For example, in a study of Eggleton et al. (2002) along a gradient of increasing anthropogenic disturbance[1], the diversity of soil feeding termites declined, whereas the diversity of wood feeding termite species increased. Accordingly, the relative abundance of three functional guilds of ants (generalist predators, specialist predators and territorially dominant arboreal species) was found to be significantly correlated to an age gradient of cocoa cultivations[2](Kone et al. 2012a).

As several species could not be unambiguously assigned to a certain category, I did not classify ants into different functional groups.

5.1.4 Parameters influencing the composition of termite and ant communities

Major factors known to influence the diversity and abundance of termites and ants are, e.g. latitude (Greenslade & Greenslade 1977; Majer & Delabie 1994), altitude (termites e.g. Donovan et al. 2002; ants e.g. Sanders et al. 2003), rainfall, temperature, soil parameters (termites e.g. Davies et al. 2003b; Dosso et al. 2010b; ants e.g. Majer & Beeston 1996; Sanders et al. 2003; Wang et al. 2001) and disturbance (termites e.g. Black & Okwakol 1997; Eggleton et al. 2002; ants e.g. Greenslade & Greenslade 1977; Holt & Lepage 2000; Lavelle et al. 1997; Lobry de Bruyn 1999; Read & Andersen 2000).

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[1] Data on termite diversity were collected in the humid forest zone of West and Central Africa in following habitats: primary forest, several ages of regenerating forest, agroforestry plots, short follows, mixed food crop fields, and mechanically cleared plots.

[2] Data on ant diversity in the Côte d'Ivoire (West Africa) were collected in the following land-use types: forest in Lamto reserve, rural forest, food crop plantations, cocoa and pineapple plantations.

Abiotic factors such as rainfall and temperature might also influence diversity patterns indirectly via their impact on biotic factors such as the diversity and biomass of vegetation (above- and belowground). The diversity of termites was found to be strongly correlated with different vegetation parameters, e.g. with plant species richness (Dosso et al. 2010b; Gillison et al. 2003), woody plant basal area (Gillison et al. 2003; Jones et al. 2003), canopy height (Gillison et al. 2003; Jones et al. 2003) or the amount of dead wood and leaf litter (Attignon et al. 2005; Davies et al. 1999; Jones et al. 2003). The diversity of ants was also found to be strongly correlated by biotic factors (Cushman et al. 1993; Perfecto & Vandermeer 1996). Majer et al. (1984) found that plant-species richness and diversity, plant cover percentage as well as litter cover percentage and the presence of large logs significantly explained the variance in ant species richness and diversity as well as community composition in 30 restored bauxite mines and 3 forest controls in Australia. Different results are reported for the effect of reduced vegetative structure following disturbance: reductions of the vegetative structure were found to reduce ant diversity (Greenslade & Greenslade 1977; Lobry de Bruyn 1993; Lobry de Bruyn 1999; Room 1975), increase ant diversity (Torres 1984; Wisdom & Whitford 1981), or to have no significant effect on ants (Belshaw & Bolton 1993; Whitford et al. 1999). There still remains considerable uncertainty about how different environmental conditions affect ant distributions (Wang et al. 2001).

As already shortly indicated, anthropogenic alterations of habitats may heavily affect termite and ant communities (e.g. Eggleton et al. 2002; Floren & Linsenmair 2005; Kone et al. 2012a; Okwakol 2000; Zeidler et al. 2004). As land-use intensification occurs, chemical and mechanical inputs progressively replace the regulation of ecosystem functions through soil biodiversity (Giller et al. 1997). A major example and one of the main drivers of land conversion in tropical Africa is the increasing cash crop production which has heavily affected both, savannas and forest ecosystems (Darkoh 2003). In Burkina Faso, cotton is the most important cash crop; in the North-Sudanese regions, more and more savanna and woodland is cleared for the extensive cotton production (cotton is shadow sensitive) (Club du Sahel, OECD 2004). Cotton production has doubled during the last 10 years (www.oecd.org) and is damaging ecosystems and threatening human health (Ferrigno et al. 2005; Williamson 2003). Cotton is mostly cultivated in complex peasant farming systems on farms with a size of at most 6 ha (Kooistra et al. 2006), thereby resulting in a small-scale mosaic of various crops which are cultivated at the same time. In addition, many small-scale farmers traditionally practice crop rotation (e.g. with maize, millet, Sorghum) with – in the best case – fallow periods that are all harmed by the intensive application of pesticides in the cotton fields.

Furthermore, a characteristic feature of cropping systems is the type and frequency of soil disturbances. Periodic tillage usually disturbs at least the upper 15–25 cm of the soil profile and homogenizes the physical structure and residue distribution of formerly stratified soils (Altieri 1999). The tilled area is continually reverted to an earlier ecological succession stage resulting in a decrease or even the complete loss of the termite and ant fauna that inhabited the stratified soil horizon before (Altieri 1999). The loss of a stratified soil microhabitat thus threatens the proper balance between organic matter, soil organisms, plant diversity and recycling of nutrients which are necessary components of a healthy and productive soil environment (Hendrix et al. 1990).

Increasing agricultural intensification is often simplifying the habitats' above-ground physical structure: e.g. leading to shorter vegetation, fewer trees and therefore a lower total woody plant basal area, reduced plant species richness and a drop in above-ground carbon. This affects the termite and ant fauna in several distinct ways (Jones et al. 2003), e.g. decreasing habitat-complexity is leading to a decreasing number of available feeding and nesting-sites; they may also face an increasingly greater physiological stress since microclimatic conditions in the pedosphere are buffered by a closed canopy. As a consequence of the reduced above-ground vegetation, wind and water erosion increases which again is negatively affecting the chemical status and physical properties of the soil (Maatman et al. 1998).

By combining the results of several tropical studies, Eggleton et al. (2002) produced a synthesis of the effects of increasing land-use intensification on termite communities. The results showed that termite species richness was strongly negatively correlated with disturbance (Eggleton et al. 2002; Eggleton et al. 1996; Eggleton et al. 1995; Wood et al. 1977). All feeding groups were affected by the gradient of anthropogenic disturbance but soil-feeding termites were more vulnerable to anthropogenic disturbances than wood-feeders or fungus-growing termites (Eggleton et al. 2002). Most of these studies were conducted in tropical humid forests, much less is known of semi-arid ecosystems. Vasconcellos et al. (2010) studied termite assemblages in the semi-arid region of north-eastern Brazil (fungus-growing termites are absent in the Neotropics) in primary woodland, disturbed woodland with selective logging and a cleared area continuously logged and intensely used by cattle and goats. In contrast to findings in humid forests, Vasconcellos et al. (2010) found that wood-feeders were the most affected feeding group.

5.1.5 Study aims

When aiming to predict the consequences of habitat change for ecosystem functioning and therefore human well-being, it is decisive to have a profound knowledge about the actual taxonomic and functional diversity and composition of local termite and ant communities as well as of the soil-arthropods' response to changing environmental parameters resulting from increasing human impact (Donovan et al. 2001; Lavelle et al. 1997).

In Burkina Faso, the consequences of habitat change for ecosystem functioning and human well-being are especially extreme. At the same time, no information is available neither about the actual diversity of the two invertebrate taxa nor about the direction or magnitude of the on-going climatic- or anthropogenic-induced changes in the composition of their communities. The study region represents a highly drought-sensitive zone which is supposed to suffer in the future increasingly under prolonged extreme climate events, which are expected to become more frequent and severe in the course of global change.

To my knowledge, studies on termites and ants in West-African savannas are rare and most concentrated on humid regions, for example in the Côte d'Ivoire in the Comoé National Park (Korb 1993; Korb & Linsenmair 1998) and the Lamto Reserve (Dosso et al. 2012; Konaté et al. 1999; Konaté et al. 2003; Konaté et al. 2005; Kone et al. 2012a, b; Yéo 2001). Furthermore, only very few studies have correlated termite and ant community parameters collected along a disturbance gradient with quantitative measures of vegetation structure or habitat modification (Eggleton 2000).

The main objectives of the present study were:

1. To representatively but rapidly assess intrinsic parameters of the existing ant and termite communities (e.g. current species richness, relative abundance, functional group composition) under different land-use regimes in Burkina Faso and to provide reliable estimates of the asymptotic species richness.

   However, no standard protocol existed to assess termite and ant diversity in arid or semi-arid savanna habitats and agro-ecosystems; another aim therefore had to be as well the selection of methods best suited to representatively assess the focal soil-arthropods under these conditions in a reasonable time and with reasonable effort.
2. To assess the quantitative and qualitative responses of termites and ants to changing environmental parameters resulting from increasing human and to identify those habitat parameters which exert causal influence on the composition of their communities.
3. To build-up reference collections for future studies and as teaching material for universities.

5.1.6 Hypotheses

Ants and termites in the Zaï system in the sub-Sahel zone (Burkina Faso)

In the Zaï system, habitat and soil heterogeneity as well as crown-cover percentage steadily increase with decreasing intensity and duration of anthropogenic impact from the initial habitat stage, the degraded barren soil, towards the most rehabilitated site, the old Zaï forest. Provided that a 'source for the resettlement' is still present in the region of the Zaï-system, I therefore assume that species richness, taxonomic and functional diversity of termites and ants will increase with decreasing intensity of anthropogenic impact, i.e. in the following order:

Degraded, barren soil → millet field → young Zaï forest → old Zaï forest.

Ants and termites in the traditional system in the North-Sudan zone (Burkina Faso)

In the traditional system studied near Fada N'Gourma, the physical structure of the habitat simplifies progressively with increasing intensity and duration of anthropogenic impact from the initial habitat stage, the protected near-natural savanna in the reserve of Pama, towards the most disturbed site, the cotton fields with extensive pesticide application. Every third year, crop rotation was practiced in the agricultural fields (cotton field and short-term fallow) and tillage as well as planting were constantly disturbing the soil profile during the cropping seasons.

Hence, I assume that the species richness, taxonomic and functional diversity of termites and ants decreases with increasing land-use intensity, which is assumed to increase from:

Pama reserve → pasture area → short-term fallow → cotton fields.

5.2 MATERIAL AND METHODS

To address the objectives, I collected termites and ants in a standardized way. Additionally, data on habitat parameters were collected. In order to account for the conditions prevailing in semi-arid regions in savannas and agro-ecosystems, we modified a standardized transect protocol originally proposed for termite communities in tropical forests (Jones et al. 2006; Jones & Eggleton 2000) which has already proven its worth in several studies – e.g. in Cameroon (Eggleton et al. 1995), Thailand (Davies 1997), Indonesia (Jones & Prasetyo 2002), Malaysia (Jones 2000) and in the humid forest zone of West and Central Africa (Cameroon, Congo) (Eggleton et al. 2002). According to our new protocol, ants are collected simultaneously within the termite transect and on parallel transects with methods proposed by Agosti et al. (2000) for leaf litter ants. Please refer to Chapter 3 for a detailed description of the protocol, the different sampling methods, all information about the handling and identification of the collected specimen, the classification of termites in functional groups as well as the statistical methods used to analyze the data. All data used in the analysis originate from transects which were run in the rainy seasons between 2004 and 2008. These standardized transects will also be referred to as 'RAP-transects'.

By following the same standard protocol in different habitats, the results from each site can be directly compared, both within this study and with other locations where the transect method has been employed. Furthermore, under the preconditions that all land-use types belonging to a disturbance gradient originally had the same initial stage (vegetation and soil type) and species pool, and that the site history (history of exploitation) since the beginning of the habitats' modification is known for each of these land-use types, it should be possible to arrange the sites along a gradient of increasing anthropogenic impact and to hypothesize about the responses of termites and ant communities to anthropogenic-induced changes.Therefore, two traditional agricultural systems, each forming a gradient of land-use intensification, were chosen for the combined assessment of the focal soil-dwelling invertebrates:

- A temporal cross-section of the traditional soil rehabilitation system Zaï in north-western Burkina Faso (Ouahigouya, sub-Sahel zone, precipitation 500–600 mm yr^{-1}), comprising four main succession stages formerly all starting as entirely degraded, barren and crusted unfertile soils; and
- A traditional agricultural system in south-eastern Burkina Faso (near Fada N'Gourma, North-Sudan region, precipitation 1,000–1,100 mm yr^{-1}) using crop-rotation and short-term fallowing and comprising four habitats which are differing in the magnitude of anthropogenic disturbance and which were formerly all starting as near-natural open tree savanna.

The general characteristics of the study sites including the number of RAP-transects, their length and the years in which they were conducted, are summarized in Table 5-1 and Table 5-2, for the habitats of the first and the second land-use intensification gradient (LUI-1 and LUI-2) respectively.

5.3 RESULTS

5.3.1 Site characteristics

An overview of the general characteristics and the history of the land-use types studied in Burkina Faso are given in Table 5-1 and Table 5-2 for the first and the second disturbance gradient, respectively. Included are further the number, the length and the year of the RAP-transects conducted in each habitat as well as some vegetation parameters.

5.3.1.1 Agricultural intensification index

An index of agricultural intensification (AI) was calculated for each of the eight habitats studied in Burkina Faso (West Africa) in order to rank them according to the degree of land-use intensification. The method, that is a description of the parameters assessed to judge the intensity of human interventions and the equation used to calculate the AI-index, is given in Chapter 3.5. For the actual data and the composition of the final index-value calculated for each habitat, please refer to Table A5-1 in Appendix 5 and the subsequent calculations. Its application was perfectly suited for the agricultural land-use gradient near Fada N'Gourma in the North-Sudan region (Gourma province), but just sub-optimal for the agro-silvopastoral one, the Zaï system in Ouahigouya in the sub-Sahel region (Yatenga province). The index-value of 1.0 for the first succession stage, the degraded, barren land ZDeg was artificially set. Representatives for each of the three categories defined by Decaëns and Jimenez (2002) were identified (Table A5-1, Appendix 5).

The ranges of these categories are as follows:

1) low-intensified (semi-natural) systems (AI-index ≤ 0.20),
2) medium-intensified (0.21 ≤ AI-index ≤ 0.40)
3) highly-intensified systems (AI-index ≥ 0.41).

Interestingly, the old Zaï-forest ZF30 had a very low index (0.17) not so different to that of the near-natural savanna in the Pama reserve FRes (0.0). Even the pasture FPas with an index of 0.20 was further away but fell also in the category low-intensified. The young Zaï forest ZF20 with an index of 0.25 was the only habitat in the category medium-intensified. Highly-intensified systems were represented by the agricultural fields which had very similar values in both regions: the fallow FFal and the cotton field FCot, both experiencing crop-rotation, had an index of 0.70 and 0.89 respectively, whilst the index of the millet field ZMil was 0.73. The site order for decreasing AI-Index values (decreasing anthropogenic intensification) (Table A5-1):

Sites in the sub-Sahel region:	ZDeg > ZMil > ZF20 > ZF30
Sites in the North-Sudanese region:	FCot > FFal > FPas > FRes

5.3.1.2 Environmental parameters

In the sub-Sahelian and the North-Sudanese region of Burkina Faso, several environmental parameters were measured to characterize the RAP-transects and the land-use types in which they were run. For a description of the methods used to measure the different parameters, please refer to Chapter 4. A graphical overview of the parameters is shown in Chapter 4.2.3 in Fig. 4-20. Each of the sub-figures in Fig. 4-20 is illustrating one environmental parameter in eight boxplots, one boxplot per land-use type.

5.3.2 Community composition along two land-use intensification gradients

The applied standard protocol RAP provides a measure of the relative abundance of ants and termites, based on the number of encounters (hits) of each species in the sections of the belt transect. The number of hits per transect could then be used to compare the relative abundance of ants between transects, and by combining the replicate transects between land-use types and, by combining the land-use types belonging to the same intensification gradient the regions. For both taxa, one encounter was defined as the recorded presence of a species in one sampling unit (SU). For termites, one SU is identical to one transect section of 10 m^2 area. For ants, one SU comprises the transect section plus one pitfall trap and one Winkler-site (1-m^2 area). At least three transects were conducted in each habitat; four to five transects were laid whenever feasible. To allow comparisons between the habitats where sampling effort (number of SUs) differed, the frequency of the species' occurrence (in %) was calculated by dividing the number of encounters through the total number of SUs in the respective habitat.

Table 5-1: Characteristics of the four main succession stages of the Zaï system in Ouahigouya (sub-Sahel region, Burkina Faso).

Between 1998 – 2008: mean annual rainfall 660 mm, mean monthly temperature 19.1–39.1°C			Vegetation (area 900 m^2)		
Short	RAP-transects	Characteristics and history of habitats since initial degraded stage	N° tree species TrcBaseA	Tree height median MIN / MAX	CC% GC%
ZDeg	1 x 100[1] m in 2004; 3 x 50 m: 2006, 2007, 2008	Degraded, barren area (13°32’36”N; 2°22’59”W). Site represents the initial stage of all Zaï stages; lateritic infertile soil; barren, crusted and impermeable soil surface; almost devoid of any vegetation; topsoil type ‘sandy loam’; 70% stones in soil samples.	-	-	0%
ZMil	1 x 100 m in 2004; 3 x 50 m: 1 x in 2006, 2 x in 2007	Millet field (13°32’29”N; 2°23’07”W), in 2009: 11-yrs Zaï restoration. Agricultural fields of millet or Sorghum combined with nitrogen-fixing green beans, cultivated with the Zaï method. During the last decade, the farmer started to cultivate his fields longer than before (the Zaï forests laid fallow after four cultivation years): at the time of sampling, the fields were in the 5th, 7th and 8th cultivation year; topsoil type ‘loam’; after the harvest, grazing allowed to the farmers’ own cattle.	12 spp. 675 cm^2	116 cm 50 / 270	1% 5%
ZF20	1 x 100 m in 2004; 3 x 50 m: 2 x in 2006, 1 x in 2007	Young Zaï forest (13°32’34”N; 2°22’55”W), in 2009: 20-yrs Zaï restoration. First cultivated with Zaï for 4 years, followed by 16 years fallow; diverse woody and herbaceous vegetation; few areas with thin, closed canopy; degraded areas; areas with thin grass cover and isolated trees or bushes; topsoil type ‘loam’; some stone lines present. In the dry season, grazing allowed to the farmers’ own cattle and wood collection allowed to the women of the farmers’ family.	21 spp. 7,437 cm^2	170 cm 50 / 390	49% 30%
ZF30	1 x 100 m in 2004; 3 x 50 m: 1 x in 2006, 2 x in 2007	Old Zaï forest (13°32’25”N; 2°22’57”W), in 2009: 30-yrs Zaï restoration. First cultivated with the Zaï-method for 4 years, followed by 26 years fallow; diverse woody and herbaceous vegetation, mostly with thin but closed canopy; very few degraded areas; areas with dense and with thin grass cover; topsoil type ‘sandy loam’; some stone lines present; no wood collection/ grazing allowed during the last 10 years (before as in ZF20).	24 spp. 12,530 cm^2	284 cm 93 / 825	80% 35%

[1] Ants: 1 x 50 m. CC%: medium crown-cover percentages, GC%: medium grass-cover percentages, TrcBaseA: total surface area covered by tree trunks.

Table 5-2: Characteristics of four land-use types located about 52 km south of Fada N'Gourma (North-Sudan zone, Burkina Faso).

Between 1997 – 2008: mean annual rainfall 875 mm, mean monthly temperature 19.6–37.1°C			Vegetation (area 900 m^2)		
Short	RAP-transects	Characteristics and history of habitats since initial stage (woody savanna)	N° tree species TrcBaseA	Tree height median MIN / MAX	CC% GC%
FRes	1 x 100 m in 2004; 3 x 50 m in 2005	Pama reserve (11°38'26"N; 0°31'45'E). Protected near-natural arboreous and shrubby savanna; represents the initial stage of all habitats belonging to this disturbance gradient; dense grass sods, bushes and trees (assemblages of *Combretum* spp., *Anogeisus leiocarpus*, *Vitellaria paradoxa*), open canopy; topsoil type 'sandy loam'; traditionally managed by burning the vegetation in the dry season; wood collection and grazing strictly forbidden.	12 spp. 11,392 cm^2	374 cm 100/800	19% 66%
FPas	1 x 100 m in 2004; 2 x 50 m in 2006	Pasture area (11°38'40"N; 0°30'03'E), in 2009: since circa 20 years exclusively used for grazing cattle; topsoil type 'sandy loam'; areas with thin but closed canopy; areas with grass and some bushes; and areas with trees and bushes but open canopy; some degraded, barren spots; light incline towards the short-term fallow; wood collection and grazing allowed for the whole farmer community.	9 spp. 10,073 cm^2	355 cm 70 / 900	37% 54%
FFal	1 x 100 m in 2004; 2 x 50 m in 2006	Short-term fallow (11°38'17"N; 0°30'09'E), in 2009: 19 years. Fallowed for 4 years (2003–2006); when sampling arthropods, the field was in the 2nd and 4th year fallow. Before fallowing, crop-rotation was practiced every 3rd year, including 4 years cotton cultivation with extensive use of pesticides1). All trees originally growing in the area had been felled, only some small bushes were left; most areas had dense grass cover; topsoil type 'clay loam'; exceptionally many ant-nests (*M .galla*) were counted in 2004 (85 nest-entrances); during fallow, grazing was allowed all year round.	7 spp. 2,298 cm^2	194 cm 80 / 400	7% 25%
FCot	1 x 100 m in 2004; 2 x 50 m in 2006	Cotton fields (11°38'15"N; 0°30'27'E), in 2009: 13 years. Agricultural fields, when sampling soil-arthropods in the 2nd year of cotton cultivation; crop-rotation practiced every 3rd year1), during 5 of the 13 years since the fields were established, cotton was cultivated; extensive use of pesticides and insecticides (9.3 kg ha^{-1} yr^{-1}); topsoil type 'loam'.	1 sp. 390 cm^2	450 cm - / -	1% 0%

CC%: medium crown-cover percentages, GC%: medium grass-cover percentages, TrcBaseA: total surface area covered by the main tree trunks.

1) For crop-sequence see Chapter 2.1.2.

5.3.2.1 Ant communities

In all sites of both regions, 65 (morpho-) species of ants (Formicidae) belonging 25 genera and 9 sub-families were collected with the rapid assessment protocol along belt-transects. In the four sites near Fada N'Gourma (North-Sudan region, Burkina Faso), 53 species of 23 genera and 9 sub-families were collected; while 41 (morpho-) species out of 16 genera and 6 sub-families were found in the Zaï system in Ouahigouya (sub-Sahel region, Burkina Faso). An overview of the species number found per genus and subfamily under the different disturbance regimes is illustrated in Fig. 5-1; each column represents one land-use type, each color one subfamily. The data collected in four years between 2004 and 2008 visualize that lowest species or genus numbers (indicated by red arrows) were found in highly-intensified areas, the degraded land ZDeg in the sub-Sahelian and the cotton fields FCot in the North-Sudanese region. Ant assemblages in the North-Sudanese sites appeared to be richer in species, genera and sub-families. The list of all ant species (including taxonomy) collected in the four succession stages of the Zaï system in Ouahigouya is given in Table 5-3, those collected in the North-Sudanese zone in Table 5-4.

The ant fauna in Burkina Faso was dominated by the Myrmicinae which comprised 54% of the species collected along both disturbance gradients, followed by the Formicinae (22%), and Ponerinae (9%); with regard to the subfamilies' share in all encounters, the Myrmicinae comprised 58%, the Formicinae 31%, and the Ponerinae 8% (Table 5-3, Table 5-4). In the four Zaï stages combined (LUI-1), the Myrmicinae comprised 61% of all species, the Formicinae 20% and the Ponerinae 10%; with regard to their share in all encounters, the subfamilies comprised 67%, 24% and 7%, respectively (Table 5-3). Accordingly, in the four habitats of the North-Sudan region (LUI-2) combined, the Myrmicinae comprised 51% of all species, the Formicinae 23%, and the Ponerinae 11%; with regard to their share in all encounters, the same subfamilies comprised 50%, 37% and 9%, respectively (Table 5-3).The combined assessment of termites and ants following our newly devised RAP protocol has been proven to be especially advantageous for the compilation of ant species checklists, where ants are additionally collected when encountered in the sections of the 'termite transect' (microhabitats and soil scrapes). In order to visualize the optimization reached when sampling ants with the RAP protocol, additionally an overview is given of the species number collected per genus and land-use type, however, differentiated according to the different' protocol parts': the 'ant transect' (AT) and the 'termite transect' (TT) (Fig. A5-3; Appendix 5). In Fig. A5-1, three columns are shown per land-use type: species collected within the ant transect, comprising pitfall trap and Winkler site; the termite transect, comprising soil scrapes and microhabitats; and, the combined number of species found per genus with both protocol parts in total (this last column, ALL, therefore resembles the column that is shown in Fig. 5-1). In each habitat except for the reserve, the majority of species has been collected following the protocol specifically designed to rapidly assess ant communities, i.e. in pitfall traps and Winkler sites (AT) (Fig. A5-1); in our study sites, pitfall traps revealed by far the best results. However, in all habitats, a significant amount of additional ant species has been collected within the sections of the 'termite transect'.

Table 5-3: Ant species and morphospecies collected in the four main succession stages of the Zaï system in Ouahigouya (sub-Sahel zone, Burkina Faso).

Sub-Sahel zone in Burkina Faso N° of sampling units (SUs) Ant subfamilies & genera			ZDeg 40 SUs		ZMil 50 SUs		ZF20 50 SUs		ZF30 50 SUs	
Rank	Ant (morpho-) species	F%	F%	D%	F%	D%	F%	D%	F%	D%
Ponerini										
Anochetus Mayr 1861										
10	*A. sedilloti* Emery 1884	13.2	3	0.8	4	0.8	22	4.1	22	3.3
19	*A.*sp.02	4.2	5	1.5	-	-	2	0.4	14	2.1
Pachycondyla Smith 1858										
11	*P. senaarensis* (Mayr 1862)	11.6	-	-	32	6.1	8	1.5	2	0.3
16	*P.* sp.03	6.8	-	-	-	-	-	-	22	3.3
Dorylinae										
Dorylus Fabricius 1793										
24	*D.* sp.02	0.5	10	3.0	-	-	-	-	2	0.3
Myrmicinae										
Crematogaster Lund 1831										
8	*C.* sp.02	18.4	20	6.0	40	7.6	2	0.4	-	-
24	*C.* sp.03	0.5	3	0.8	-	-	-	-	-	-
Nesomyrmex Mayr 1855										
22	*N. evelynae* (Forel 1916)	1.6	-	-	-	-	4	0.7	-	-
Temnothorax Mayr 1861										
19	*T. megalops*^{1} (H. & K. 1967)	4.2	-	-	-	-	4	0.7	12	1.8
Pheidole Westwood 1839										
2	*P.* sp.01	75.3	40	12.0	76	14.5	88	16.4	84	12.6
24	*P.* sp.02	0.5	-	-	-	-	-	-	2	0.3
21	*P.* sp.03	2.1	-	-	-	-	2	0.4	6	0.9
Monomorium Mayr 1855										
6	*M. abyssinicum* (Forel 1894)	27.4	-	-	32	6.1	34	6.3	22	3.3
14	*M. areniphilum* (Santschi 1911)	8.9	53	15.8	2	0.4	-	-	-	-
1	*M. bicolor* Emery 1877	78.4	68	20.3	88	16.8	82	15.3	74	11.1
24	*M. dakarense* (Santschi 1914)	0.5	-	-	-	-	-	-	2	0.3
22	*M. destructor* (Jerdon 1851)	1.6	40	12.0	-	-	-	-	4	0.6

Sub-Sahel zone in Burkina Faso N° of sampling units (SUs) Ant subfamilies & genera			ZDeg 40 SUs		ZMil 50 SUs		ZF20 50 SUs		ZF30 50 SUs	
Rank	Ant (morpho-) species	F%	F%	D%	F%	D%	F%	D%	F%	D%
17	*M. oscaris* Forel 1894	5.3	-	-	4	0.8	6	1.1	10	1.5
23	*M.* sp.01	1.1	-	-	-	-	-	-	4	0.6
20	*M.* sp.08	3.7	-	-	-	-	-	-	14	2.1
22	*M.* sp.09	1.6	3	0.8	2	0.4	2	0.4	2	0.3
15	*M. vonatu* Bolton 1987	7.9	3	0.8	6	1.1	16	3.0	8	1.2
Oligomyrmex Mayr 1867										
24	*O.* sp.02	0.5	-	-	-	-	-	-	2	0.3
Tetramorium Mayr 1855										
7	*T. angulinode* Santschi 1910	23.2	3	0.8	22	4.2	20	3.7	46	6.9
21	*T. longicorne* Forel 1907	2.1	-	-	-	-	-	-	8	1.2
3	*T. sericeiventre* Emery 1877	62.6	3	0.8	62	11.8	82	15.3	62	9.3
24	*T.* sp.05	0.5	-	-	-	-	-	-	2	0.3
9	*T.* sp.06	13.7	-	-	10	1.9	12	2.2	30	4.5
23	*T.* sp.07	1.1	-	-	2	0.4	2	0.4	-	-
12	*T. zapyrum* Bolton 1980	11.1	-	-	2	0.4	-	-	40	6.0
DOLICHODERINAE										
Tapinoma Foerster 1850										
18	*T.* sp.01	4.7	-	-	4	0.8	8	1.5	6	0.9
23	*T.* sp.02	1.1	-	-	2	0.4	2	0.4	-	-
CERAPACHYINAE										
Cerapachys Smith 1857										
23	*C.* sp.01	1.1	-	-	-	-	-	-	4	0.6
FORMICINAE										
Anoplolepis (Santschi 1914)										
21	*A.* sp.01	2.1	-	-	-	-	4	0.7	4	0.6
Lepisiota (Santschi 1926)										
5	*L.* sp.01	44.7	-	-	56	10.7	40	7.5	72	10.8
19	*L.* sp.02	4.2	-	-	6	1.1	6	1.1	4	0.6
19	*L.* sp.03	4.2	35	10.5	6	1.1	-	-	2	0.3

Sub-Sahel zone in Burkina Faso N° of sampling units (SUs) Ant subfamilies & genera			ZDeg 40 SUs		ZMil 50 SUs		ZF20 50 SUs		ZF30 50 SUs	
Rank	Ant (morpho-) species	F%	F%	D%	F%	D%	F%	D%	F%	D%
	Camponotus Mayr 1861									
4	*C. maculatus* (Fabricius 1782)	57.9	48	14.3	60	11.5	62	11.6	56	8.4
13	*C. sericeus* (Fabricius 1798)	10.0	-	-	6	1.1	18	3.4	14	2.1
23	*C.* sp.07	1.1	-	-	-	-	-	-	4	0.6
	Polyrhachis Smith 1857									
20	*P.* sp.02	3.7	-	-	-	-	8	1.5	6	0.9
N° of ant species (spp.) N° of hits in all sampling units		41 spp. 997hits	15 spp. 133 hits		22 spp. 226 hits		25 spp. 268 hits		35 spp. 334 hits	

[1] H. & K: Hamann & Klemm. ZDeg: degraded area. ZMil: millet fields. ZF20: young Zaï forest. ZF30: old Zaï forest. Rank: species rank according to their frequency in 190 sampling units (SUs) (all four habitats). F%: species' share in all SUs (in %); D%: species' dominance.

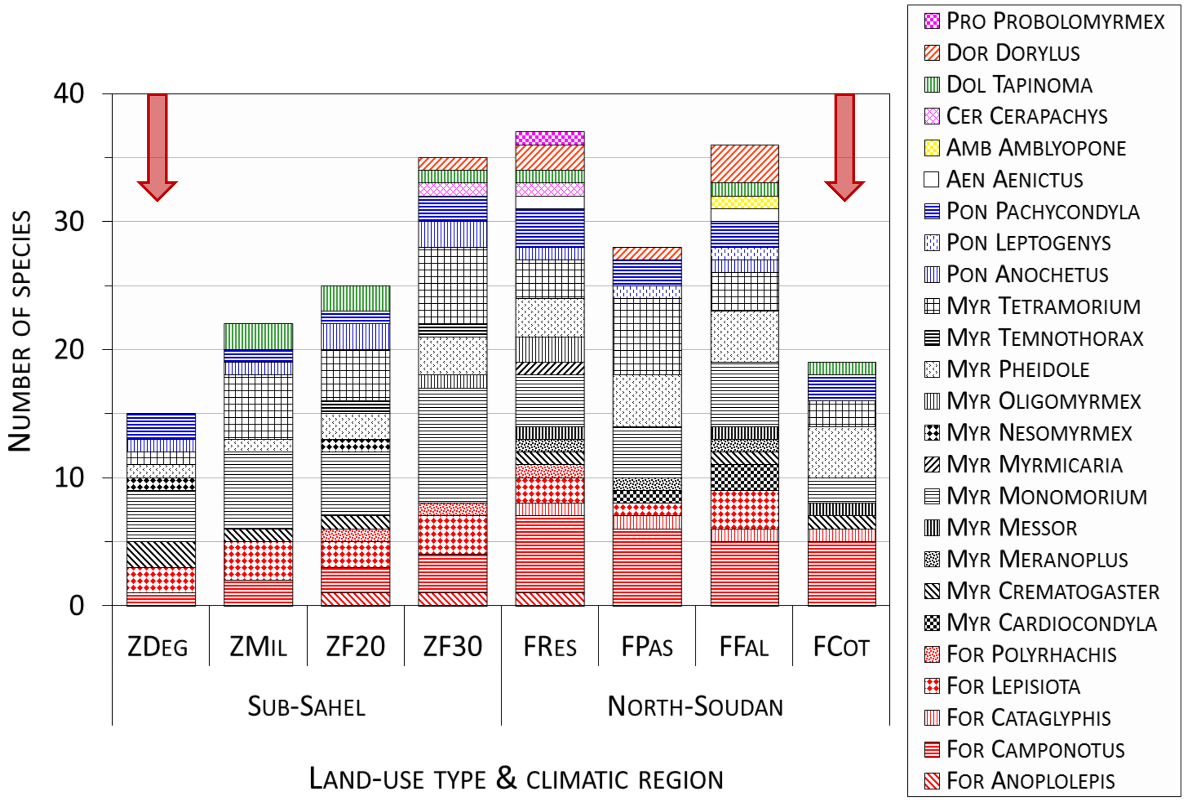

Fig. 5-1: Number of ant species collected per genus and subfamily in eight different habitats from 2004–2008. Each color represents one of nine subfamilies: Amblyoponinae (Amb), Aenictinae (Aen), Formicinae (For), Myrmicinae (Myr), Ponerinae (Pon), Cerapachyinae (Cer), Dolichoderinae (Dol), Proceratinae (Pro), and Dorylinae (Dor). Habitats are ZDeg: Degraded land, ZMil: millet fields, ZF20: young Zaï forest, ZF30: old Zaï forest. FRes: Pama reserve, FPas: pasture, FFal: fallow, FCot: cotton field.

Table 5-4: Ant species and morphospecies collected in the four habitats located 52 km east of Fada N'Gourma (North-Sudan zone, Burkina Faso).

North-Sudan region in Burkina Faso N° of sampling units (SUs) Ant subfamilies & genera			FRes 50 SUs		FPas 40 SUs		FFal 40 SUs		FCot 40 SUs	
Rank	Ant (morpho-) species	F%	F%	D%	F%	D%	F%	D%	F%	D%
Proceratiinae										
Probolomyrmex Mayr 1901										
30	*P.* sp.01	0.6	2	0.3	-	-	-	-	-	-
Ponerini										
Anochetus Mayr 1861										
30	*A. sedilloti* Emery 1884	0.6	2	0.3	-	-	-	-	-	-
29	*A.* sp.02	1.2	-	-	-	-	5	0.6	-	-
Leptogenys Roger 1861										
27	*Leptogenys* sp.01	2.4	-	-	8	1.2	3	0.3	-	-
Pachycondyla Smith 1858										
4	*P. senaarensis* (Mayr 1862)	38.2	18	2.7	8	1.2	68	8.8	65	17.7
17	*P.* sp.01	11.8	24	3.6	13	2.1	3	0.3	5	1.4
28	*P.* sp.03	1.8	6	0.9	-	-	-	-	-	-
Aenictinae										
Aenictus Shuckard 1840										
25	*A.* sp.01	3.5	10	1.5	-	-	3	0.3	-	-
Dorylinae										
Dorylus Fabricius 1793										
28	*D.* sp.01	1.8	2	0.3	-	-	5	0.6	-	-
28	*D.* sp.02	1.8	-	-	-	-	8	1.0	-	-
21	*D.* sp.03	8.8	20	3.0	3	0.4	10	1.3	-	-
Myrmicinae										
Crematogaster Lund 1831										
19	*C.* sp.01	10.6	36	5.3	-	-	-	-	-	-
24	*C.* sp.02	4.7	-	-	-	-	18	2.3	3	0.7
Cardiocondyla Emery 1869										
28	*C.* sp.03	1.8	-	-	3	0.4	5	0.6	-	-
27	*C.* sp.04	2.4	-	-	-	-	10	1.3	-	-

North-Sudan region in Burkina Faso N° of sampling units (SUs) Ant subfamilies & genera			FRes 50 SUs		FPas 40 SUs		FFal 40 SUs		FCot 40 SUs	
Rank	Ant (morpho-) species	F%	F%	D%	F%	D%	F%	D%	F%	D%
	Meranoplus Smith 1853									
26	*M.* sp.01	2.9	6	0.9	3	0.4	3	0.3	-	-
	Myrmicaria Saunders 1841									
11	*M.* sp.01	17.1	58	8.6	-	-	-	-	-	-
	Messor Forel 1890									
5	*M. galla* (Emery 1895)	36.5	6	0.9	-	-	90	11.7	58	15.6
	Pheidole Westwood 1839									
2	*P.* sp.01	64.1	76	11.3	83	13.6	68	8.8	28	7.5
14	*P.* sp.02	15.3	6	0.9	35	5.8	13	1.6	10	2.7
23	*P.* sp.03	5.9	-	-	3	0.4	13	1.6	10	2.7
7	*P.* sp.04	27.6	8	1.2	15	2.5	63	8.1	30	8.2
	Monomorium Mayr 1855									
12	*M. abyssinicum* (Forel 1894)	16.5	12	1.8	53	8.7	3	0.3	-	-
30	*M. areniphilum* (Santschi 1911)	0.6	-	-	-	-	-	-	3	0.7
6	*M. bicolor* Emery 1877	29.4	8	1.2	60	9.9	38	4.9	18	4.8
22	*M. destructor* (Jerdon 1851)	7.1	24	3.6	-	-	-	-	-	-
27	*M. oscaris* Forel 1894	2.4	8	1.2	-	-	-	-	-	-
29	*M.* sp.08	1.2	-	-	3	0.4	3	0.3	-	-
30	*M.* sp.09	0.6	-	-	-	-	3	0.3	-	-
25	*M. vonatu* Bolton 1987	3.5	-	-	10	1.7	5	0.6	-	-
	Oligomyrmex Mayr 1867									
29	*O.* sp.01	1.2	4	0.6	-	-	-	-	-	-
30	*O.* sp.02	0.6	2	0.3	-	-	-	-	-	-
	Tetramorium Mayr 1855									
8	*T. angulinode* Santschi 1910	27.1	22	3.3	28	4.5	48	6.2	13	3.4
15	*T. sericeiventre* Emery 1877	14.1	2	0.3	30	5.0	23	2.9	5	1.4
24	*T.* sp.06	4.7	6	0.9	5	0.8	8	1.0	-	-
30	*T.* sp.08	0.6	-	-	3	0.4	-	-	-	-
30	*T.* sp.10	0.6	-	-	3	0.4	-	-	-	-
26	*T. zapyrum* Bolton 1980	2.9	-	-	13	2.1	-	-	-	-

North-Sudan region in Burkina Faso N° of sampling units (SUs) Ant subfamilies & genera			FRes 50 SUs		FPas 40 SUs		FFal 40 SUs		FCot 40 SUs	
Rank	Ant (morpho-) species	F%	F%	D%	F%	D%	F%	D%	F%	D%
DOLICHODERINAE										
Tapinoma Foerster 1850										
21	*T.* sp.01	8.8	8	1.2	-	-	23	2.9	5	1.4
AMBLYOPONINAE										
Amblyopone Erichson 1842										
30	*A.* sp.01	0.6	-	-	-	-	3	0.3	-	-
CERAPACHYINAE										
Cerapachys Smith 1857										
30	*C.* sp.02	0.6	2	0.3	-	-	-	-	-	-
FORMICINAE										
Anoplolepis (Santschi 1914)										
30	*A.* sp.02	0.6	2	0.3	-	-	-	-	-	-
Lepisiota (Santschi 1926)										
20	*L.* sp.01	9.4	4	0.6	3	0.4	33	4.2	-	-
27	*L.* sp.02	2.4	4	0.6	-	-	5	0.6	-	-
29	*L.* sp.03	1.2	-	-	-	-	5	0.6	-	-
Cataglyphis Foerster 1850										
18	*C.* sp.01	11.2	2	0.3	3	0.4	18	2.3	25	6.8
Camponotus Mayr 1861										
13	*C. compressiscapus* André 1889	15.9	20	3.0	28	4.5	8	1.0	8	2.0
3	*C. maculatus* (Fabricius 1782)	52.9	56	8.3	60	9.9	55	7.1	40	10.9
1	*C. sericeus* (Fabricius 1798)	70.0	90	13.4	75	12.4	73	9.4	38	10.2
19	*C. solon* (Forel 1886)	10.6	34	5.0	3	0.4	-	-	-	-
9	*C.* sp.06	19.4	12	1.8	48	7.9	15	1.9	5	1.4
16	*C.* sp.07	12.4	10	1.5	13	2.1	25	3.2	3	0.7
Polyrhachis Smith 1857										
10	*P.* sp.01	18.2	62	9.2	-	-	-	-	-	-
N° of ant species N° of hits in all SUs		53 spp. 1034 hits	37 spp. 337 hits		28 spp. 242 hits		36 spp. 308 hits		19 spp. 147 hits	

Habitats are FRes: near-natural savanna (Pama reserve), FPas: pasture area, FFal: short-term fallow, FCot: cotton fields. Rank: species rank according to their frequency in 170 sampling units (SUs) (all four habitats); species with the same frequency have the same rank. F%: species' share in all SUs (in %); D%: species' dominance (share in all hits in %).

5.3.2.2 Termite communities

Combining all sites of both regions, 42 (morpho-) species of termites (including three unknown) belonging to 13 genera (plus unknown) and 4 sub-families were collected by means of the rapid assessment protocol. The four age stages of the Zaï system (sub-Sahel region, Burkina Faso) hosted 33 (morpho-) species (including three unknown) of 11 genera (plus unknown) and 4 sub-families, while it were 31 (morpho-) species of 12 genera and 4 sub-families in the four sites of the North-Soudan. An overview of the species number found per genus and functional group (FG) under different disturbance regimes is illustrated in Fig. 5-2. Each column represents one land-use type, each color one functional group (FG).

The situation we found is very similar to that of ants. Lowest numbers of species and FG are found in areas which are heavily impacted by humans (sites with the highest AI-index) and show very low habitat-heterogeneity, ZDeg in the Sub-Sahel and FCot in the North-Soudan (indicated by the red arrows) (Fig. 5-2).

Obvious is the negative trend of decreasing species diversity along the disturbance gradient in the North-Soudan: the diversity of termite communities is highest in the reserve with restricted human impact, and drastically decreases with increasing human pressure, that is pasture > fallow > cotton fields. In the sustainable agriculture, the traditional Zaï system, on the other hand, an increasing number of termite species was found with increasing habitat restoration, that is degraded, barren land < millet fields < young Zaï forest < old Zaï forest. Remarkable is that compared to the near-natural savanna FRes, the old Zaï forest ZF30 is richer in species, and the young and the old Zaï forestare richer in termite genera. Furthermore, the young forest ZF20 and even the millet fields ZMil were richer in species and FGs than any other habitat in the North-Soudan.

However, more information concerning the functional groups can be drawn from Fig. 5-2: i) fungus growers were very well represented in all habitats thereby highlighting the enormous adaptability and success of this FG in semi-arid areas; ii) whole functional groups are missing in heavily impacted areas, e.g. soil and grass feeders were missing in FCot and neither soil-, nor grass- nor wood feeders were present in ZDeg; iii) except for ZDeg, communities in all Zaï stages had representatives for each of the four FGs, even of the extremely sensible soil feeders; in the North-Soudan by contrast, FRes was the only habitat that hosted soil feeding termites; even the grass feeders were only in FRes notably diverse. To conclude, the highest variations between the habitats seem to occur in soil and grass feeding termites.

The complete list of termite species (including taxonomy) collected in the four succession stages of the Zaï system in Ouahigouya is given in Table 5-5, those collected in the North-Sudanese zone in Table 5-6**.**

Table 5-5: Termite species and morphospecies collected in the four main succession stages of the Zaï system in Ouahigouya (sub-Sahel zone, Burkina Faso).

Sub-Sahel zone in Burkina Faso N° of sampling units (SUs) Termite subfamilies & genera			ZDeg 50 SUs	ZMil 50 SUs		ZF20 50 SUs		ZF30 50 SUs	
Rank	Termite (morpho-) species	F%	F%	F%	D%	F%	D%	F%	D%
MACROTERMITINAE									
*Ancistrotermes*Silvestri 1912 – fungus-growers									
15	*A. cavithorax* (Sjöstedt 1899)	2.0	-	2	1.1	4	2.9	2	0.7
13	*A. crucifer* (Sjöstedt 1897)	3.0	-	6	3.4	-	-	6	2.2
Macrotermes Holmgren 1909 – fungus-growers									
5	*M. bellicosus* (Smeathman 1781)	8.5	-	-	-	6	4.3	28	10.1
16	*M. subhyalinus* (Rambur 1842)	1.5	-	-	-	-	-	6	2.2
Microtermes Wasmann 1902 – fungus-growers									
1	*M. havilandi* Holmgren 1913	22.0	-	36	20.2	30	21.4	22	8.0
4	*M.* sp.01	9.5	-	2	1.1	8	5.7	28	10.1
18	*M.* sp.02	0.5	-	-	-	-	-		0.7
2	*M. subhyalinus* Silvestri 1914	17.0	-	-	-	16	11.4	52	18.8
Odontotermes Holmgren 1912 – fungus-growers									
9	*O.* sp.01	6.0	-	2	1.1	12	8.6	10	3.6
11	*O.* sp.02	4.5	-	-	-	10	7.1	8	2.9
17	*O.* sp.04	1.0	2	-	-	2	1.4	-	-
NASUTITERMITINAE									
Trinervitermes Holmgren 1912 – grass-feeders									
18	*T. geminatus* (Wasmann 1897)	0.5	-		1.1	-	-	-	-
18	*T. occidentalis* (Sjöstedt 1904)	0.5	-	-	-	-	-		0.7
14	*T. oeconomus* (Trägårdh 1904)	2.5	-	4	2.2	4	2.9	2	0.7
AMITERMITINAE									
Amitermes Silvestri 1901 – wood-feeders									
7	*A. evuncifer* Silvestri 1912	7.5	-	18	10.1	-	-	12	4.3
16	*A. guineensis* Sands 1992	1.5	-	-	-	2	1.4	4	1.4
18	*A.* sp.01	0.5	-	-	-	-	-	2	0.7
18	*A. stephensoni* Harris 1957	0.5	-		1.1	-	-	-	-

Sub-Sahel zone in Burkina Faso N° of sampling units (SUs) Termite subfamilies & genera			ZDeg 50 SUs	ZMil 50 SUs		ZF20 50 SUs		ZF30 50 SUs	
Rank	Termite (morpho-) species	F%	F%	F%	D%	F%	D%	F%	D%
Microcerotermes Silvestri 1901 – wood-feeders									
6	*M. edentatus* Emerson 1928	8.0	-	26	14.6	4	2.9	2	0.7
18	*M. limpopoensis* Fuller 1925	0.5	-	-	-		1.4	-	-
12	*M. parvulus* (Sjöstedt 1911)	3.5	-	12	6.7	2	1.4	-	-
8	*M. parvus* (Haviland 1898)	7.0	-	16	9.0	4	2.9	8	2.9
18	*M. theobromae* Holmgren 1912	0.5	-	-	-	-	-		0.7
16	*M. thermarum* Fuller 1925	1.5	-	-	-	6	4.3	-	-
TERMITINAE									
Angulitermes Sjöstedt 1924 – wood-feeders									
18	*A. elsenburgi* (Fuller 1925)	0.5	-	-	-	-	-		0.7
Eremotermes Silvestri 1911 – wood-feeders									
5	*E. sabaeus* Harris 1957	8.5	-	28	15.7	2	1.4	4	1.4
Cubitermes Wasmann 1906 – soil-feeders									
18	*C. bilobatodes* Silvestri 1912	0.5	-		1.1	-	-	-	-
18	*C.* sp.01	0.5	-	-	-		1.4	-	-
15	*C. subcrenulatus* Silvestri 1914/15	2.0	-	4	2.2	-	-	4	1.4
APICOTERMITINAE									
Anoplotermes Sands 1972 – soil-feeders									
5	*A.* sp.01	8.5	-	-	-	8	5.7	26	9.4
UNKNOWN									
10	Unknown – soil-feeders	5.0	-	-	-	6	4.3	14	5.1
3	Unknown-1	13.0	-	16	9.0	10	7.1	26	9.4
18	Unknown-2	0.5	-	-	-	-	-		0.7
N° of species (spp.)		33 spp.	1 sp.	16 spp.		20 spp.		25 spp.	
N° of hits in all sampling units		298 hits	1 hit	89 hits		70 hits		138 hits	

Habitats are ZDeg: degraded, barren site, ZMil: millet fields, ZF20: young Zaï forest, ZF30: old Zaï forest. Rank: species rank according to their frequency in 190 sampling units (SUs) (all four habitats); species with the same frequency have the same rank. F%: species' share in all SUs (in %); D%: species' dominance (share in all hits in %).

Table 5-6: Termite species and morphospecies collected in the four habitats located 52 km east of Fada N'Gourma (North-Sudanese zone, Burkina Faso).

North-Sudan region in Burkina Faso N° of sampling units (SUs) Termite subfamilies & genera			FRes 50 SUs		FPas 40 SUs		FFal 40 SUs		FCot 40 SUs	
Rank	Termite (morpho-) species	F%	F%	D%	F%	D%	F%	D%	F%	D%
MACROTERMITINAE										
Ancistrotermes Silvestri 1912 – fungus-growers										
16	*A. cavithorax* (Sjöstedt 1899)	1.8	6	1.4	-	-	-	-	-	-
6	*A. crucifer* (Sjöstedt 1897)	11.8	32	7.3	-	-	10	7.7	-	-
17	*A. guineensis* (Silvestri 1912)	1.2	4	0.9	-	-	-	-	-	-
17	*A.* sp.01	1.2	-	-	3	1.8	3	1.9	-	-
Macrotermes Holmgren 1909 – fungus-growers										
8	*M. bellicosus* (Smeathman 1781)	7.6	20	4.6	5	3.6	3	1.9	-	-
18	*M. subhyalinus* (Rambur 1842)	0.6	2	0.5	-	-	-	-	-	-
Microtermes Wasmann 1902 – fungus-growers										
1	*M. havilandi* Holmgren 1913	32.4	48	11.0	33	23.6	8	5.8	38	38.5
13	*M.* sp.01	3.5	-	-	-	-	-	-	15	15.4
18	*M.* sp.02	0.6	2	0.5	-	-	-	-	-	-
2	*M. subhyalinus* Silvestri 1914	30.0	42	9.6	5	3.6	40	30.8	30	30.8
Odontotermes Holmgren 1912 – fungus-growers										
11	*O.* sp.01	5.3	4	0.9	3	1.8	15	11.5	-	-
12	*O.* sp.02	4.1	-	-	5	3.6	13	9.6	-	-
18	*O.* sp.03	0.6	-	-	3	1.8	-	-	-	-
NASUTITERMITINAE										
Trinervitermes Holmgren 1912 – grass-feeders										
5	*T. geminatus* (Wasmann 1897)	12.4	40	9.2	3	1.8	-	-	-	-
18	*T. gratiosus* Sjöstedt 1924	0.6	2	0.5	-	-	-	-	-	-
9	*T. occidentalis* (Sjöstedt 1904)	7.1	24	5.5	-	-	-	-	-	-
3	*T. oeconomus* (Trägårdh 1904)	27.1	48	11.0	53	38.2	3	1.9	-	-
14	*T. togoensis* (Sjöstedt 1899)	2.9	10	2.3	-	-	-	-	-	-
12	*T. trinervius* (Rambur), 1842	4.1	14	3.2	-	-	-	-	-	-
Fulleritermes Coaton 1962 – wood-feeders										
15	*F. coatoni* Sands, 1965	2.4	6	1.4	3	1.8	-	-	-	-

North-Sudan region in Burkina Faso N° of sampling units (SUs) Termite subfamilies & genera			FRes 50 SUs		FPas 40 SUs		FFal 40 SUs		FCot 40 SUs	
Rank	Termite (morpho-) species	F%	F%	D%	F%	D%	F%	D%	F%	D%
AMITERMITINAE										
Amitermes Silvestri 1901 – wood-feeders										
16	*A. evuncifer* Silvestri 1912	1.8	6	1.4	-	-	-	-	-	-
16	*A. guineensis* Sands 1992	1.8	4	0.9	3	1.8	-	-	-	-
18	*A. messinae* Fuller, 1922	0.6	-	-	3	1.8	-	-	-	-
Microcerotermes Silvestri 1901 – wood-feeders										
7	*M. edentatus* Emerson 1928	8.8	28	6.4	-	-	3	1.9	-	-
15	*M. parvulus* (Sjöstedt 1911)	2.4	8	1.8	-	-	-	-	-	-
4	*M. parvus* (Haviland 1898)	22.9	58	13.3	15	10.9	10	7.7	-	-
TERMITINAE										
Eremotermes Silvestri 1911 – wood-feeders										
10	*E. sabaeus* Harris 1957	6.5	-	-	5	3.6	10	7.7	13	12.8
Cubitermes Wasmann 1906 – soil-feeders										
18	*C. subcrenulatus* Silvestri 1914/15	0.6	2	0.5	-	-	-	-	-	-
Promirotermes Silvestri 1914/15 – soil-feeders										
18	*P. holmgreni* (Silvestri 1912)	0.6	-	-	-	-	3	1.9	-	-
APICOTERMITINAE										
Anoplotermes Sands 1972 – soil-feeders										
15	*A.* sp.01	2.4	8	1.8	-	-	-	-	-	-
UNKNOWN										
7	Unknown-1	8.8	18	4.1	-	-	13	9.6	3	2.6
N° of species (spp.)		31 spp.	24 spp.		14 spp.		13 spp.		5 spp.	
N° of hits in all sampling units		364 hits	210 hits		55 hits		52 hits		39 hits	

Habitats FRes: near-natural savanna (Pama reserve); FPas: pasture area; FFal: short-term fallow; FCot: cotton fields. Rank: species rank according to their frequency in 170 sampling units (SUs) (all four habitats); species with the same frequency have the same rank. F%: species' share in all SUs (in %); D%: species' dominance, i.e. species' share in all hits (in %).

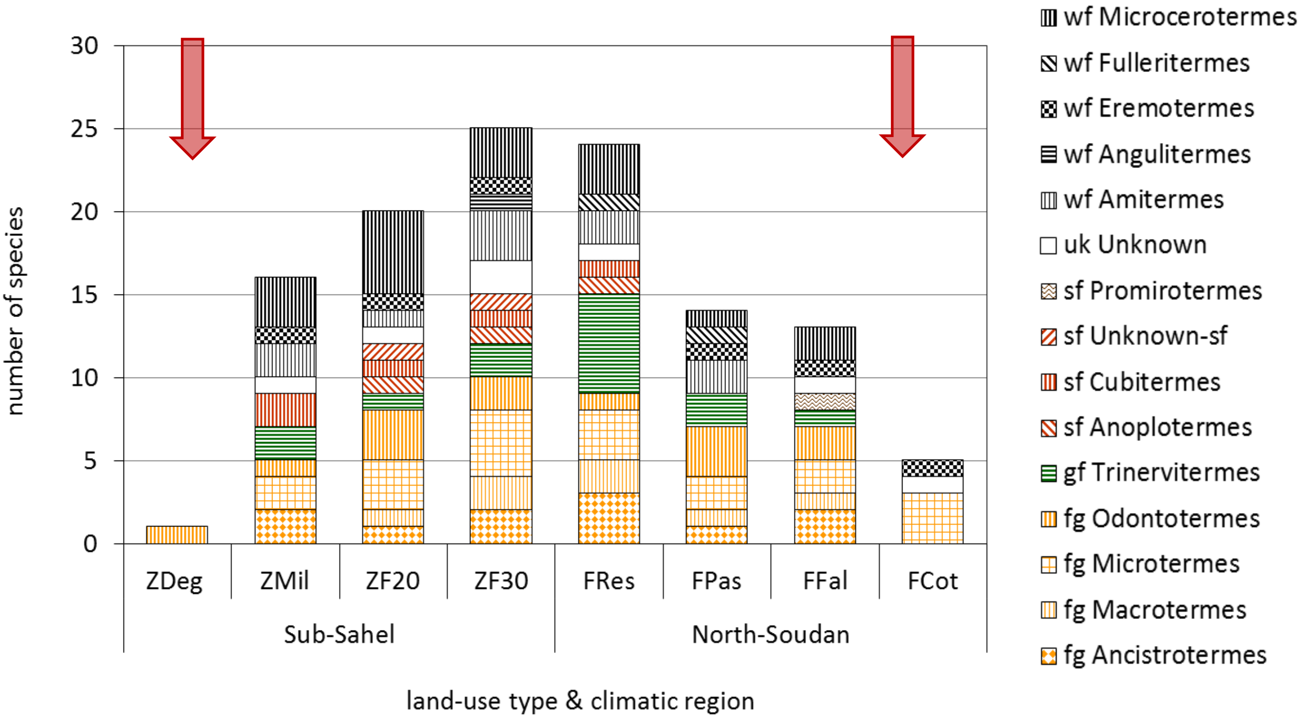

Fig. 5-2: Number of termite species per genus and functional group in eight land-use types (Burkina Faso from 2004–2008). Each column represents one habitat type, each color a functional group. ZDeg: degraded land, ZMil: millet fields, ZF20: young Zaï forest, ZF20: old Zaï forest; FRes: Pama reserve, FPas: pasture, FFal: fallow, FCot: cotton field. Functional groups are fg: fungus-grower, gf: grass-feeder, sf: soil-feeder, wf: wood-feeder, uk: unknown genus.

5.3.3 Species richness along two land-use intensification gradients

5.3.3.1 Incidence-based, randomized accumulation and rarefaction curves

Incidence-based, randomized accumulation curves were used to graphically compare the species richness of the habitats belonging to the same intensification gradient, for example the termite communities in the four succession stages of in the Zaï system in Ouahigouya (Fig. 5-3). In those cases where the sampling effort differed slightly between the land-use types (e.g. in the case of ant communities in four Zaï stages), the rarefaction method was used to calculate the number of species expected in a subsample selected at random from the multiple samples. Species richness of the habitats was then compared at a common lower level, which is at the smaller sampling effort.

The slopes of the curves illustrate the rate at which new species were added with increasing sampling effort. However, these curves only indicate the total species richness when sampling has been exhaustive and an asymptote is reached (for more information see Magurran 2004).

5.3.3.2 Ant communities

Increasing the sampling effort means an increasing number of sampling units. For ants, one sampling unit comprises one pitfall trap, one 'Winkler-site' of 1-m^2, and one transect section. However, only eight ant sampling stations (each comprising one pitfall trap and one Winkler-site) were installed per 50 m transect; two sampling units for ants consequently correspond to one transect section only. The term 'samples' might be used henceforth.

First disturbance gradient in the sub-Sahel region of Burkina Faso (LUI-1)

For ants collected in four succession stages of in the Zaï system in Ouahigouya (Sub-Sahel) between 2004 and 2008, the incidence-based, randomized rarefaction curves (Coleman with standard deviations) are shown in Fig. 5-3. Species richness of the different ant communities along the first land-use intensification gradient (LUI-1) were compared at the common level of 39 samples which is indicated by the vertical dashed line.

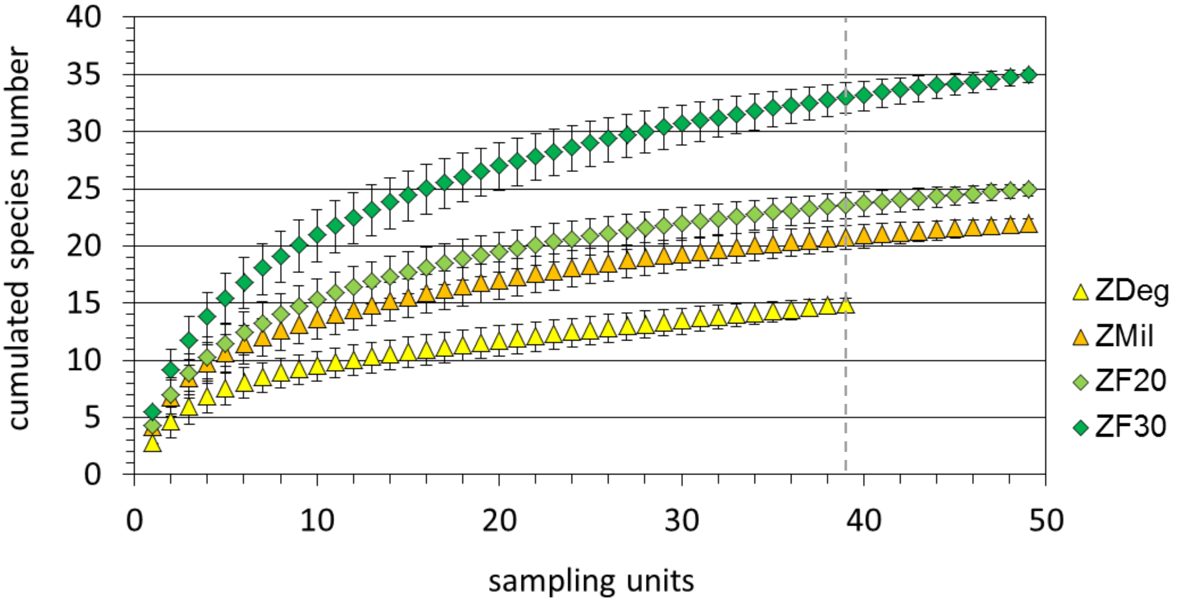

Fig. 5-3: Incidence-based, randomized rarefaction curves (with standard deviations) for ants in four Zaï stages (Burkina Faso from 2004–2008). The rarefied number of 39 sampling units (dashed line) was used to compare the habitats. ZDeg: degraded land, ZMil: millet fields, ZF20: young Zaï forest, ZF30: old Zaï forest. Since neither curves nor standard deviations overlap for any of the habitats at the point of 39 SUs, habitats can be ordered with regard to species richness: ZDeg < ZMil < ZF20 < ZF30.

The figure visualizes the increasing species richness with increasing habitat rehabilitation, i.e. from degraded land, to millet fields, to the young, and then the old Zaï forest (Fig. 5-3). That the sites can be ordered according to their species richness, can be seen as neither curves nor standard deviations overlap for any of the land-uses at the sampling unit (SU) number used to compare the land-uses (39 SUs) (Fig. 5-3). Species composition and the number of ant species expected (Coleman) at the common sampling effort differed significantly between the four Zaï stages (Friedmann *n* = 39, χ^2 (3) = 117, *p* < 0.0001). The descending order of all land-uses with regard to the number of ant species expected in 39 samples is ZF30 > ZF20 > ZMil > ZDeg. A Wilcoxon sign-rank test was used to follow up on this finding for ZF20 and ZMil; a Bonferroni correction was applied and so all effects are reported at a 0.025 level of significance. As illustrated in Fig. 5-3 by the separated curves, significantly more ant species were found in the young Zaï forest than in the millet fields ZMil (*Z* = -5.44, *p* < 0.0001, *R* = 0.62).

Second disturbance gradient in the North-Sudan region of Burkina Faso (LUI-2)

For ants collected between 2004 and 2006 along the second land-use intensification gradient (LUI-2) in the North-Sudan region, the incidence-based, randomized rarefaction curves are presented in Fig. 5-4. The reserve FRes and the fallow FFal exhibited almost identical rates at which new species were added with increasing sampling effort, but the curve of FFal rather approaches an asymptote (Fig. 5-4). The number of ant species in the pasture FPas was about three-quarter of the species-number in FRes; it was lowest in the cotton field FCot (Fig. 5-4).

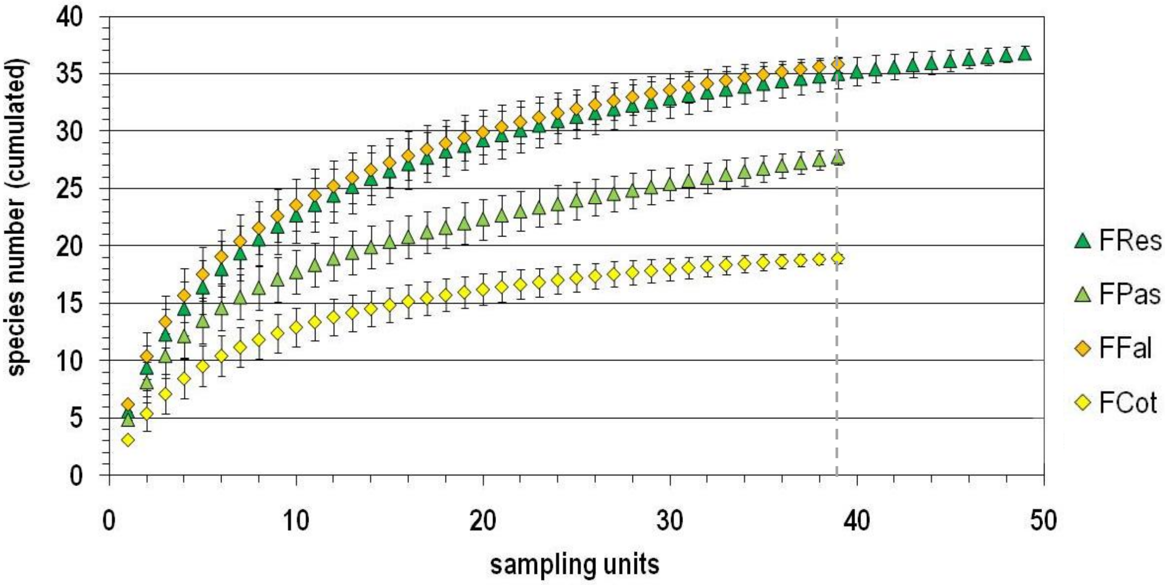

Fig. 5-4: Incidence-based, randomized rarefaction curves (with standard deviations) for ants in four habitats near Fada N'Gourma (Burkina Faso from 2004–2008). The rarefied number of 39 sampling units (dashed line) was used to compare the sites. FRes: Pama reserve, FPas: pasture, FFal: fallow, FCot: cotton fields. Since the curves of FRes and FFal overlap at the point of 39 SUs, these two habitats cannot be ordered with regard to species richness.

Species composition and the number of ant species expected (Coleman) at the common sampling effort differed significantly between the four land-uses (Friedmann *N* = 39, χ^2(3) = 117, *p* < 0.0001). The descending order of all land-uses with regard to the number of ant species expected in 39 samples is FFal > FRes > FPas > FCot. However, a Wilcoxon sign-rank test was used to follow up on this finding for FFal and FRes. Indicated in Fig. 5-4 by the overlapping curves, differences in ant species richness did not differ significantly between the two land-uses (*Z* = -5.45, *r* = -0.62, *p* < 0.0001 after Bonferroni correction).

5.3.3.3 Termite communities

For termites, one sampling unit comprises one transect section; the term 'samples' might be used henceforth.

First disturbance gradient in the sub-Sahel region of Burkina Faso (LUI-1)

Belt-transects were used to collect termites between 2004 and 2008 along the first land-use intensification gradient (LUI-1) in the sub-Sahel region. The incidence-based, randomized accumulation curves are presented in Fig. 5-5; one transect-section (5 x 2 m) equals one sampling unit. Quite similar to the trend observed for ants, visualizes the figure increasing termite species richness with increasing habitat rehabilitation (Fig. 5-5).

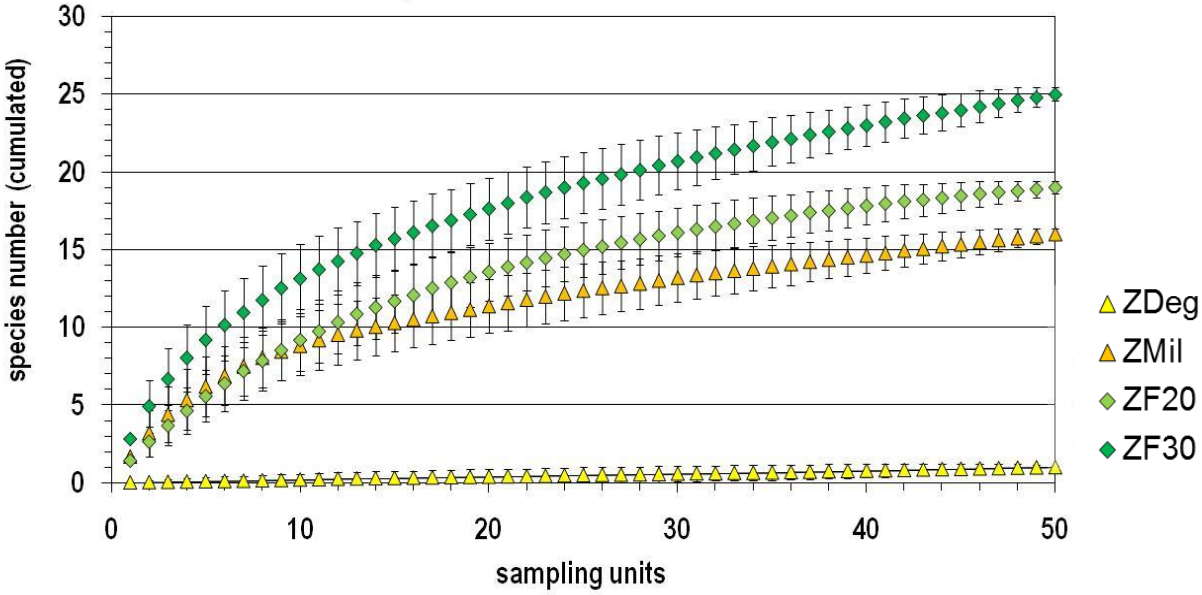

Fig. 5-5: Incidence-based, randomized accumulation curves (with standard deviations) for termites in four Zaï stages (sub-Sahel, Burkina Faso) from 2004–2008. The curves visualize increasing species richness with increasing habitat restoration. ZDeg: degraded land, ZMil: millet fields, ZF20: young Zaï forest, ZF30: old Zaï forest.

The number of species observed differed significantly between the four Zaï stages in (Friedmann *N* = 50, $\chi 2$ (3) = 141.94, *p* < 0.0001). The descending order with regard to the species number is old forest ZF30 > young forest ZF20 > millet fields ZMil > degraded soil ZDeg.

Second disturbance gradient in the North-Sudan region of Burkina Faso (LUI-2)

For termites collected between 2004 and 2006 along the second land-use intensification gradient (LUI-2) in the North-Sudan region, the incidence-based, randomized rarefaction curves are shown in Fig. 5-6. The number of species was compared at the common level of 39 samples which is indicated by the vertical dashed line. The figure indicates a trend of decreasing species richness with increasing intensification (Fig. 5-6).

Species composition and the number of termite species at the common number of samples differed significantly between the four land-uses ($N = 39$, χ^2 (3) = 106.68, $p < 0.0001$ Friedmann). The order for decreasing species richness in 39 samples is FRes > FPas > FFal > FCot. However, almost no differences existed between the number of species in FPas and FFal ($Z = -2.21$, $p = 0.027$, $r = -0.25$ Wilcoxon sign-rank test) which can be seen in Fig. 5-6 by the overlapping curves. A Bonferroni correction was applied, so all effects are reported at a .025 level of significance.

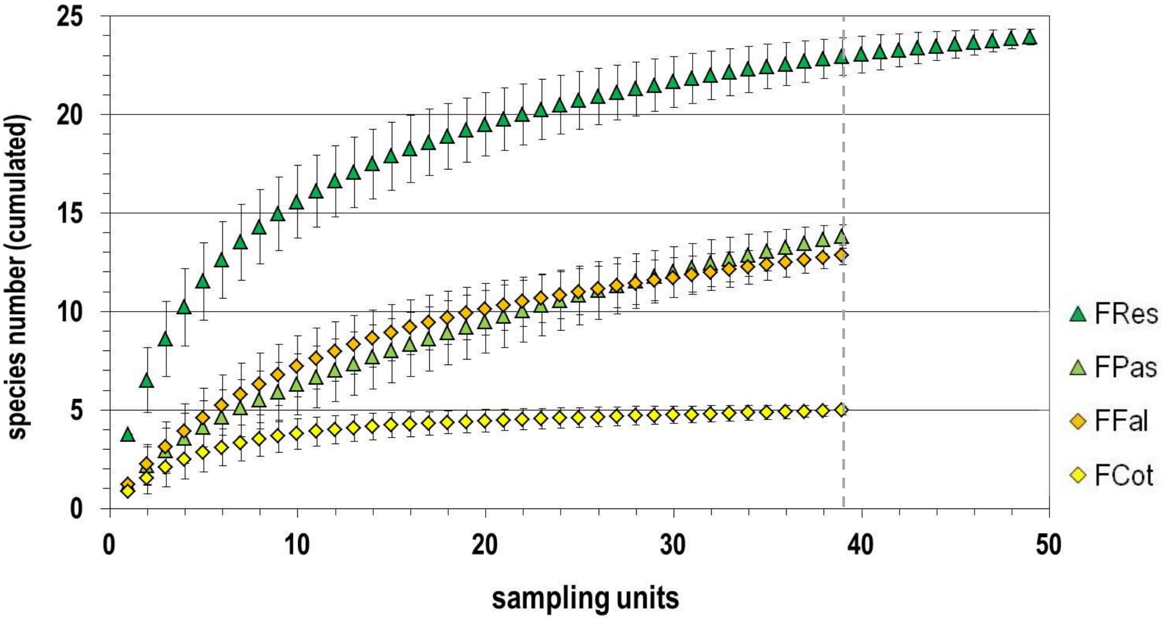

Fig. 5-6: Incidence-based, randomized rarefaction curves (with standard deviations) for termites in four habitats near Fada N'Gourma (Burkina Faso from 2004–2008). The rarefied number of 39 sampling units (dashed line) was used to compare the habitats. FRes: Pama reserve, FPas: pasture, FFal: fallow, FCot: cotton fields. Since the curves of FPas and FFal overlap at the point of 40 SUs, these two habitats cannot be ordered with regard to species richness.

5.3.3.4 Comparing the regional species richness of termite and ant communities

The incidence-based, randomized rarefaction curves of the ant and termite communities on a regional level are shown in Fig. 5-7. At the common number of 169 sampling units, the highest species richness was noted for ants in the North-Sudanese region. Termite species richness in both regions was about three-quarter of the number of ant species in the sub-Sahel or about three fifths of the number in the North-Sudanese zone (Fig. 5-7).

When comparing the two curves of ant communities, the North-Sudanese zone exhibited higher species richness and a higher rate at which new ant species were added than the Sub-Sahel (Fig. 5-7). At the common sample-number (here: 169), species richness in the Sub-Sahel zone was about four fifths of that in the North-Sudanese. As already indicated by the figure, significantly more ant species were found in the North-Sudanese than in the Sub-Sahel zone ($U = 1693.5$, $Z = -13.89$, $p < 0.0001$, $r = -0.76$).

When comparing the termite communities on a regional level at the common sample-number (169 sampling units), almost no differences could be noted between the two regions (Fig. 5-7). The sub-Sahel region exhibited slightly higher termite species richness. New species were added at a higher rate in the sub-Sahel than the North-Sudanese zone. Furthermore, at an effort of 169 sampling units, the rarefaction curve for the sub-Sahel almost reached a plateau.

Fig. 5-7: Incidence-based, randomized rarefaction curves (Coleman with standard deviations) of ants and termites collected from 2004–2008 along two land-use intensification gradients in Burkina Faso (sub-Sahel zone, North-Sudan zone). The rarefied number of 169 sampling units (dashed line) was used to compare the regions.

5.3.4 Species richness estimators

All incidence-based rarefaction and accumulation curves illustrated in Fig. 5-3, Fig. 5-4, Fig. 5-5, Fig. 5-6, and Fig. 5-7 roughly approach an asymptote. The figures therefore indicate that the combined and rapid assessment protocol (RAP) was appropriate to sample termites and ants. They also indicate that the sampling effort was sufficient to allow for reliable estimations of the habitats' total species richness.

Hence, different incidence-based estimators were calculated in EstimateS 7.5 (Colwell 2005): Jackknife-1, Jackknife-2, Chao-2, Bootstrap, incidence-based coverage estimator (ICE) and Michaelis-Menten mean (MMM). The expected total species-richness calculated by the four estimators that fitted the data best are given i) by combining the respective replicate transects for each land-use type, and ii) for each region (Table 5-7). For each estimator, the sampling efficacy (%-eff) was calculated as relation between the number of species observed (SOB) and the respective estimator value. The last column (mean all) represents the calculated mean of the four estimators. For clarity no decimal places are shown for estimators or standard deviations. In Appendix 5, the expected total species-richness is additionally calculated for each of the replicate transects that were conducted in the study sites (Table A5-4 and Table A5-5 for ants; Table A5-6 and Table A5-7 for termites).

5.3.4.1 Ant communities in the sub-Sahel and North-Sudan region in Burkina Faso

The efficacy reached when sampling ants by following the RAP-protocol was very high on all levels (single transects, the different land-use types, and the two regions) (Table 5-7; Table A5-4; Table A5-5). The lowest sampling efficacies reached for transects in the Zaï system, were 43% for the third transect in the degraded area (ZDeg-3) and 59% for the second in the old forest (ZF30-2), both according to the ICE (Table A5-4). The lowest sampling efficacy for a habitat in the Zaï system was reached – again according to the ICE – for the degraded land with 50% (Table 5-7). In all other cases, between 60% and 100% were reached; in most cases between 70% and 90% were reached for transects, for land-uses and the sub-Sahel region (Table 5-7).

Sampling efficacies calculated for the transects which were run in the land-use types of the North-Sudan region were even higher: the lowest value for transects was reached with 64% for the second transect in the pasture (FPas-2), for habitats with 70% for the pasture area – both according to the ICE (Table 5-7; Table A5-5). In all other cases, efficacies exceeded 70%, according to the Bootstrap or Michaelis-Menten Mean even 80% (Table 5-7; Table A5-5).

5.3.4.2 Termite communities in the sub-Sahel and North-Sudan region in Burkina Faso

The efficacy reached when sampling termites following the RAP-protocol was similarly high as for ants, and again on all levels (single transects, the different land-use types, and the two regions) (Table 5-7; Table A5-6; Table A5-7). For most transects or land-use types in the sub-Sahel zone, sampling reached an efficacy of 70% and more (Table 5-7; Table A5-6). The lowest efficacy for single transects was reached according to the ICE in the two Zaï forests: 28% of the expected species richness were sampled with the second transect in the old forest (ZF30-2) and 40% with the third transect in the young forest (ZF20-3) (Table A5-6). For most transects run in the degraded soil, 100% efficacy was calculated with all estimators

(Table A5-6). The lowest efficacy for a land-use type was reached according to the first Jackknife (Jack1) with 51% for the degraded land (Table 5-7).

The efficacy for sampling termites was also very high in the North-Sudanese zone (Table 5-7; Table A5-6, Table A5-7). The lowest efficacies for single transects were reached according to the ICE with 44% for the first transect in the pasture (FPas-1) and with 50% for the third transect in the fallow (FFal-3) (Table A5-7). For a land-use type in the North-Sudan region, the lowest value reached was 53% in the pasture (Table 5-7). In all other cases, efficacy exceeded 60%, mostly even 70% or 80%. According to the bootstrap estimator, sampling efficacy was above 80% for single transects and land-use types (Table 5-7; Table A5-7).

5.3.4.3 Performance of the estimators for ants in the sub-Sahel zone

The performance of the estimators was exemplarily evaluated for ants in the sub-Sahel zone both graphically (Appendix 5, Fig. A5-2 to Fig. A5-5) and by calculating the mean deviation (*MD*), the mean square deviation (*MSD*), the mean square proportional deviation (MSPD), and Pearson's correlation coefficient (r^2) for each of the four estimators (on the level of single transects, different Zaï stages and the sub-Sahel region) (Appendix 5, Table A5-7).

5.3.5 Sampling efficiency of the RAP-protocol with increasing sampling effort

For the protected woody savanna in the Pama reserve (FRes), the near-natural ecosystem studied near Fada N'Gourma in the North-Sudanese zone of Burkina Faso, the increase in ant and termite species richness was observed with increasing sampling effort (Fig. 5-4; Fig. 5-6). The total species richness was estimated with six estimators (ICE, Chao2, Jackknife1, Jackknife2, Bootstrap, and Michaelis-Menten-Mean) in relation to an increasing sampling effort. For each additional sampling unit, the efficiency of sampling (in %) was calculated for each estimator by dividing the observed species richness (SOB) through the respective estimated species richness (see Appendix 5, Table A5-2 and Table A5-3).

For ants, one sampling unit (SU) comprises one pitfall trap, one 'Winkler-site' of 1-m^2, and one transect section (area of 10 m^2). However, two SUs consequently correspond to one transect section since only eight ant sampling stations (each comprising one pitfall and one 'Winkler-site') were installed per 50 m transect. For ants in the Pama reserve (FRes), 82% of the estimated species richness (mean all) was collected after 30 sampling units**.** Additional sampling in another 20 sampling units only yielded further four species or 2% of the final species richness estimated for the community of ants in the protected savanna (Table A5-2).

For termites, one sampling unit is equivalent to one transect section (10 m^2). For termites in the Pama reserve (FRes), 83% of the estimated species richness (mean all) was collected after 30 sampling units. Additional sampling in another 20 RAP-sections only yielded further three species or 5% of the final species richness estimated for the community of termites in the protected savanna (Table A5-3).

Table 5-7: Incidence-based species-richness estimators (± standard deviation) of ant and termite communities in Burkina Faso calculated per habitat and region. Sampling efficacy (%-eff) was calculated as relation between the number of species observed (SOB) and the respective estimator value, indicating that sampling was very efficient. The last column (mean all) represents the mean of all estimators. ICE: incidence-based coverage estimator, Jack1: jackknife-1, Boot: Bootstrap, MMM: Michaelis-Menten mean.

Habitat $^{\text{transect-length}}$	Ant communities										
Geographic region $^{\text{transect-length}}$	SOB	ICE	%-eff	Jack1	%-eff	Boot	%-eff	MMM	%-eff	mean all	%-eff
Degraded land$^{200\ \text{m}}$	15	30 ± 0	50	21 ± 3	71	17 ± 0	88	15	100	21	72
Millet field$^{250\ \text{m}}$	22	25 ± 0	88	27 ± 3	81	24 ± 0	92	22	100	25	90
Young Zaï forest$^{250\ \text{m}}$	25	31 ± 0	81	31 ± 3	81	28 ± 1	89	26	96	29	86
Old Zaï forest$^{250\ \text{m}}$	35	41 ± 0	85	43 ± 3	81	39 ± 0	90	36	97	40	88
Sub-Sahel region $^{950\ \text{m}}$	41	45 ± 0	91	47 ± 3	87	44 ± 0	93	40	98	44	93
Pama reserve$^{250\ \text{m}}$	36	43 ± 0	84	45 ± 3	80	41 ± 0	88	39	92	42	86
Pasturearea$^{200\ \text{m}}$	28	40 ± 0	70	38 ± 3	74	32 ± 0	88	29	97	35	81
Fallowland$^{200\ \text{m}}$	36	43 ± 0	84	44 ± 3	82	40 ± 0	90	38	95	41	87
Cotton field$^{200\ \text{m}}$	19	21 ± 0	90	22 ± 2	86	21 ± 0	90	21	90	21	89
North-Sudan region $^{850\ \text{m}}$	53	61 ± 0	87	63 ± 3	84	57 ± 0	93	52	102	58	91
	Termite communities										
Degraded land$^{250\ \text{m}}$	1	2 ± 0	67	2 ± 1	51	1 ± 0	74	0	0	1	82
Millet field$^{250\ \text{m}}$	16	24 ± 0	68	22 ± 2	73	19 ± 0	87	18	90	20	78
Young Zaï forest$^{250\ \text{m}}$	19	22 ± 0	86	24 ± 3	80	22 ± 1	88	26	74	23	82
Old Zaï forest$^{250\ \text{m}}$	25	35 ± 0	72	34 ± 3	74	29 ± 1	87	28	89	31	80
Sub-Sahel region $^{1000\ \text{m}}$	33	47 ± 0	70	44 ± 4	75	37 ± 0	88	34	96	41	81
Pama reserve$^{250\ \text{m}}$	24	27 ± 0	89	28 ± 2	86	26 ± 0	92	26	94	27	90
Pasturearea$^{200\ \text{m}}$	14	27 ± 0	53	21 ± 2	67	17 ± 0	82	17	81	20	69
Fallowland$^{200\ \text{m}}$	13	16 ± 0	79	18 ± 2	73	15 ± 0	87	17	79	16	79
Cotton field$^{200\ \text{m}}$	5	6 ± 0	91	6 ± 1	84	5 ± 0	93	6	90	6	89
North-Sudan region $^{850\ \text{m}}$	31	36 ± 0	85	38 ± 3	82	34 ± 0	91	32	97	35	88

5.3.6 Measures of within-habitat diversity: Alpha-diversity indices

The within-habitat diversity of ant and termite communities, also called the alpha-(α)-diversity, was measured by means of two commonly used indices: Simpsons' D and Shannon-Wieners' H'. The following boxplots are illustrating the α-diversity of ant and termite communities for each of the eight land-use types studied in the sub-Sahelian and the North-Sudanese region of Burkina Faso (Fig. 5-8, Fig. 5-9, Fig. 5-10, Fig. 5-11). The indices were calculated separately for each RAP-transect; depending on the habitat, each boxplot comprises therefore three or four replicate transects.

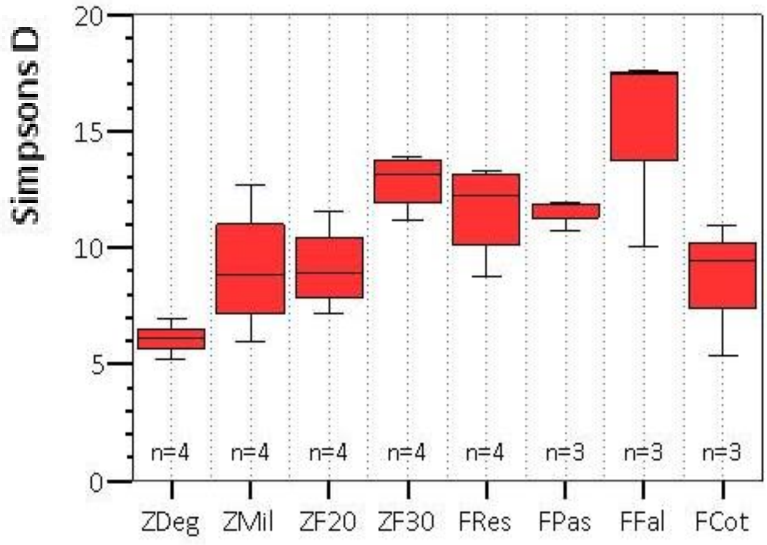

Fig. 5-8: Boxplots illustrating the Simpsons index of ant communities per land-use type studied in the sub-Sahel and the North-Sudanese region of Burkina Faso. Simpsons D was calculated for each RAP-transect.

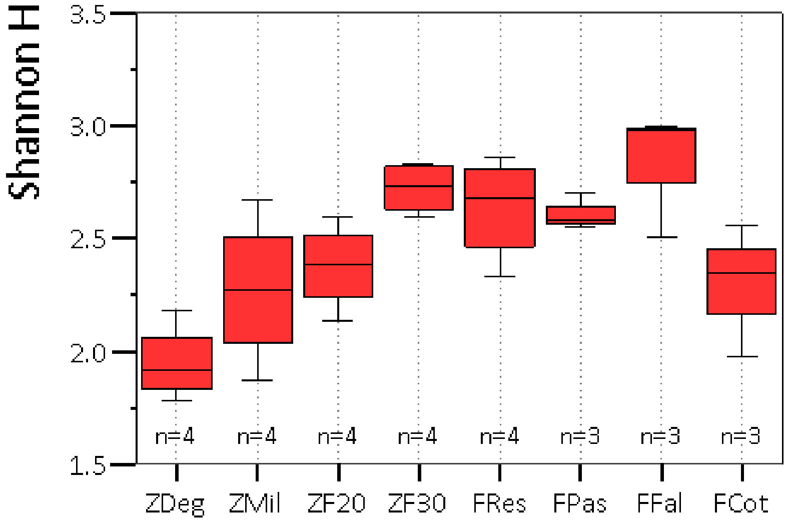

Fig. 5-9: Boxplots illustrating the Shannon-Wiener index of ant communities per land-use type studied in the sub-Sahel and the North-Sudan region of Burkina Faso. Simpsons D was calculated for each RAP-transect.

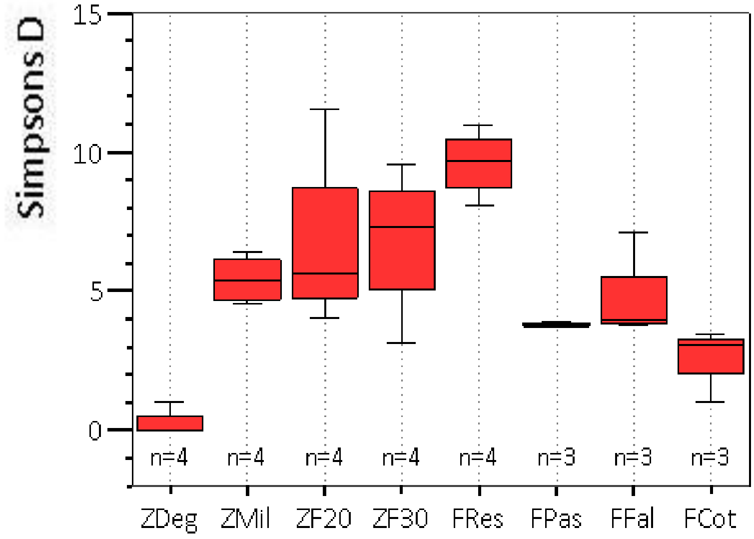

Fig. 5-10: Boxplots illustrating the Simpsons index of termite communities per land-use type studied in the sub-Sahel zone and the North-Sudan region of Burkina Faso. Simpsons D was calculated for each RAP-transect.

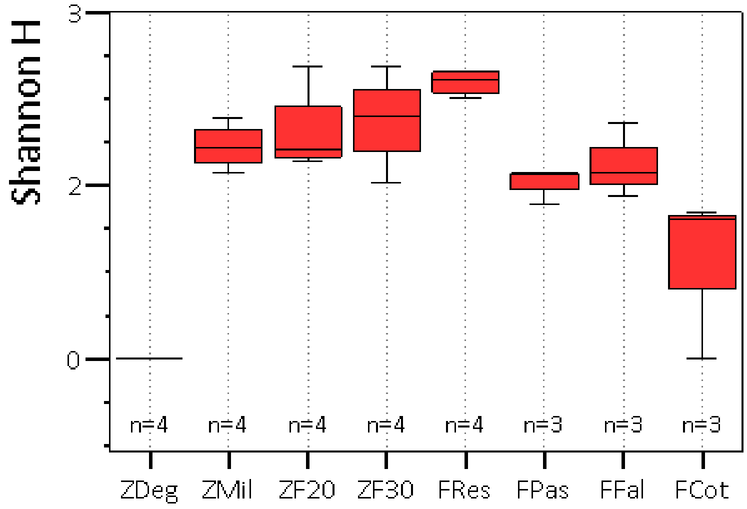

Fig. 5-11: Boxplots illustrating the Shannon-Wiener index of termite communities per land-use type studied in the sub-Sahel and the North-Sudan region of Burkina Faso. Simpsons D was calculated for each RAP-transect.

Land-use types in the sub-Sahelian region (Zaï system) are ZDeg: degraded land, ZMil: millet field, ZF20: 20-yrs old Zaï forest, ZF30: 30-yrs old Zaï forest; those in the North-Sudanese region are FRes: Pama reserve, FPas: pasture area, FFal: fallow land, FCot: cotton field.

By combining all sections of the respective replicate transects, the Simpson and the Shannon-Wiener indices were additionally calculated for each land-use type and, by combining the respective land-use types, they were further calculated for each of the two regions. These values (± standard deviation) are summarized in Table 5-8 for both, ant and termite communities.

Please refer to the Appendix of Chapter 5, for a detailed overview of the index-values for each RAP-transect, the land-use types and the regions: ants in the sub-Sahel zone (Table A5-

9), ants in the North-Sudanese zone (Table A5-10), termites in the sub-Sahel zone (Table A5-11), and termites in the North-Sudanese zone (Table A5-12).

Table 5-8: Measures of alpha-diversity for ant and termite communities in Burkina Faso, calculated per habitat and region (± standard deviation). SOB: species number observed.

Habitat $^{\text{transect-length}}$ Geographic region $^{\text{transect-length}}$	Ant communities		
	SOB	Shannon-Wiener H’	Simpsons’ D
Degraded land$^{200\ \text{m}}$	15	2.2 ± 0.1	8 ± 0
Millet field$^{250\ \text{m}}$	22	2.5 ± 0	9.9 ± 0.1
Young Zaï forest$^{250\ \text{m}}$	25	2.6 ± 0	10 ± 0
Old Zaï forest$^{250\ \text{m}}$	35	2.9 ± 0	14.5 ± 0
Sub-Sahel region $^{950\ \text{m}}$	41	2.8 ± 0	11.7 ± 0
Pama reserve$^{250\ \text{m}}$	36	3.0 ± 0	15.6 ± 0.2
Pasturearea$^{200\ \text{m}}$	28	2.8 ± 0	13.1 ± 0.1
Fallowland$^{200\ \text{m}}$	36	3.0 ± 0	16.6 ± 0.2
Cotton field$^{200\ \text{m}}$	19	2.5 ± 0	10.5 ± 0.1
North-Sudan region $^{850\ \text{m}}$	53	3.3 ± 0	18.8 ± 0.1
Habitat $^{\text{transect-length}}$ Geographic region $^{\text{transect-length}}$	Termite communities		
	SOB	Shannon-Wiener H’	Simpsons’ D
Degraded land$^{250\ \text{m}}$	1	0	0
Millet field$^{250\ \text{m}}$	16	2.3 ± 0	9 ± 0
Young Zaï forest$^{250\ \text{m}}$	19	2.6 ± 0	12.2 ± 0.4
Old Zaï forest$^{250\ \text{m}}$	25	2.7 ± 0	12 ± 0
Sub-Sahel region $^{1000\ \text{m}}$	33	2.9 ± 0	15 ± 0
Pama reserve$^{250\ \text{m}}$	24	2.8 ± 0	13.3 ± 0
Pasturearea$^{200\ \text{m}}$	14	1.9 ± 0	4.8 ± 0
Fallowland$^{200\ \text{m}}$	13	2.2 ± 0	7.5 ± 0.2
Cotton field$^{200\ \text{m}}$	5	1.3 ± 0	3.8 ± 0.1
North-Sudan region $^{850\ \text{m}}$	31	2.8 ± 0	12.1 ± 0

5.3.6.1 Ant communities

First disturbance gradient in the sub-Sahel region of Burkina Faso (LUI-1)

For ant communities in the four main succession stages of the Zaï system in the sub-Sahel region of Burkina Faso, a trend of increasing α-diversity with increasing habitat restoration was noted (Fig. 5-8, Fig. 5-9, Table 5-8, and Table A5-9 in Appendix 5).

When comparing the indices of the α-diversity of ant communities for the common number of transect sections (see land-use types in Table 5-8; Table A5-9), the four Zaï sites differed highly significantly (p < 0.0001) for both, the Simpson index (*N* = 35, $\chi^2(3) = 99.03$) and the Shannon index (*N* = 40, $\chi^2(3) = 118.83$).

The order for increasing α-diversity was: degraded land (ZDeg) < millet field (ZMil) < young Zaï forest (ZF20) < old forest (ZF30). When comparing the site-pair ZMil and ZF20, differences were still highly significant for the Shannon index ($Z = -6.28$, $p < 0.0001$ Wilcoxon sign-rank) and just significant for the Simpson index ($Z = -3.26$, $p = 0.01$).

Second disturbance gradient in the North-Sudan region of Burkina Faso (LUI-2)

The highest α-diversity of ant communities according to the Shannon and the Simpson index was observed in the fallow (FFal) which was sampled in the second and third year of fallowing (Fig. 5-8, Fig. 5-9, Table 5-8, and Table A5-10). For ant communities in the other three habitats near Fada N'Gourma in the North-Sudanese region, a trend of decreasing α-diversity with increasing land-use intensification was noted (Fig. 5-8, Fig. 5-9, Table 5-8, and Table A5-10).

Similar results to those in the sub-Sahel were obtained when comparing the α-diversity indices between ant communities in the four North-Sudanese sites at the common number of transect sections (see land-use types in Table 5-8; Table A5-10); differences were highly significant ($p < 0.0001$) for Simpsons D (*N* = 33, $\chi^2(3) = 99.00$) and for Shannons H' (*N* = 40, $\chi^2(3) = 120.00$).

The order for increasing α-diversity was: cotton field (FCot) < pasture area (FPas) < reserve (FRes) < fallow (FFal). When comparing only the site pair FRes and FPas, differences were still highly significant ($p < 0.0001$) for the Shannon ($Z = -5.54$) and Simpson index ($Z = -5.31$). The reported significances for site pairs are after Bonferroni correction.

5.3.6.2 Termite communities

First disturbance gradient in the sub-Sahel region of Burkina Faso (LUI-1)

For termites in the Sub-Sahel, a trend of increasing α-diversity with increasing habitat restoration was noted, although differences between the millet field and the two forests were small (Fig. 5-10, Fig. 5-11, Table 5-8; Table A5-11 in Appendix 5).

When comparing the indices of the α-diversity of ant communities for the combined number of transect sections (see land-use types in Table 5-8; Table A5-11), the four succession stages differed highly significantly ($p < 0.0001$) for both, the Simpson index (*N* = 41, $\chi^2(2) = 82.00$) and the Shannon index (*N* = 50, $\chi^2(3) = 140.44$).

However, the site order for increasing termite diversity differed for both indices – while it was degraded land (ZDeg) < millet field (ZMil) < young Zaï forest (ZF20) < old forest (ZF30) for the Shannon-Wiener index, it was ZDeg < ZMil < ZF30 < ZF20 for Simpsons’ D. When comparing the site pair ZMil and ZF20, differences were still highly significant (p < 0.0001Wilcoxon sign-rank) for Shannons H’ (Z = -5.13) and for Simpsons’ D (Z = -5.58).

Second disturbance gradient in the North-Sudan region of Burkina Faso (LUI-2)

In the North-Sudanese zone, a trend of decreasing termite diversity with increasing intensification was observed (Fig. 5-10, Fig. 5-11, Table 5-8; Table A5-12 in Appendix 5). An exception was the fallow (FFal) where termite diversity was higher than in the pasture (FPas) – according to Shannons H’ and Simpsons’ D.

Again, similar results to those in the sub-Sahel were obtained when comparing the indices of the α-diversity between termite communities of the four North-Sudanese sites at the common number of transect sections (see land-use types in Table 5-8; Table A5-12); differences were highly significant (N = 40, p < 0.0001) for both, the Simpson ($\chi^2(3) = 88.84$) and the Shannon index ($\chi^2(3) = 118.83$).

The site order for increasing termite diversity was cotton field (FCot) < pasture area (FPas) < fallow (FFal) < reserve (FRes) for Shannons H’ and Simpsons’ D. When following up these findings for selected site pairs with the Wilcoxon sign-rank test, differences were still highly significant (p < 0.0001) between FFal and FPas (Shannons H’: Z = -5.55; Simpsons’ D: Z = -4.86), highly significant (p < 0.0001) between FRes and FFal (Shannons H’: Z = -5.51; Simpsons’ D: Z = -4.86), highly significant (p < 0.0001) between FRes and FPas (Shannons H’: Z = -5.51; Simpsons’ D: Z = -5.01), and highly significant (p < 0.0001) between FFal and FCot (Shannons H’: Z = -5.51; Simpsons’ D: Z = -4.86). All reported significances for site pairs are after Bonferroni correction.

5.3.7 Habitat parameters determining variations in community composition

All environmental parameters measured in the four succession stages of the Zaï system in Ouahigouya (sub-Sahel zone, northern Burkina Faso) and in the land-uses studied near Fada N’Gourma (North-Sudan region, south-eastern Burkina Faso) are shown in Chapter 4.2.3 in Fig. 4-20. Illustrated are for example physical and chemical soil parameters assumed to be important for soil-dwelling arthropods (grain sizes, pH etc.), parameters characterizing the RAP-transect sections (crown cover and grass cover percentage etc.), the quantity of food resources available for termites during the dry season (e.g. leaf litter or dead wood), and vegetation parameters assessed once per site in an area of 900 m^2 – as for example the woody plant basal area, the maximum tree height and the tree species richness. The woody plant basal area is the total soil surface covered by tree trunks, although the numbers are very conservative since only the main trunk was measured per tree.

For the methods used to measure the different parameters, please refer to Chapter 4. In Table A4-3 (sub-Sahelian sites) and Table A4-5 (North-Sudanese sites) in Appendix 4, tree species are ranked in descending order depending on their abundance – first for the combined area of all plots assessed in the land-use types of the respective disturbance gradient (3600 m^2), then separately for each habitat.

5.3.7.1 Ant communities

First disturbance gradient in the sub-Sahel region of Burkina Faso (LUI-1)

Environmental parameters predicting a significant share of variations in the composition of ant communities were found for the first land-use intensification gradient (LUI-1) in the Zaï system (Ouahigouya, sub-Sahel region, northern Burkina Faso). The ordination tri-plot resulting from a Canonical Correspondence Analysis (CCA) for ants in the four main succession stages of the Zaï-system, namely degraded barren land (ZDeg), millet fields (ZMil), 20-yrs old Zaï forest (ZF20 or young forest) and 30-yrs old Zaï forest (ZF30 or old forest), are illustrated in Fig. 5-12. The figures show 16 RAP-transects conducted in the Zaï-system, common ant species (crosses) and the three most influencing environmental parameters: medium air humidity, maximum tree height and medium clay-content in soil samples taken in the upper soil horizon (0-10 cm). At a 5% probability level, the first three axes significantly explain 51.1% of the variance in the relative abundance of common ant species (Monte Carlo, 1,000 randomizations, $p1 = 0.0001$, $p2 = 0.04$, $p3 = 0.03$). The first axis explains with 37.2% the largest part of the total variation in the data set; taken together, the first two axes explain 47% (Fig. 5-12).

The highest trees were found in the old Zaï forest, the smallest in the millet field –the degraded area had no trees at all; the highest clay-content in the sub-surface soil (0-10 cm) was found in samples of the old and the young Zaï forest; the highest percentage of air humidity were noted during sampling of six RAP-transects –two each in the old forest and the degraded area and one in the young forest as well as the millet fields (Fig. 5-12).The two omnivorous predator-species *Monomorium bicolor* (5) and *Pheidole* sp.1 (9), illustrated in the center of the tri-plots, were found in every habitat and mostly in high relative abundances (Fig. 5-12). The degraded, barren land was characterized by the presence of *Monomorium areniphilum* (4), an omnivorous predator of open areas. *Lepisiota* sp.3 and especially the general predator-species *Pachycondyla senaarensis*, a species that was often found in rural or settlement areas, were mainly found in the millet fields; *Crematogaster* sp.2 (1) was encountered in high relative abundances in the open habitats, the degraded land and the millet fields. *Anochetus sedilloti* (0) and *Tetramorium* sp.6 (10), on the other hand, were abundant predators in the two forested areas. *Pachycondyla* sp.3 (8) was a predator that preferred clayey soil.

In summary, we can state that the first axis resembles mainly a "tree height" axis, the second mainly an "air humidity" axis and the third mainly an axis for the content of the finest grain size in the upper soil horizon, the clay-content (Fig. 5-12).

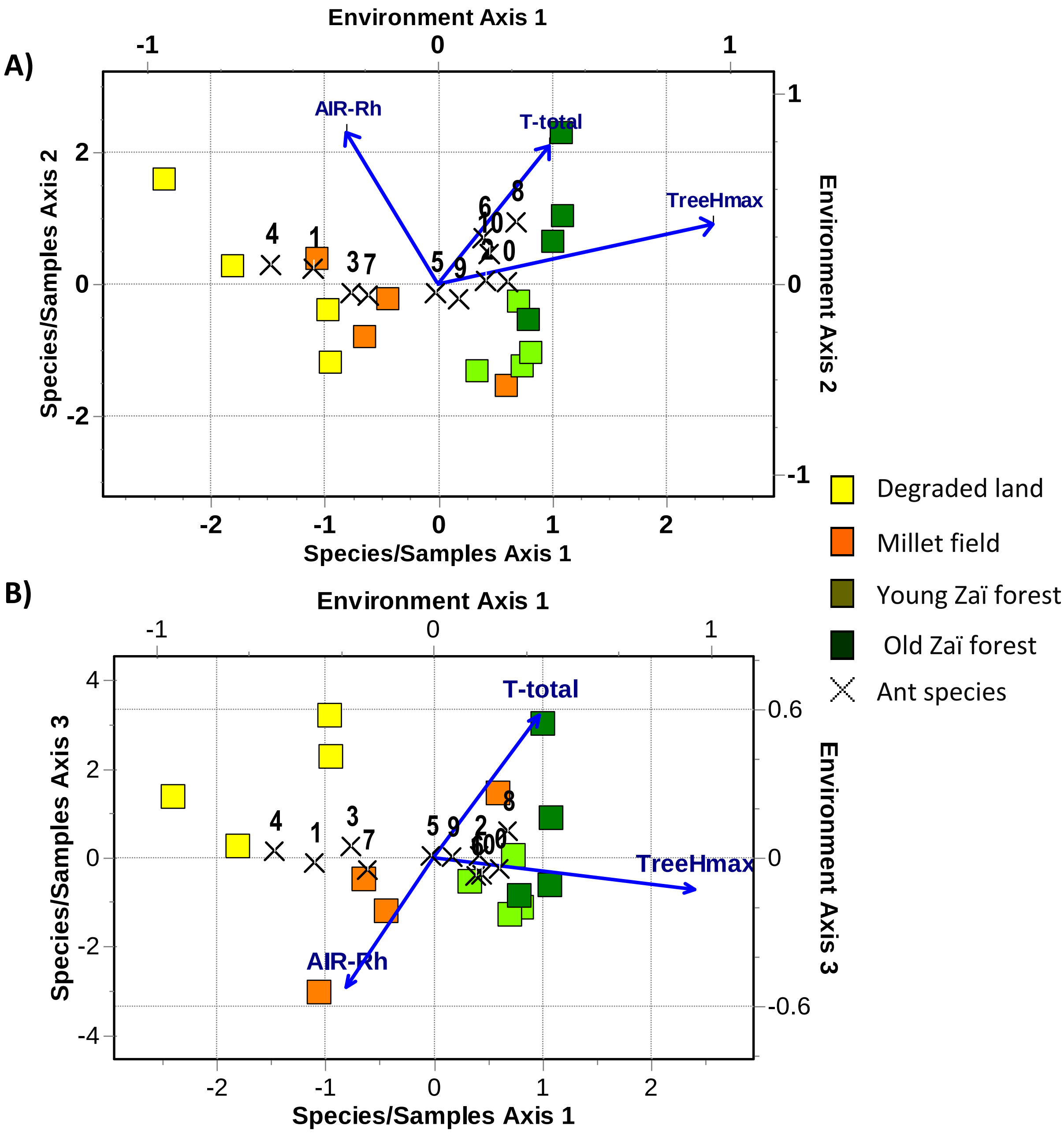

Fig. 5-12: Ordination tri-plots for ant assemblages in the Zaï-system resulting from a Canonical Correspondence Analysis (CCA) (sites at species centroids; weighted). The first three axes significantly explain 51.1% of the variance in the relative abundance of common ant species. **A)** Axis-1 and axis-2 explain 47%, and **B)** axis-1 and axis-3 explain 41.3%. Predicting parameters TreeHmax: maximum tree height; Air-Rh: medium air humidity; T-total: medium clay-content (in soil 0-10 cm). Ant species 0: *Anochetus sedilloti*, 1: *Crematogaster* sp.2, 2: *Lepisiota* sp.1, 3: *Lepisiota* sp.3, 4: *Monomorium areniphilum*, 5: *Monomorium bicolor*, 6: *Monomorium oscaris*, 7: *Pachycondyla senaarensis*, 8: *Pachycondyla* sp.3, 9: *Pheidole* sp.1, 10: *Tetramorium* sp.6.

A clearer picture concerning the response or preference of species to a single environmental variable is shown in Fig. A5-6, Fig. A5-7 and Fig. A5-8 (Appendix 5). The position of species along the vector representing the environmental variable was found by projecting orthogonal lines from the species positions on to the vector. The points of intersection indicate the relative response of each species to the environmental variable; the distance from the line is irrelevant. Hence, the further a species is located to the right, the higher its preference for habitats with very large trees (Fig. A5-7) and clayey soils (Fig. A5-8). The further to the upper left, the higher the preference for high percentages of humidity in the air (Fig. A5-6). One short example 'maximum tree height': *Pachycondyla* sp.3 (Pac_sp3) preferred the habitats with high trees – *Monomorium areniphilum* (Mon_aren) preferred the lowest. The two species *Tetramorium* sp.6 (Tet_sp6) and *Anochetus sedilloti* (Ano_sedi) had highest abundances in habitats with trees of medium height (Fig. A5-7).

The significance of the groups formed by transects that belong to one land-use type, i.e. groups formed by replicate-transects, was tested with the 'Analysis of Similarities' (ANOSIM) (Appendix 5, Table A5-13). In Fig. 5-12, these groups are differently colored, one color per land-use. The null hypothesis tested was that there were no differences between transects of different habitats. The resulting overall test statistic after 1,000 randomizations was R*:* 0.52 indicating that slightly more than 50% of the replicate-transects were within the same groups (ANOSIM $p < 0.001$, α: 0.1%) (Table A5-13).

The rest of the replicate-transects were not more similar in composition than transects conducted in different land-uses and not more similar than would be expected by chance. The null hypothesis was still rejected, i.e. transects conducted in the same land-use type were more similar in composition than transects conducted in different land-uses and more similar than would be expected by chance (Table A5-13).

The significance of the groups formed by replicate-transects was also tested with the method 'Similarity Percentages' (SIMPER) (Appendix 5, Table A5-14 and Table A5-15). The 'average within-group similarity' was 74% for transects in the two forests, 70% for those in the millet field and 60% for the degraded land (Table A5-14). The 'average dissimilarity between groups' was ranging between 48% and 58% for the site-pairs degraded – millet, degraded – young/ old forest, between 34% and 37% for millet – young / old forest, and 28% for the two forests (Table A5-15).

Second disturbance gradient in the North-Sudan region of Burkina Faso (LUI-2)

The environmental parameters predicting a great part of the variations in the composition of ant communities were also found for the second land-use intensification-gradient (LUI-2), the habitats close to Fada N'Gourma (North-Soudan region of Burkina Faso).

The ordination tri-plot resulting from a Canonical Correspondence Analysis (CCA) is illustrated in Fig. 5-13. The figure shows 13 RAP-transects transects comprising four transects run in the reserve (FRes), three in the pasture (FPas), the fallow (FFal) and the cotton field (FCot). Illustrated are further common ant species and the three most influencing environmental parameters: medium crown-cover percentage (CC), maximum tree height (TreeH) and total litter weight (Litter-Total). At a 5% probability level, the first two axes significantly explain 60.8% of the variance in the relative abundance of the ant species present (Monte Carlo 1,000 permutations; p1: 0.0005, p2: 0.004). The first axis explains with 44.2 % the largest part of the total variation in the data set. The largest area covered with shade of tree crowns was found in the reserve and the pasture; the highest litter weight was collected in the reserve, the least in the cotton fields; and while trees were highest in the pasture, they were smallest in the fallow land (Fig. 5-13).

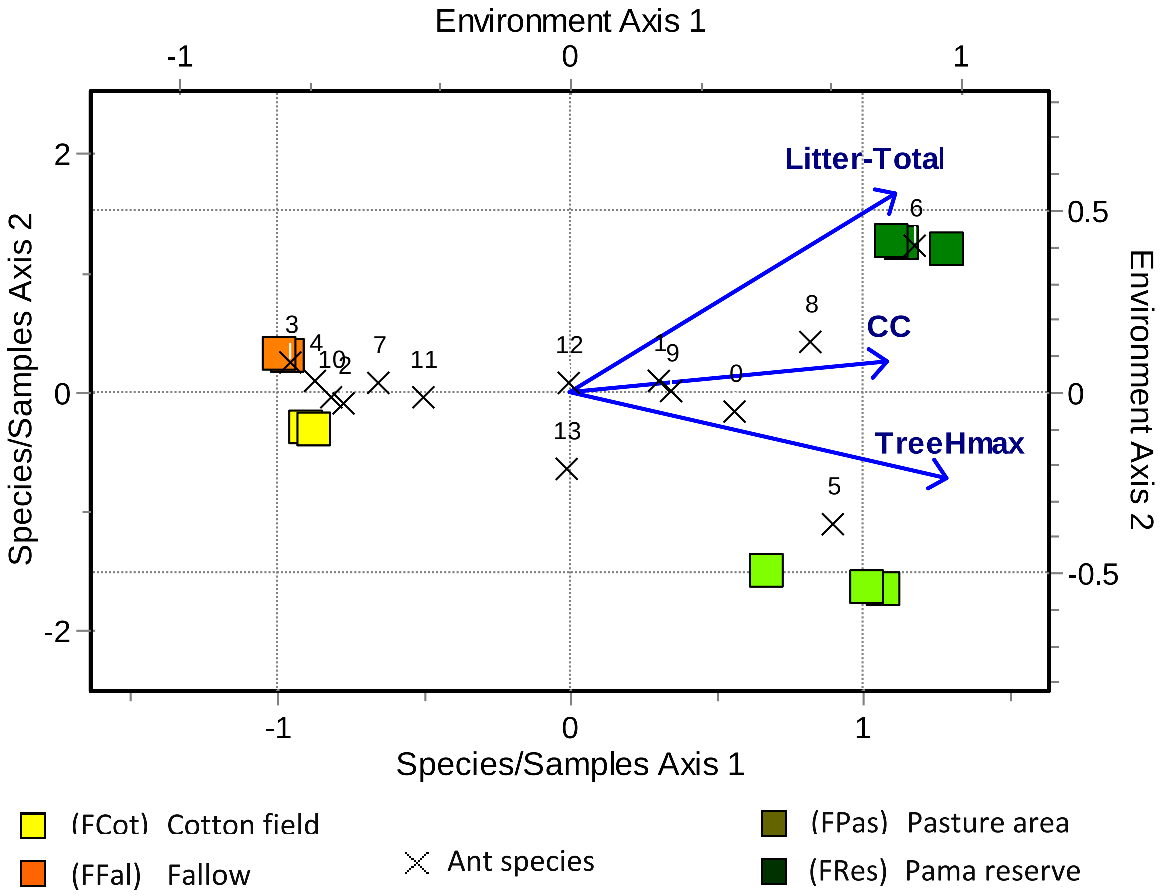

Fig. 5-13: Ordination tri-plot for ants in the North-Sudanese region of Burkina Faso, resulting from a Canonical Correspondence Analysis (CCA). The first two axes significantly explain 60.8% of the total variation in the data set (Monte Carlo α: 5%, p1: 0.0005, p2: 0.004); the first axis alone explains 44.2% of the total variation. Transect replicates per land-use: n = 3, only FRes n = 4. Predicting parameters are CC: crown-cover percentage, TreeHmax: maximum tree height, Litter-Total: total litter dry weight. Ant species are 0: *Camponotus compressiscapus*, 1: *Camponotus sericeus*, 2: *Cataglyphis* sp.1, 3: *Crematogaster* sp.2, 4: *Messor galla*, 5: *Monomorium abyssinicum*, 6: *Monomorium destructor*, 7: *Pachycondyla senaarensis*, 8: *Pachycondyla* sp.1, 9: *Pheidole* sp.1, 10: *Pheidole* sp.3, 11: *Pheidole* sp.4,12: *Tetramorium angulinode*, 13: *Tetramorium sericeiventre*.

Some facts which can be drawn concerning the ant species: the fallow and to a lesser extent the cotton fields were characterized by an especially high relative abundance of the granivorous ant species *Messor galla* (4) from which about 85 nest-entrances were counted in the whole hectare plot in 2004. *Crematogaster* sp.2 (3) preferred low crown-cover percentages and was characteristic for the fallow. *Cataglyphis* sp.1 (2) and the omnivorous predator *Pheidole* sp.3 (10), both species preferring low crown-cover percentages, were found mainly in the fallow and the cotton fields. The omnivorous predators *Monomorium destructor* (6) and *Monomorium abyssinicum (*5) were found in the reserve and the pasture, respectively.

In summary, we can state that the first axis is mainly a "crown-cover" axis and the second a "litter" and "tree height" axis (Fig. 5-13).

The ordination of the species along the environmental axes, with the points of intersection indicating their relative response to the variables, is shown in Fig. A5-9 to Fig. A5-11 (Appendix 5). The distance from the line is irrelevant. The further the species' position to the right, the higher the preference for habitats with large quantities of litter (Fig. A5-9), high crown-cover percentages (Fig. A5-10) and high trees (Fig. A5-11). For example, Fig. A5-10 indicates that *M. destructor* (6, Mon_dest) preferred shady habitats with high crown-cover percentages. *Crematogaster* sp.2 (3, Cre_sp2) preferred the open sites and the two species *Camponotus sericeus* (1, Cam_seri) and *Pheidole* sp.1 (9, Phe_sp1) had their highest abundances at medium crown-cover percentages.

The 'Analysis of Similarities'(ANOSIM) was used to test the significance of the groups formed by replicate-transects (Appendix 5, Table A5-16). In Fig. 5-13 these groups are differently colored (i.e. one color per habitat). The tested null hypothesis was that there are no differences between transects of different habitats. The resulting overall test statistic after 1,000 randomizations was R: 0.75 indicating that three-quarter of the replicate-transects were within the same groups (ANOSIM $p < 0.001$ at α: 0.01) (Table A5-16). Hence, the null hypothesis was rejected. In other words, transects conducted in the same land-use type were more similar in composition than transects conducted in different land-uses and more similar than would be expected by chance.

Additionally, the significance of the groups in the complete data set was tested with the method 'Similarity Percentages' (SIMPER) (Appendix 5, Table A5-17 and Table A5-18). The 'average within-group similarity' was 59.4% for cotton while it was ranging between 73% and 79% for fallow, pasture and the reserve (Table A5-17). The resulting 'dissimilarity between groups' was ranging between 34% and 35% for the site-pairs cotton – fallow, reserve – pasture; between 48% and 52% for fallow – pasture and reserve – fallow; and it was ranging between 61% and 64% for cotton – reserve and cotton – pasture (Table A5-18).

5.3.7.2 Termite communities

The abbreviations used for termite species in the figures illustrating the ordination of species along environmental axes, for both land-use intensification gradients shown in Appendix 5 (Fig. A5-12 to Fig. A5-17) comprise:

i) Firstly, a two-digit-shortcut indicating the functional group to which the species belong, that is fg: fungus-growers, wf: wood-feeder, sf: soil-feeder, gf: grass-feeder, uk: unknown;
ii) Secondly, separated by an hyphen, the first three digits of the genus;
iii) Thirdly, separated by an underscore, the first four digits of the species epithet.

First disturbance gradient in the sub-Sahel region of Burkina Faso (LUI-1)

Environmental parameters predicting a significant share of variations in the composition of termite communities were found for the first land-use intensification-gradient (LUI-1) in the Zaï system (Ouahigouya, sub-Sahel region of Burkina Faso).

The ordination tri-plot resulting from a CCA for termites in three succession-stages of the Zaï-system, namely millet fields (ZMil), young i.e. 20-yrs old Zaï forest (ZF20) and old i.e. 30-yrs old Zaï forest (ZF30), are illustrated in Fig. 5-14. The degraded land (ZDeg) was not included in the analysis since only one fungus-growing species of the genus *Odontotermes* was found. The figures show 12 RAP-transects conducted in the three land-uses, common termite species and the three most influencing environmental parameters: crown-cover percentage (CC%), litter availability measured on a scale from 0 to 4 (Litter), and medium sand-content in soil samples taken from the upper soil horizon (0-10 cm) (S-total). At a 5% probability level, the first two axes significantly explain 47.4%, the first three 54.6% of the variance in the relative abundance of common termite species (Monte Carlo 10,000 permutations, p1: 0.008, p2: 0.009, p3: 0.05). With 30.8% explains the first axis the largest part of the total variation. The largest part covered with the shade of tree crowns was found in two transects of the old and two of the young Zaï-forest (ZF30, ZF20), the smallest in the millet fields (ZMil).

The highest litter availability was noted in the transect-sections of the old Zaï-forest, especially in two of the four RAP-transects run in this habitat. Also the highest medium sand-content in the upper soil horizon (0-10 cm) was noted in samples of the old and the young Zaï forest; the least again in the millet fields (Fig. 5-14). The fungus-growing species *Microtermes havilandi* (7) as well as an unknown species (3), both illustrated near the center of the tri-plot, were found in almost every transect. The highest relative abundances of *M. havilandi* were noted in the millet fields – what explains its slightly dextral position. In the third replicate-transect, the species occurred in every section. The millet fields were characterized by the presence of two wood-feeding species, *Eremotermes sabaeus* (2) and *Microcerotermes edentatus* (5), both feeding in the inside of millet-stalks. *Microtermes subhyalinus*, (8), a tiny fungus-growing species, was found in both forests – with higher abundances in the older one. The deepest fungus-comb chambers built by *M. subhyalinus* were seen in about 75 cm, while sampling in soil profiles that were dug up to 1 m depth in the old forest. *Macrotermes bellicosus* (4), one of the largest termite species, occurred only in the two Zaï-forests – most of their mounds were built in shady areas, often at the base of a tree. The epigeal mounds provide optimal growth-conditions for the symbiotic fungal partner (*Termitomyces* sp.) and represent a conspicuous and typical feature in the landscape. *Odotontermes* sp.2 (9, fg-Odo_sp2), another fungus-grower, was mainly found in the young forest.

In summary, we can state that the first axis resembles mainly a "crown-cover percentage" axis, the second mainly an axis for the sand-content in the upper soil horizon and the third mainly a "litter" axis (Fig. 5-14).

The ordination of the species along the environmental axes is shown in Fig. A5-12, Fig. A5-13 and Fig. A5-14 (Appendix 5). The points of intersection indicate the relative response of each species to the environmental parameter. The distance from the line is meaningless. Hence, the further to the left, the higher the preference for shady habitats, that is high crown-cover percentages (Fig. A5-12), for habitats with large quantities of litter (Fig. A5-13), and the higher the preference for sandy soils (Fig. A5-14).

Some examples: *Microtermes subhyalinus (*8, fg-Mic_subh) and *Ancistrotermes crucifer* (0, fg-Anc_cruc), small fungus-growers with diffuse underground-nests, prefer high sand-content in the upper soil-horizon. *Macrotermes bellicosus* on the other hand is known to favor clayey soils. The clay-content of their mound-walls significantly surpass the content of the surrounding habitat soil. Their position along the vector sand-content is rather at the beginning than at the end (Fig. A5-14). The preferences for the vector crown-cover percentage are illustrated in Fig. A5-12. The position of *M. bellicosus* close to the arrowhead indicates the preference for high crown-cover percentages, i.e. shady locations (see above). Fig. A5-13 displays that fungus-growers are litter-feeders; except *Microtermes havilandi* (7, fg-Mic_havi), all fungus-growers are on the vector. Fungus-growers gather all kinds of organic matter. Their broad food range combined with their ability to adapt to land-use changes explains the success of some group-members. The genus *Odontotermes* for example, was found in whatever was available in the respective land-use: in the millet-fields they were feeding in compost-holes and after the harvest in millet-stalks, leaf-litter or cow-dung. In the forests they were found in and on dead wood, in leaf-litter, dry grass and they were feeding under the bark of trees. In the dry season most tree-stems were covered with soil-sheetings. Last but not least, one *Odontotermes*-species was the pioneer to inhabit the degraded area.

The significance of groups formed by transects that belong to one land-use type, i.e. groups formed by replicate-transects, was tested with the 'Analysis of Similarities' (ANOSIM) (Appendix 5, Table A5-19). In Fig. 5-14 these groups are differently colored, one color per land-use. The null hypothesis tested was that there were no differences between transects of different habitats. The resulting overall test statistic after 1,000 randomizations was R: 0.81 (ANOSIM p < 0.001 at 0.01-level) (Table A5-19). Hence, the null hypothesis was rejected, 80% of all transects conducted in the same land-use type were more similar in composition than transects conducted in different land-uses, and more similar than would be expected by chance.

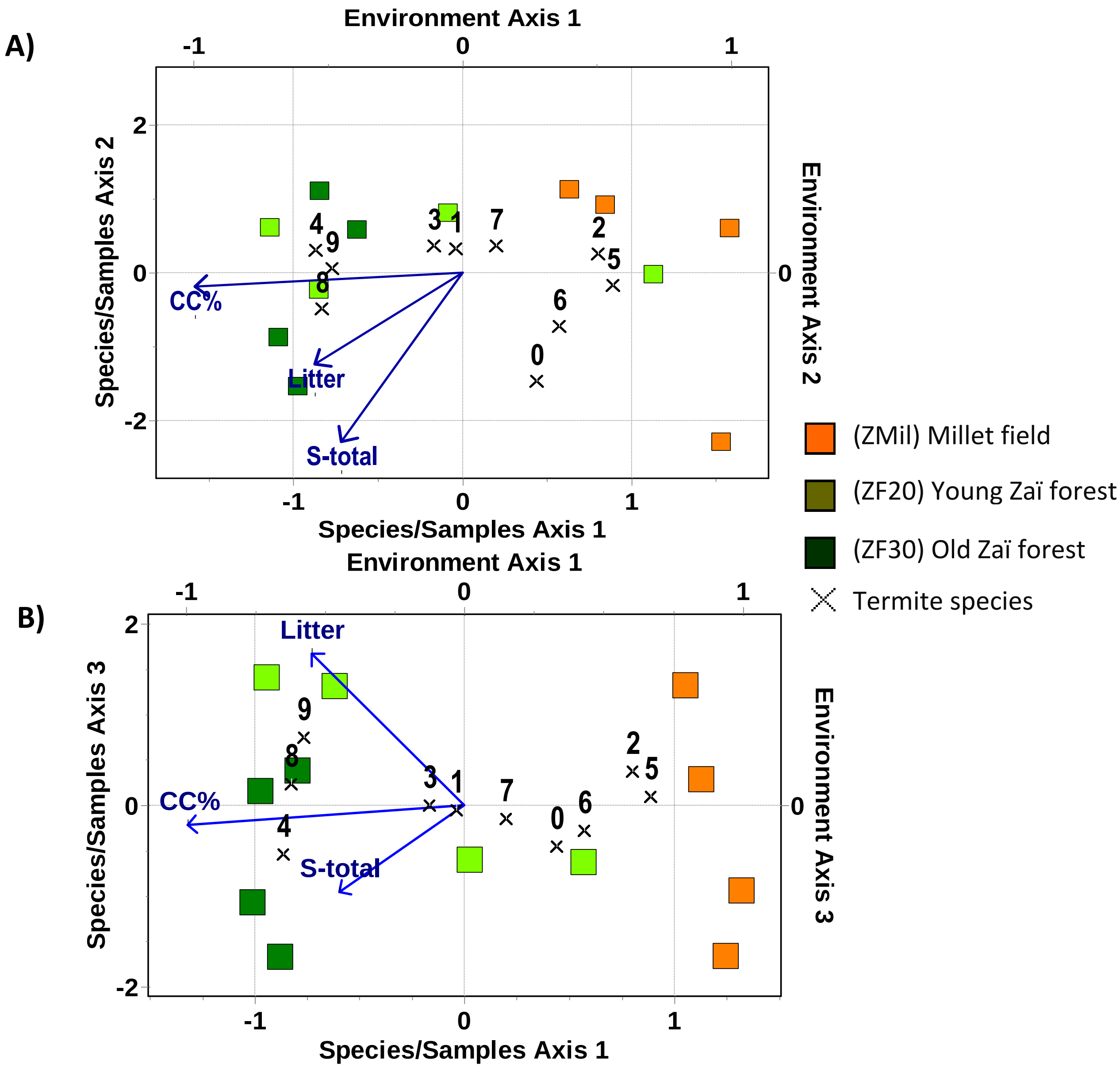

Fig. 5-14: Ordination tri-plots for termite assemblages in the Zaï-system (sub-Sahel region) resulting from a Canonical Correspondence Analysis (CCA; sites at species centroids; weighted) (four transect replicates per Zaï stage; the degraded land was not included). Together, the first three axes significantly explain 54.6% of the variance in the relative abundance of common termite species. **A)** Axis-1 and axis-2 explain 47.4%, and **B)** axis-1 and axis-3 explain 38.1%. Predicting parameters CC%: medium crown-cover percentage; Litter: litter availability measured on a scale from 0 to 4; S-total: medium sand-content (0-10 cm). Termite species 0: *Ancistrotermes crucifer* (fg), 1: *Cubitermes subcrenulatus* (sf), 2: *Eremotermes sabaeus* (wf), 3: unknown species, 4: *Macrotermes bellicosus* (fg), 5: *Microcerotermes edentatus* (wf), 6: *Microcerotermes parvus* (wf), 7: *Microtermes havilandi* (fg), 8: *Microtermes subhyalinus* (fg), 9: *Odontotermes* sp.2. Functional groups are fg: fungus-growers, wf: wood-feeders, sf: soil-feeders.

When pair-wise tests were made with the groups, three test statistics were *R*: 1.0. Only transects of the two forests were not significantly different (ANOSIMR: 0.05, *p*: 0.21). When testing the pair millet field and young forest, R was 0.60 (*p*: 0.04); when comparing millet and the old forest, *R* was 0.82 (*p*: 0.01) (Table A5-19).

The significance of the groups comprising the replicate-transects was also tested with the method ‘Similarity Percentages’ (SIMPER) (Appendix 5, Table A5-20 and Table A5-21). The ‘average within-group similarity’ was 83% for transects in the degraded land and about 40% for those in the millet and old forest; lowest was the young forest with 33% (Table A5-20). The ‘average dissimilarity between groups’ was ranging between 98% and 100% for the site-pairs degraded – millet, degraded – young/old forest, 76% for millet – young/old forest and 66% for the two forests (Table A5-21).

Second disturbance gradient in the North-Sudan region of Burkina Faso (LUI-2)

The environmental parameters predicting a great part of the variations in the composition of termite communities were also found for the second land-use intensification-gradient (LUI-2), the habitats located about 54 km east of Fada N’Gourma (Gourma province, North-Soudan zone of Burkina Faso).

The ordination tri-plots resulting from a Canonical Correspondence Analysis (CCA, sites at species centroids, weighted) are illustrated in Fig. 5-15. The figures show 12 RAP-transects comprising four transects run in the reserve (FRes), three in the pasture (FPas), three in the fallow (FFal) and two in the cotton field (FCot). One of the cotton field transects was excluded since only one species, *Microtermes havilandi* (4, fg-Mic_havi), was found. Illustrated are further common termite species and the three most influencing environmental parameters: the total surface area covered by tree trunks (TrcBaseA) (only the main stem was measured per tree), the medium clay (T-total) and the medium soil organic matter content (SOM) (Fig. 5-15). The latter two parameters were measured for samples of the upper soil horizon (0-10 cm). At a 5% probability level, the first two axes significantly explain 44.8%, the first three axes 53.8% of the variance in the relative abundance of common termite species. The first axis explains with 30.8% the largest part of the total variation in the data set (Monte Carlo 1,000 permutations α: 5%, *p1*: 0.001*, p2*: 0.02, axis-3 *p*: 0.006).

The reserve had the largest surface-area covered with trunks, directly followed by the pasture (Fig. 5-15). The sub-surface soil of the fallow (0–10 cm) was the richest in organic matter, the soil in the pasture was the poorest. The fallow and the cotton fields had the highest clay-content in the sub-surface soil; the reserve had the lowest (Fig. 5-15).

The wood-feeder *Eremotermes sabaeus* (2, wf-Ere_saba) was found in both cotton field-transects, feeding inside of cotton-stalks (as in the stalks of the millet-fields in the Sub-Sahel). *E. sabaeus* was also found in the second fallow-transect which was run towards the field-margin (Fig. 5-15). The near-natural savanna was characterized by the grass-feeding species *Trinervitermes geminatus* (8: gf-Tri_gemi); also the wood-feeder *Amitermes evuncifer* (0, wf-Ami_evun) was only found in the reserve. *Trinervitermes oeconomus* (9, gf-Tri_oeco) was highly abundant in the reserve and the pasture (Fig. 5-15).

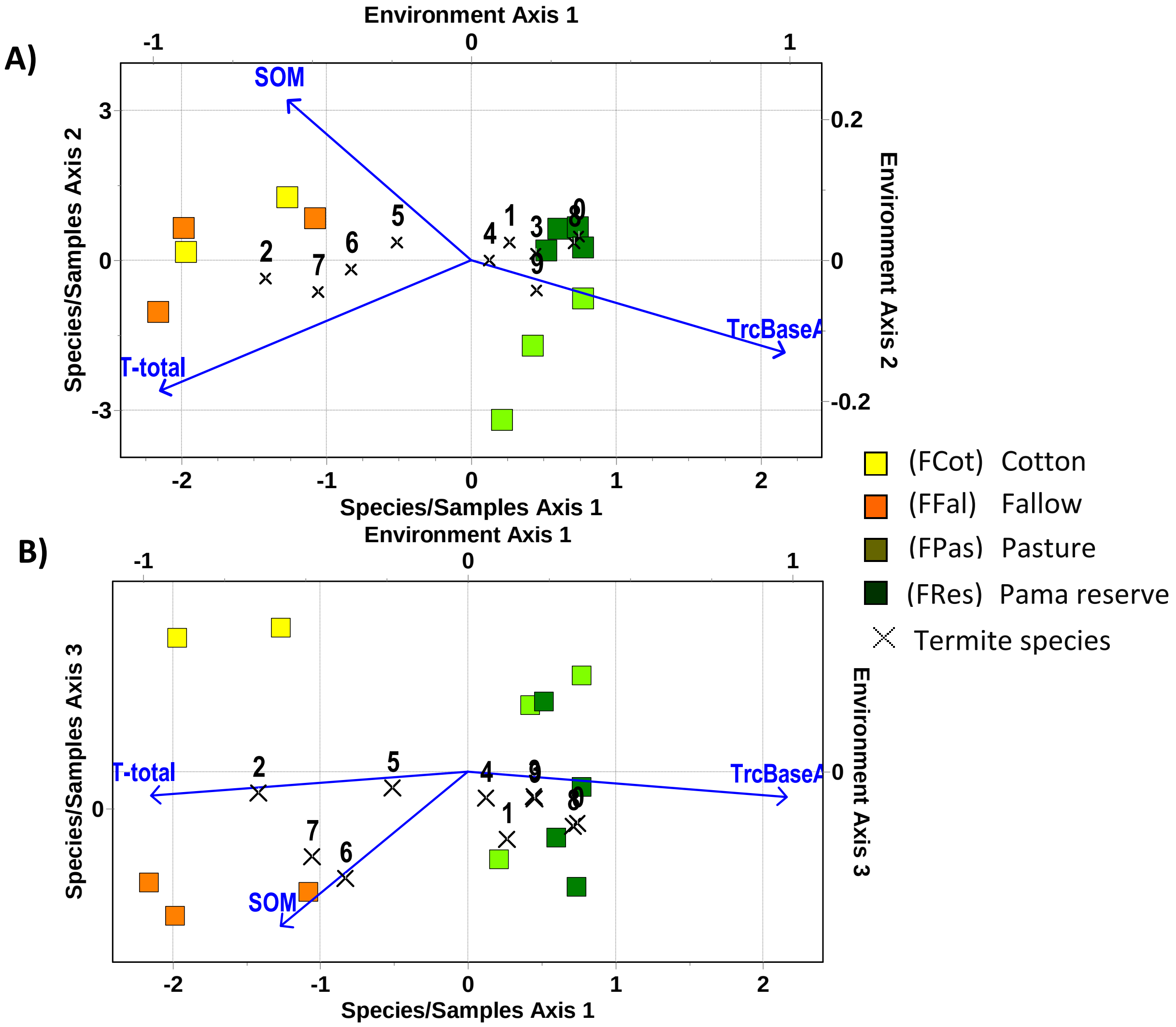

Fig. 5-15: Ordination tri-plots for termite assemblages in four different land-use types near Fada N'Gourma (North-Sudan region) resulting from a Canonical Correspondence Analysis (CCA; sites at species centroids; weighted). The first three axes significantly explain 53.8% of the variance in the relative abundance of common termite species (Monte Carlo α: 5%, p1: 0.001, p2: 0.02, p3: 0.006). **A)** Axis-1 and axis-2 explain 39.8%, and **B)** axis-1 and axis-3 explain 39.8% of the variance in the data set. Predicting parameters: T-total: medium clay-content (in soil 0-10 cm), SOM: medium soil organic matter content (0-10 cm), TrcBaseA: total surface area covered by tree trunks. Termite species are 0: *Amitermes evuncifer* (wf), 1: *Ancistrotermes crucifer* (fg), 2: *Eremotermes sabaeus* (wf), 3: *Macrotermes bellicosus* (fg), 4: *Microtermes havilandi* (fg), 5: *Microtermes subhyalinus* (fg), 6: *Odontotermes* sp.1 (fg), 7: *Odontotermes* sp.2 (fg), 8: *Trinervitermes geminatus* (gf), 9: *Trinervitermes oeconomus* (gf). The first two letters of the species-abbreviation indicate the functional group: fg: fungus-growers, wf: wood-feeders and gf: grass-feeders.

Unlike the Sub-Sahel zone, *Trinervitermes*-mounds were plentiful in the land-scape of the North-Soudan region. The fungus-growing species *Microtermes subhyalinus* (5, fg-Mic_subh), illustrated near the center of the tri-plots, was a highly abundant species. It was found in all transects except one of the pasture what explains its slightly sinistral position.

Microtermes havilandi (4, fg-Mic_havi) were present in all transects except one in the fallow and one in the pasture; highest abundances were noted in the reserve and pasture, explaining its position dextral of the triplot-center. Mounds of *Macrotermes bellicosus* (3, fg-Mac_bell) were totally missing in the cotton fields. Epigeal mounds occurred in the reserve and the pasture; in the fallow they were only left (by the farmers) at the field-margins.

To conclude: the first canonical axis separates the sites according to their 'total tree trunk area' and their 'clay-content', while the second and third mainly are "soil organic matter content"-axes (Fig. 5-15).

The ordination of the species along the environmental axes is shown in Fig. A5-15 to Fig. A5-17 (Appendix of Chapter 5). The points of intersection in indicate the relative response of the species to the environmental variables. That means the further to the right the higher was the preference for land-uses with large areas covered by tree trunks (Fig. A5-15). And the further to the left, the higher the preference for high contents of organic matter (Fig. A5-16) and clay (Fig.A5-17) in the upper soil horizon (0-10 cm). Most of the mounds of *M. bellicosus* and *A. evuncifer* located within the transects-sections were built in the shade at the base of trees. Their position along the vector 'trunk base area' for example, is end of the first third and shortly behind the middle, for *Amitermes* and *Macrotermes* respectively. According to Fig. A5-16, both *Odontotermes*-species (fg-Odo_sp1, fg-Odo_sp2) as well as *M. subhyalinus* (fg-Mic_subh) seem to prefer habitats with high organic matter content in the upper soil horizon; and, according to Fig. A5-17 the same species seem to prefer clayey soils. However, for the second intensification gradient one should bear in mind that both sites, cotton fields and fallow experienced extensive insecticide- and pesticide-inputs. An especially high level of prudence is therefore required not to draw premature conclusions.

The significance of groups formed by replicate-transects, was tested with the 'Analysis of Similarities' (ANOSIM) (Appendix 5, Table A5-22 to Table A5-24). In Fig. 5-15 these groups are differently colored, one color per land-use. However, the data basis tested was including all three transects run in the cotton fields and including 31 termite species. The null hypothesis tested was that there were no differences between transects of different habitats. The resulting overall test statistic after 1,000 randomizations was R: 0.60 (ANOSIM $p < 0.001$, α: 0.01) (Table A5-22). Hence, the null hypothesis was rejected, 60% of all transects conducted in the same land-use type were more similar in composition than transects conducted in different land-uses, and more similar than would be expected by chance (Table A5-22). When pair-wise tests were made with the groups, only the three transects of the fallow and the three run in the cotton fields were not significantly different (ANOSIM R: 0.07, p: 0.15) (Table A5-22). Additionally, the significance of the groups in the complete data set was tested with the method 'Similarity Percentages' (SIMPER) (Appendix 5; Table A5-23, Table A5-24). The 'average within-group similarity' was 50% for the reserve while it was ranging between 28% and 33% for cotton, fallow and pasture land (Table A5-23). The resulting 'dissimilarity between groups' was ranging between 71% and 75% for the site-pairs cotton – fallow, reserve – fallow, reserve – pasture; and between 80% and 82% for cotton – pasture, cotton – reserve and fallow – pasture (Table A5-24).

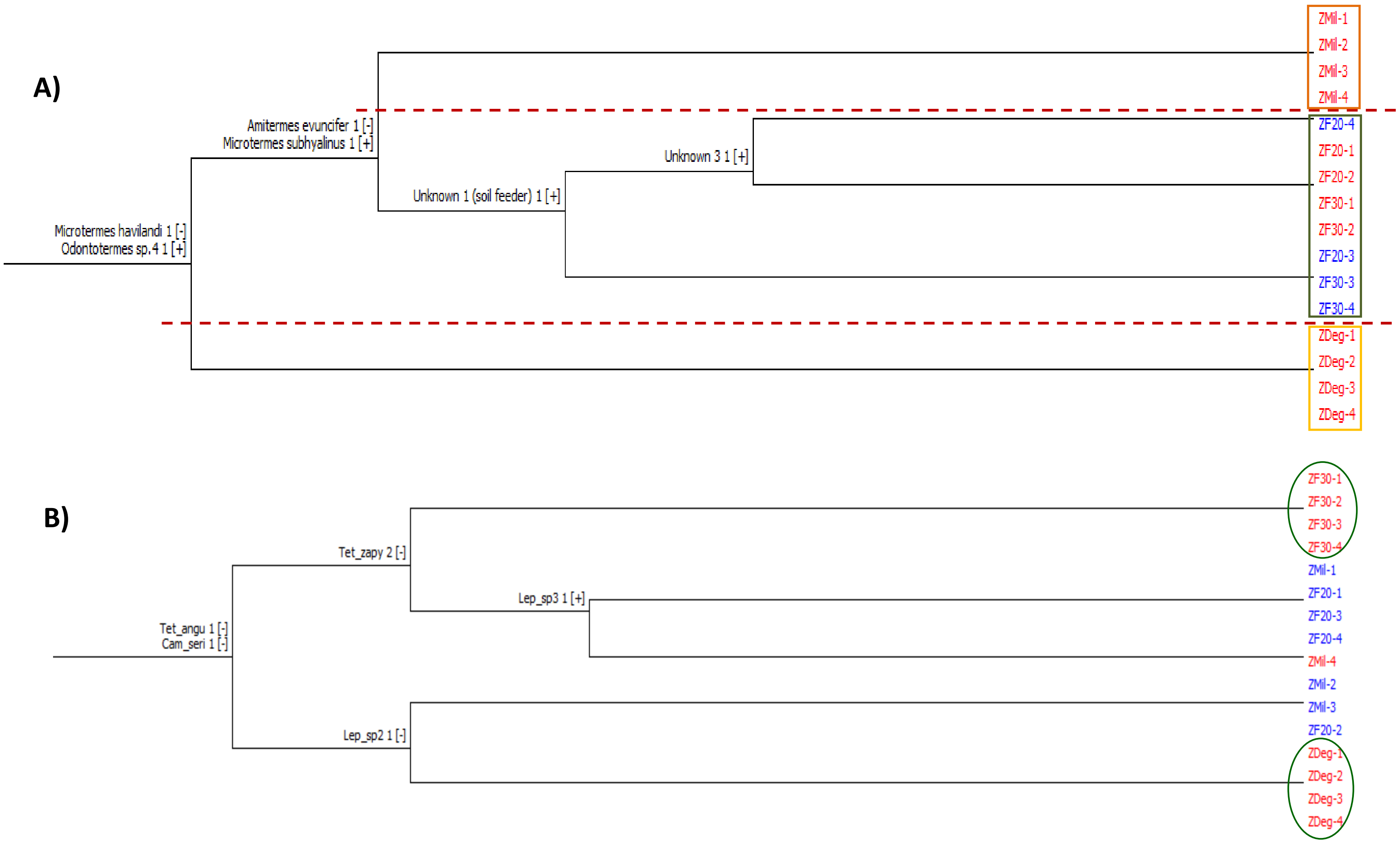

Fig. 5-16: TWINSPAN dendrogram showing the similarity of **A)** termite assemblages and **B)** ant assemblages, based on the frequency of occurrence of the species collected within four transects that were conducted between 2004 and 2008 in each of four succession stages of the Zaï system in Ouahigouya (Yatenga province, sub-Sahel region, Burkina Faso). At each division the indicator species are shown. Species names are abbreviated. Ant species are Tet_angu: *Tetramorium angulinode*, Tet_zapy: *Tetramorium zapyrum*, Cam_seri: *Camponotus sericeus*, Lep_sp2: *Lepisiota* sp.02, Lep_sp3: *Lepisiota* sp.03.
]

5.3.8 Similarity of termite and ant communities within and between habitats

For both termites and ants, several species have been identified which seem to be characteristic for different regions or land-use types. On the other hand, we also found less specialized species which occurred in every study site situated along the gradient. In TWINSPAN samples are divided between clusters using Correspondence Analysis. The TWINSPAN-method (Two Way Indicator Species Analysis) (Hill 1979) was used to examine the similarity of transects regarding their species composition. The analysis was carried out in CAP-4 (Community Analysis Package Version 4, Pisces Corporation Ltd., 2007). TWINSPAN identifies so-called 'preferentials', indicator species that are influential in determining which transects were separated at each node. TWINSPAN thus helps to define the dissimilarity between assemblages at that level of the dendrogram. At each division the preferentials are shown. An odd feature of the method is the use of so-called 'pseudo-species'. Species are divided into abundance classes and these different levels are viewed as different variables, i.e. different species. These 'pseudo-species' make the interpretability of the results considerably difficult. The method is therefore only exemplarily shown for termite and ant communities collected in four succession stages of the Zaï system in Ouahigouya (sub-Sahel region, Burkina Faso). Fig. 5-16 A) displays the dendrogram based on the data set of termites occurring in all RAP-transects conducted in the Zaï system; Fig. 5-16 B) shows the corresponding dendrogram based on the data set of ants.

5.4 DISCUSSION

Despite the general recognition that human activities – particularly agricultural processes – are increasingly changing the environment on local and global scales, thereby affecting both managed and unmanaged habitats (Hooper et al. 2005; Millennium Ecosystem Assessment 2005), relatively little is known about the effects on termites and ants which carry out vital functions in many tropical ecosystems.

However, to determine the role of termites and ants in agroecosystem function, the impact of farming practices on their diversity must be established first (Black & Okwakol 1997). In this study, an attempt was made to understand the distribution pattern of ant and termite communities with reference to the habitat type and the climatic region. I therefore assessed the existing ant and termite fauna under different land-use regimes traditionally applied in semi-arid Burkina Faso (West Africa) and investigated how management form and increasing land-use intensity affected the composition of their communities. The succession stages of the Zaï system in the sub-Sahel region will also be referred to as the first disturbance or land-use intensification gradient (LUI-1), the habitats in the North-Sudan region were forming the second disturbance gradient (LUI-2).

SAMPLING EFFICIENCY

Overall sample coverage indicated a very good representativeness for both invertebrate taxa; that means that the rapid assessment protocol RAP, as well as the application of only one of the two protocol-components apart (i.e. ant- or termite-transect), turned out to be very effective to representatively characterize, statistically compare, and monitor the termite and ant fauna in the near-natural savannas and agroecosystems selected in semi-arid Burkina Faso (Chapter 3.1). The efficacy reached when sampling ants and termites following the newly revised RAP-protocol was very high on all levels (transects, land-use types, regions) (Table 5-7; Table A5-5 to Table A5-8). The observed species richness was close to the estimated total species richness – in most cases between 70% and 90% of the expected species richness were collected. Therefore, the objective of representatively characterizing the actual ant and termite communities in the different land-use regimes and of assessing the changes in their diversity and relative abundance along the gradients of increasing land-use intensification and increasing soil restoration could be addressed.

The comparison of the methods used confirms King and Porter (2005) who stated that combinations of sampling methods are much more effective to assess ant species richness than protocols following one single method only; individual methods are complementary and sample only part of the entire termite and ant assemblage (Agosti & Alonso 2000; Jones & Eggleton 2000). The combined assessment of termites and ants has been proven to be especially advantageous for the compilation of ant species checklists. A significant amount of additional ant species has been detected owing to our newly designed protocol for the combined assessment of ant and termite communities, where ants are additionally collected when encountered in microhabitats or soil scrapes, i.e. following the protocol primarily designed to assess termite communities (Fig. A5-1). These additional methods were also named by Agosti and Alonso (2000) as being especially promising to increase the number on ant species checklists. Therefore, a significant advantage of our combined baseline transect protocol is, that due to the inclusion of microhabitat- and soil scrape-sampling as standard methods for the assessment of ants, all the species found cannot only be used to increase the number on the species checklists but also to statistically estimate and compare the species richness between habitats. In our study sites, pitfall traps revealed by far the best results; the Winkler sites always contributed least to the total number of ant species observed, probably due to the low amount of litter covering the ground in the study sites. This method turned out to be not appropriate for the dry conditions prevailing in the land-use types of the present study; it was originally designed to sample leaf-litter ant communities in tropical rainforests where huge quantities of litter are covering the forest floor (Delsinne et al. 2008). Similar findings were obtained in Paraguay and Argentina where the number of species collected per sampling effort increased with aridity for pitfalls and decreased with aridity for Winkler samples (Delsinne et al. 2008). The authors explained this trend with the low daytime foraging activity in the leaf litter during drought periods and assumed that in arid and semiarid regions the success of sampling ants with pitfalls was due to their 24-hours operation (Delsinne et al. 2008).

DIVERSITY OF ANT AND TERMITE COMMUNITIES IN BURKINA FASO

Together in both regions, 65 ant species belonging to 25 genera and 39 termite species belonging to 13 genera were found. In the temporal cross-section of the traditional soil rehabilitation system Zaï in Ouahigouya (sub-Sahel zone), 41 ant species (16 genera) and 33 termite species (11 genera) were collected (Table 5-3, Table 5-5). The four sites near Fada N'Gourma (North-Sudan region) on the other hand, hosted 53 ant species (23 genera) and 31 termite species (12 genera) (Table 5-4, Table 5-6). To my knowledge these findings represent the first records for Burkina Faso.

The only information available for termites were those in Mando (1997) who reported that Ouedraogo (1990) found species of the genera *Macrotermes*, *Odontotermes* and *Cubitermes* and that the three species *Odontotermes smeathmani* (Fuller), *Microtermes lepidus* (Sjöst) and *Macrotermes bellicosus* (Sjöst), were present in an experimental site. The single records for ants in Burkina Faso were the following 13 species listed in ANTWIKI.ORG; species with an asterisk have not been collected within the present study: *Camponotus sericeus* (Fabricius, 1798); *Camponotus vestitus** (Smith, F., 1858); *Cataglyphis* spp.; *Messor galla* (Mayr, 1904); *Monomorium abyssinicum* (Forel, 1894); *Monomorium afrum** André, 1884; *Monomorium balathir** Bolton, 1987; *Monomorium bicolor* Emery, 1877; *Monomorium oscaris* Forel, 1894; *Oecophylla longinoda**; *Pachycondyla sennaarensis ruginota** (Stitz, 1916); *Pheidole rugaticeps** Emery, 1877 and *Tetramorium sericeiventre* Emery, 1877 (http://www.antwiki.org). Unfortunately, no information is given about the collectors or the land-use types where these species had been collected.

However, although there are no other quantitative data available concerning the diversity of the focal soil-arthropods in Burkina Faso, the results leastwise indicate that compared to the findings of other studies from West Africa with similar sampling protocols, species richness of termites was relatively high in both study regions. For example, 32 termite species were collected inside and around the Lamto Reserve (Côte d'Ivoire), a region receiving around 1,200 mm per year (Dosso et al. 2010b). Increasing aridity along rainfall gradients in Africa and Asia is generally associated with decreasing termite species richness (Bignell & Eggleton 2000; Schuurman 2006). However, the same number of species was found in the Oumé region (Côte d'Ivoire) during an assessment of termites and the damages they cause in cocoa plantations (TraBi 2013), although the mean annual rainfall in this region amounts to about 1,640 mm (Kone et al. 2012a). Neither is this general trend supported by findings of the present study. Despite the higher mean annual rainfall in the North-Sudan region (875 mm year^{-1}), more species were found in the sub-Sahel zone (ca. 660 mm year^{-1}) (Fig. 5-7). The actual difference between the two regions may be even larger – the rarefaction curve for termites in the North-Sudan reached an asymptote, the one for the sub-Sahel zone, however, was still slightly rising (Fig. 5-7). Even the number of termite species collected in different habitat types appears to be high in Burkina Faso. In the region of Lamto, termite richness fell from 25 species in the forest island, to 18 species in a savanna-woodland, and to 14 species in the annually burned Guinean savanna (Dosso et al. 2010b); the primary forest in the Oumé region hosted 20 termite species (TraBi 2013). In comparison, the old Zaï forest (sub-Sahel zone) and the near-natural savanna (North-Sudan region), hosted 25 and 24 termite species, respectively – although termite communities in tropical rainforests in

Africa are known to be particularly species-rich (e.g. Abe et al. 2000; Davies et al. 2003a; Eggleton 2000).

For ants in Burkina Faso, differences between the study regions were larger; significantly more species were found in the wetter North-Sudan region (Fig. 5-8). Similarly, also the differences in the regional species richness between the present study and the Oumé region (Cote d'Ivoire) were larger: 100 species were recorded along an age gradient of cocoa cultivation (Kone et al. 2012a), and 132 ant species were recorded in eight main land-use types, comprising primary and secondary forests, multispecific tree plantations as well as teak plantations of different age (Yéo et al. 2011). However, only 38 ant species were recorded within cocoa agroforests of five regions in Cameroon, receiving around 1,600 mm rain per year and ranging from less extensive, intermediate to more intensive cocoa agroforests (Bisseleua et al. 2013). Delsinne et al. (2010) stated that the perception of the relationship between ant alpha-diversity and precipitation depends on the gradient range under study. So far, only few studies investigated the relationship between ant diversity and annual precipitation (e.g. Delsinne et al. 2010; Dunn et al. 2009; Kaspari et al. 2000). Unfortunately, results are inconsistent due to confounding factors (Delsinne et al. 2010). Some studies revealed that ant species richness was positively correlated with rainfall, especially when precipitation was very low (e.g. less than 200 mm year^{-1}) (Davidson 1977; Marsh 1986), others that ant diversity was negatively correlated with rainfall (Dunn et al. 2009). Along a 400 km-long transect in the Paraguayan Chaco region with a mean annual rainfall ranging between 460 and 887 mm similar to the precipitation range studied in Burkina Faso, Delsinne et al. (2010) found that aridity did not constitute an environmental filter reducing ant diversity at the studied regional scale.

However, other factors than the annual precipitation may have been more important for the differences noted in the regional species richness of ant and termites; for example, differences in the regional species pool, the land-use types, the topography, the habitats' abiotic and biotic parameters, or the study season. Aridity may affect ant diversity by limiting the availability of resources and causing physiological distress to the ant populations as assumed by Delsinne et al. (2010). Parameters predicting the variations noted in the composition of communities along the two disturbance gradients will be discussed in detail further below.

SPECIES RICHNESS AND DIVERSITY ALONG THE DISTURBANCE GRADIENTS

Termites and ants appeared to be highly sensitive to land-use intensification. Lowest numbers of species, genera, subfamilies and functional groups were found in the most degraded or extensively managed habitats, the degraded barren land in the sub-Sahel zone, and the cotton fields in the North-Sudan region (Fig. 5-1, Fig. 5-2). These land-use types also had the highest agricultural intensification (AI) index within their gradient (method in Chapter 3.5; results see Table A5-1 in Appendix 5).

In both regions, the resulting index values supported my assumptions concerning the putative order[3] when arranging the sites according to decreasing anthropogenic intensification (decreasing index values). The AI index presented here was standardized by the maximum as in Herzog et al. (2006) or Decaëns and Jimenez (2002) (Chapter 3.5) with the advantage that each component is scaled between 0 and 1. Other approaches are for instance, standardization against the mean value of each component as in Blüthgen et al. (2012). In three regions in Germany they studied 50 managed grasslands (meadows and pastures) over a period of three years, each region was forming a gradient spanning the whole range of land-use intensities; standardization by the maximum could have been disadvantageous for them because it relies on a single site and inter-annual variations in land-use intensity of this particular site could have strongly affected all index values[4]. In contrast, in the present study the inter-annual variations in the land-use intensity were already taken into account as the site-history since the establishment of the system (age of the site) was considered. However, the AI index was only used as control measure but not included in any of the ordinations since both gradients comprised only four land-use types, each represented by one or two plots only. A categorical analysis based on the different habitats and the environmental parameters measured in each site appeared to be preferable. Due to the pronounced qualitative differences between the different land-use types (degraded area, reforested sites, near-natural savanna, pasture, agricultural fields with and without pesticide or fertilizer application) an element of uncertainty was caused concerning the sub-indices selected in the formula of the AI index to reflect the frequency or intensity of human interventions (duration of cropping periods, mean tillage frequency, mean fertilization rate, etc.); they were all weighed equally in their contribution to define the gradient, although they might have contributed to a different extent. Moreover, the first disturbance gradient was formed by a temporal cross-section of the Zaï system – the different age stages thus already represented a single 'unidirectional intensity gradient'.

North-Sudan region

The decreasing diversity of termites with increasing anthropogenic impact was as expected (Fig. 5-10, Fig. 5-11, Table 5-8). Species richness was highest in the reserve (24 spp.) with restricted human impact, lower in the pasture and the short-term fallow, and drastically decreased to only five species in the cotton fields with extensive pesticide application (Fig. 5-2). Numerous authors reported of similar findings; termite communities were consistently found to be less diverse in disturbed habitats (e.g. Bignell & Eggleton 2000; Davies et al.

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[3] Sub-Sahel: Degraded, barren soil > millet field > young Zaï forest > old Zaï forest.
North-Sudan: Cotton fields > short-term fallow > pasture area > Pama reserve.

In the short-term fallow, termites and ants were assessed in the 2nd and the 4th year, the latter representing the last year fallowing. Even in the 4th year, the fallow was still lacking the rich flora and fauna which normally develops in long-term fallows.

[4] Moreover, Blüthgen et al. (2012) tested their LUI-index and found that the type of standardization did not affect the general conclusions about the land-use effects.

1999; Donovan et al. 2002; Donovan et al. 2007; Eggleton et al. 1995; Eggleton et al. 1997; Gathorne-Hardy et al. 2006; Vaessen et al. 2011). Most studies in agro-ecosystems revealed that crops and plantations hosted less termite species than nearby natural vegetation (see Black & Okwakol 1997 and references therein).

Like in termites, the ants' species richness and within-habitat diversity was highest in the savanna in the Pama reserve (37 spp.), lower in the pasture and lowest in the cotton fields (Fig. 5-1, Fig. 5-8, Fig. 5-9, Table 5-8). These findings are in line with those of other studies. For example in the Cote d'Ivoire, ant species richness and diversity clearly decreased from the relatively well conserved land use types to the most degraded or extensively managed ones (Yéo et al. 2011). Lobry de Bruyn (1999) reviewed ten studies which recorded the species richness and composition of ant communities in agricultural soils and concurrently in naturally vegetated environments. Although their results could rarely be directly compared due to differences in soil type, rainfall or intensity of agricultural activity, the studies showed that species richness and diversity of ants was nearly always lower in farmland environments than in naturally vegetated areas (Lobry de Bruyn 1999). In Australia, agricultural clearing, followed by rangeland grazing, were found responsible for the greatest loss of ant biodiversity integrity (Majer & Beeston 1996). Likewise the results from the North-Sudan region, the reserve was richest, the pasture was poorer, and the cotton fields were poorest. Contrary to what was assumed and surprisingly similar to the reserve, however, was the species richness in the short-term fallow where 36 ant species were collected (Fig. 5-1). The short-term fallow also had the highest within-habitat diversity of all four land-use types (Fig. 5-8, Fig. 5-9, Table 5-8). An explanation for this high species number in the short-term fallow may be a high number of leftover seeds in the soil from the agricultural production during the preceding years. Another reason might be a reduced soil compaction resulting from the tillage practice during the cropping years; this could be favorable for seed-harvesting species. An indication for these assumptions may be the exceptionally high nest number of *Messor galla*; this granivorous ant represented the most abundant species in this site, occurring in 90% of all sampling units (Table 5-4). Moreover, *Pachycondyla senaarensis*, another ant with a partly granivorous diet, was highly abundant in the short-term fallow (Table 5-4).

Although the understanding of ant diversity in agricultural landscape is still fragmented, three common explanations for the loss of ant species in agricultural environments were offered by Lobry de Bruyn (1999) – explanations which may also be applicable to termites: 1) changes in microclimate conditions that adversely affect larvae and pupae development (Hölldobler & Wilson 1990), foraging activity and nesting places (Davies et al. 1999; Eggleton et al. 2002); 2) the reduced food availability following the application of agrochemicals (pesticides, herbicides, fertilizer) and the reduction in litter and soil organic matter (Attignon et al. 2005; Davies et al. 1999; Jones et al. 2003); and 3) interactions with other species leading to alterations in community structure (Attignon et al. 2005; Korb & Linsenmair 2001, 2002; Linsenmair et al. 2001; Longhurst 1977; Longhurst et al. 1978; Luke 2010).

Sub-Sahel region

Very promising results concerning the recovery potential of the diversity of termites and ants on initially fully degraded and crusted soils were gathered in the Zaï system in Ouahigouya (sub-Sahel region).

The number of species collected (Fig. 5-1, Fig. 5-2) and the within-habitat diversity (Fig. 5-8 to Fig. 5-11, Table 5-8) of ants and termites increased with increasing habitat rehabilitation, which is from degraded land, to the millet fields, to the young and then the old Zaï forest. Under the precondition that a certain form of 'diversity-island', acting as an initial source for the termite and ant resettlement, is still present in the region to be restored, it appears that the negative trend in form of the massive loss of diversity in termite and ant communities with increasing anthropogenic pressure, which is apparent in the agricultural system studied in the North-Sudan region, seems to be reversible with the Zaï technique. Therefore, the data collected for the focal soil arthropods in the sub-Sahel region were consistent with my assumptions for the Zaï system. The question how distant sources can be to resettle an area when conditions improve remains to be answered in future studies.

The recovery potential of termite communities has already been studied elsewhere. However, to my knowledge, no study investigated the recovery potential of termite and ant communities in completely degraded, barren and crusted soils like the initial habitat stage of the Zaï system in Ouahigouya. For instance, Gathorne-Hardy et al. (2002) studied termites in different habitat types in Borneo and Sumatra (mean annual rainfalls ranging between 1,700 mm and 3,800 mm). The most disturbed habitats, a grassland covered with *Imperata cylindrica* and a cassava field, had a strongly reduced termite fauna with only two functional groups based on the classification of Donovan et al. (2001) remaining: Macrotermitinae and *Amitermes*-group (feeding group II; wood and litter feeders) and *Termes–Capritermes* group (feeding group III/IV; soil-wood interface feeders). The study revealed that these disturbed habitats had the potential to recover the termite fauna when left fallow near to a source area of primary forest for over 50 years (Gathorne-Hardy et al. 2002). And Dibog et al. (1999) found promising evidence of the potential for tree-based agriculture in the Amazon to support the function of soil termite fauna, even on land previously used as pasture.

THEORIES ABOUT SPECIES RICHNESS AND DIVERSITY

There are several theories about the effects that determine species richness or diversity.

The unimodal response of species richness to disturbance has been attributed to a trade-off between competitive ability and tolerance to disturbance (Connell 1978). Connell's **intermediate disturbance hypothesis (IDH),** the most prominent model on effects of disturbance on diversity, predicts that the highest diversity is maintained at intermediate levels of disturbance because more species are able to coexist due to coexistence of competitors and colonizers (Connell 1978). At low levels of disturbance diversity is assumed to be low due to competitive exclusion of species by few competitive dominants. At high levels of disturbance, only fugitive species can persist (Connell 1978). Such a humped diversity pattern has been documented, for example, for ant communities along gradients of both stress and disturbance, with a reduction in diversity linked to exclusion by dominant species (Andersen 1992, 1997).

My study does not support the IDH – provided that the classification following the agricultural intensification index is correct. According to the AI-index, the young Zaï forest was classified as medium-intensified system; but the old forest, the least-intensified system in the sub-Sahel, was richer in ant as in termite species. However, in the natural succession, the old Zaï forest may de facto represent a medium-intensified system. A follow-up study in the Zaï system in Ouahigouya could try to answer this question. It might, however, also be possible that the sub-indices of the AI-index would need an adaptation for the Zaï system. The value 1 for the degraded land had to be set artificially; the history of this site could not be taken into account as it represented the initial stage of the traditional restoration system Zaï, the site history was therefore only considered thereafter. But neither did the findings in the North-Sudan region support the IDH. However, there is an important scaling issue related to such a humped diversity pattern – its expression requires a full range of productivity or disturbance (Andersen 1997). If only a part of the range is sampled, then increasing, decreasing, or no related responses are possible, depending on whether only low levels, high levels or only moderate levels of disturbance were sampled, respectively (Andersen 1997).

An extension of the IDH is **Hustons' Dynamic-Equilibrium Model (DEM)** which predicts that the effects of disturbance depend on the productivity of communities, because a stronger disturbance is required at high growth rates to counteract increased rates of competitive exclusion. Huston's DEM further assumes that the rate of competitive exclusion is the primary determinant of species diversity in undisturbed environments while low rates of competitive displacement are assumed to be the reason for low diversity in severely degraded environments (Huston 1979). However, in severely degraded environments such as the degraded, barren land in the Zaï-system, diversity may also be low because only few species were able to re-colonize such a harsh environment. Only one *Odontotermes*-species was found during the diversity assessment. Even in the experimental blocks installed in each succession stage during a dry and a rainy season (Chapter 8) and where different organic materials were applied, only this single *Odontotermes*-species was encountered. Hassall et al. (2006) stated that appropriately adapted species can recover from the disturbance and persist in the community when disturbance is high but population growth rates are also high. A similar situation may be found in the millet fields (LUI-1), according to the AI-index a highly intensified site, where higher quality food resources were available and where termite and ant species richness was relatively high.

COMMUNITY COMPOSITION ALONG DISTURBANCE GRADIENTS

Not all species or functional groups responded to agricultural intensification in the same way, as was also noted by Donovan et al. (2007). For both invertebrate taxa significant differences could be noted in the shape of the density variations along the gradient (Table 5-3 to Table 5-6).

Occurrence of Individual Termite Species

Of the 42 termite species collected across both disturbance gradients, 22 occurred in both climatic zones, 11 species were characteristic for the sub-Sahel and 9 characteristic for the North-Sudan zone (Table 5-5, Table 5-6).

The two fungus-growers *Microtermes* sp.2 and *Macrotermes subhyalinus*, and the grass-feeder *Trinervitermes occidentalis* occurred only in the two least-intensified habitats, the protected savanna and the old Zaï forest (Table 5-5, Table 5-6). In contrast, e.g. Pearce et al. (1995) observed *Macrotermes subhyalinus* while attacking crops. The fungus-grower *Odontotermes* sp.1, the grass-feeder *Trinervitermes oeconomus*, and the wood-feeder *Microcerotermes parvus* were found in all habitats except for the two most intensified ones, the degraded land and the cotton fields (Table 5-5, Table 5-6). Probably due to intensive use of pesticides, the cotton fields harboured only a very simplified termite assemblage with just 5 termite species remaining: one unknown species, three *Microtermes*-species (*M.* sp.1, *M. havilandi, M. subhyalinus*), and the wood-feeder *Eremotermes sabaeus* which was published to be endemic to the Arabian Peninsula (Cowie 1989). Species of *Microtermes* were termed as ‘damage causing species’ (Rajagopal 2002; Sattar et al. 2007), causing wilting and death to local crop plants (Pearce et al. 1995). Similarly, only *Microtermes* spp. thrived in intensely tilled fields in Kenya (Kooyman & Onck 1987), and increasing abundances of *Microtermes* species were also noted under agricultural conditions in semi-arid northern Botswana (Schuurman 2006). A similar pattern was found in Burkina Faso where the relative abundances *M. havilandi* increased in the millet fields (LUI-1) and the cotton fields (Table 5-5, Table 5-6). However, not all *Microtermes* species responded in the same way; for example, the abundances of *Microtermes* sp.01 decreased with increasing restoration, and *Microtermes subhyalinus* occurred only in the two Zaï forests (Table 5-5). The relative abundance of *E. sabaeus* steadily increased in both regions with increasing intensification, perhaps pointing to their attaining the status of a pest species. *M. parvus* on the other hand, occurred in the North-Sudan region in decreasing frequencies with increasing intensification. Inconsistent results about the abundance of termites in disturbed and undisturbed habitats were already reported in other studies see review of Black and Okwakol (1997).

Representation of the Termites’ Functional Groups

Some parallels became apparent, when comparing the functional group composition in Burkina Faso with what is known from other semi-arid regions in Africa. Fungus-growers were very well represented in all habitats (Fig. 5-2). With their dominance, fungus-growing termites showed an enormous adaptability to different land-use practices or habitat types (disturbed or non-disturbed), thereby proving high ecological plasticity. The dominance of fungus-growers in the study sites support the general finding that increasing aridity is associated with increasing relative abundance of fungus-growers (Bignell & Eggleton 2000;

Schuurman 2006). Macrotermitinae often dominate the termite fauna of arid savannas presumably because they are able to utilize fresh litter (e.g. Lepage 1984; Schuurman 2006; Turner 2006; Wood et al. 1977); they were also the most abundant group in all habitats studied by Dosso et al. (2012) in the Côte d'Ivoire.

In the present study, the greatest variations between the habitats were observed in soil and grass-feeding termites. In heavily impacted habitats, whole functional groups were missing: soil and grass-feeders were absent in the cotton fields and neither soil-, nor grass-, nor wood-feeders were present in the degraded barren site (Fig. 5-2).

In the North-Sudan region, soil-feeders were only found in the near-natural savanna. Even the grass-feeders were only in the savanna notably diverse (Fig. 5-2). Crop-rotation with tillage and pesticide-use are assumed to be the cause for the lack of soil-feeders in the short-term fallow and the cotton fields. Soil-feeders have already been found elsewhere to be especially vulnerable to cultivation and often showed a stronger decrease in species richness and abundance than other functional groups, e.g. as wood-feeders (e.g. Bandeira & Vasconcellos 2002; DeSouza & Brown 1994; Eggleton et al. 2002; Eggleton et al. 1997). In the pasture, soil-feeders were presumably missing because of soil compaction caused by trampling of crazing cattle. Highly compacted soils are known to be extremely poor microhabitats for soil-feeding termites (Eggleton et al. 1997). Compaction is also likely to have negative effects for nesting and feeding (Eggleton et al. 1997; Gathorne-Hardy et al. 2002). The absence of a canopy is also known to reduce particularly the diversity and abundance of soil-feeders (Dibog et al. 1999), most probably because of the greater diurnal temperature and moisture fluctuations in ecosystems with low crown-cover percentages (Gathorne-Hardy et al. 2002). Soil-feeders live on an “energetic knife edge” (Dibog et al. 1999; Gathorne-Hardy et al. 2002), they are more likely to desiccate in hotter, more disturbed habitats since they are less sclerotized, softer bodied and generally more fragile than wood-feeders (Eggleton et al. 2002). The present study supports the general finding that soil-feeders favor shaded habitats – with three species they were most diverse in the two Zaï forests (Fig. 5-3). Only apparently contradictory was the presence of two *Cubitermes* species and the high number of *Cubitermes* mounds in the millet fields (LUI-1). The subsistence farmer and land owner, Yacouba Sawadogo, who knows about the beneficial effect soil-feeding termites exert on the soils’ nutrient status, transferred over the last decade mounds from other places into his millet fields – and several of these mounds stayed alive; their occurrence in this site has therefore to be handled with caution.

In the present study, wood-feeders and especially grass-feeders appeared to be distributed according to the availability of ligneous and grassy litter, respectively. In the Côte d'Ivoire, wood-feeders were better represented in forests than in savannas (Dosso et al. 2010b). It seems that this pattern also holds for the situation in Burkina Faso since most wood-feeding species occurred in the two Zaï forests. All six grass-feeding species collected in Burkina Faso belonged to the genus *Trinervitermes* (Fig. 5-2). Grass-feeders were notably divers and dominant only in the near-natural, annually burned savanna of the North-Sudan region where high grass biomass was produced; four species were even restricted to this habitat

(Table 5-6). *T. oeconomus,* a species known to attack standing grass (Ohiagu 1978), and *T. geminatus* were highly abundant in the reserve; the former species further represented the most abundant species in the pasture (Table 5-6). Grass-cover percentages in the pasture were almost as high as in the reserve (Chapter 4, Table 4-6), however, trampling by cattle was most probably the reason that not more grass-feeders were able to persist or to settle in this habitat. Similar findings are reported from a Southern Guinea Savanna in Nigeria where all of the *Trinervitermes*-species of the present study (except for *T. gratiosus*) were sympatric and where *T. geminatus* was by far the most abundant species (Ohiagu 1979). My observations are further congruent with findings from northern Ghana (Benzie 1986) and from the Côte d'Ivoire where all grass-feeders collected by Dosso et al. (2012) belonged to this genus as well; in both studies, grass-feeding *Trinervitermes*-species were restricted to savanna habitats, especially an annually burned Guinean savanna comparable to the present study. A general decrease in the density of *Trinervitermes'* mounds in savannas with high grass biomass may only be caused by man's interference (Roy-Noël 1978) – for instance by annual fires like in the protected savanna of the Pama reserve. Tillage and pesticide application during the preceding cropping years are assumed to be responsible for the grass-feeders' absence in the short-term fallow of the North-Sudan zone. Beside the lower grass-cover percentages in the Zaï stages (Chapter 4, Table 4-4), tree invasion might be an explanation for the low number of grass-feeders present in the two Zaï forests – tree invasion seemed to be a negative factor for grass-feeders in the Côte d'Ivoire (Dosso et al. 2010b).

Occurrence of Individual Ant Species

Of the 65 ant species collected, 29 occurred in both climatic zones, 12 species were characteristic for the sub-Sahel, 24 for the North-Sudan zone (Table 5-3, Table 5-4). The following five species were *ubiquitous* in all eight land-use types: *Camponotus maculatus* (Formicinae), *Pachycondyla senaarensis* (Ponerinae), *Tetramorium sericeiventre* (Myrmicinae), *Pheidole* sp.01 (Myrmicinae) and *Monomorium bicolor* (Myrmicinae).

Camponotus maculatus was highly abundant in both regions (Table 5-3, Table 5-4). Kone et al. (2012a) classified the species as 'generalist' ant, exploiting diverse sources of food including plant carbohydrates and proteins, and according to Longhurst (1977) including termites[5]. Members of the genus *Camponotus* are classified as subordinate Camponotini (Andersen 2000); these are often diverse and abundant in rich ant communities which are under some environmental stress, and many are ecologically segregated from them owing to their large body size and often nocturnal foraging (Andersen 2000; Koch & Vohland 2004). *C. maculatus* is indeed a very large and highly abundant ant, similar to *Camponotus sericeus*, another generalist known to predate on termites and the most abundant ant in the near-natural savanna, and the North-Sudan region in general (Table 5-4). ***Pachycondyla***

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[5] Longhurst (1977) observed *C. maculatus* predating on fungus-growers (*M. subhyalinus, M. bellicosus, Microtermes* spp., *Ancistrotermes cavithorax*, *Odontotermes* spp.), grass-feeders (*Trinervitermes* spp.), and wood-feeders (*Amitermes* sp., *Microcerotermes* spp.).

senaarensis is an aggressive savanna species (Collingwood 1985), known throughout the African tropics including West Africa (Wheeler 1922), presumably representing the most common ant in the Sudan savanna regions (Levieux & Diomande 1978). *P. senaarensis* is an ‘opportunist’ (Longhurst 1977), i.e. a non-competitive and *non-specialized* ant that exploits diverse food sources. Longhurst (1977) observed this ponerine predating on the same termite taxa as did *C. maculatus.* Opportunists differ from other generalist species in their ability to persist in disturbed environments (Kone et al. 2012a); they generally predominate only at sites where stress or disturbance severely limits ant productivity and diversity (Andersen 2000) – like in the present study where it was especially abundant in the short-term fallow and the cotton fields despite the intensive application of insecticides during cotton cultivation (Table 5-4). Unique among ponerines is its partially granivorous diet, assumed to be an adaptation to the dry areas which constitute the species’ main habitat (Déjean & Lachaud 1994), and assumed to be responsible for the ants’ great success (Levieux & Diomande 1978). ***Tetramorium sericeiventre*** is an ‘opportunist’ (Longhurst 1977) and open area species (Yéo et al. 2011), what seems to be especially mirrored in its distribution pattern in the Zaï stages (Table 5-3): the degraded area was open but had limited spatiotemporally stable food resources; the millet fields were open and provided at least seasonally rich food resources; the young Zaï forest offered both open areas as well as diverse and spatiotemporally stable food resources, whereas the old forest was rich in diverse and spatiotemporally stable food resources but only had few open areas. Its frequencies in the study sites (Table 5-3, Table 5-4) further confirm the sensibility of ants to land-use changes, thereby supporting findings of a study recently undertaken in the Côte d’Ivoire, where *T. sericeiventre* appeared to be particularly characteristic for anthropogenic impacts (Yéo et al. 2011). As the rate of competitive exclusion is assumed to be the primary determinant of species diversity in undisturbed or less disturbed habitats (Connell 1978; Huston 1979), it is likely that this non-competitive opportunist gets excluded by competitive dominants. This might explain the ants’ low frequencies in the near-natural savanna in the Pama reserve. The pasture offered regions with open areas and spatiotemporally stable food resources; trampling by cattle may have kept the ants’ frequency on a medium level. The short-term fallow represented an open area; however, due to former pesticide application and the highly simplified flora and fauna, food resources were lower or rather not as diverse as in the pasture. The recent use of pesticides may explain the ants’ sparse occurrence in the cotton fields (LUI-2). ***Pheidole* sp.01** is a ‘generalist ant’ (Kone et al. 2012a) exploiting diverse food sources like opportunists, however, differing in their inability to persist in highly disturbed environments (Kone et al. 2012a). This inability seems to be mirrored in its distribution pattern in Burkina Faso: in both study regions, *Pheidole* sp.01 was the second most abundant species, with lower frequencies only in the most-intensified habitats (Table 5-3, Table 5-4). Members of the genus *Pheidole* are often classified as ‘generalized Myrmicinae’[6] which are often among the most abundant ants of communities throughout the warmer regions of the world (Andersen 2000). They have a restricted

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[6] Like members of the genera *Monomorium*- and *Crematogaster*-species.

territory size, moderate rates of foraging activity, and – what seems to be supported by the findings of the present study – their primary distribution is in habitats with moderate stress (Andersen 2000). ***Monomorium bicolor***, a general scavenger (Bolton 1987), was the species with the highest frequencies in the sub-Sahel region (Table 5-3). The findings of the present study are in accordance with Bolton (1987) who stated that in sub-Saharan Africa, *M. bicolor* is characteristically a species of open savannah or semi-arid zones, also occurring in forested areas where there is some direct insolation˙ Bolton (1987) further reported that it is the most successful and widely distributed species of its group in the Afrotropical region.

Representation of the Ants' Subfamilies

The dominance of individual ant subfamilies was rather constant in both regions and throughout the different land-use types (Fig. 5-1, Table 5-3, Table 5-4). This might indicate that the ant communities were sampled evenly and therefore again that the objective of representatively characterizing the ant fauna could be addressed.

The ant fauna in Burkina Faso was dominated by the Myrmicinae with 54% of the total number of species collected along both disturbance gradients, the Formicinae comprised 22% and the Ponerinae 9%. The corresponding values for the subfamilies' shares in each region were similar to these numbers, irrespective of whether the species number or their frequencies were regarded (Table 5-3, Table 5-4). The dominance of the Myrmicinae in Burkina Faso is paralleled by their numerical importance in the world fauna (e.g. Bolton 1994; Kone et al. 2012a). The Myrmicinae and Formicinae are the largest ant subfamilies and represent the dominant groups in most terrestrial habitats (Marsh 1986; Ramesh et al. 2010). Yéo et al. (2011) found that the whole subfamily Myrmicinae as well as species of the genus *Tetramorium* proved to be surrogate taxa to indicate the decreasing ant species richness with increasing land-use intensification. Similar findings as in Burkina Faso were reported by Ramesh et al. (2010) in South India, where the Myrmicinae comprised 51% of all species and the Formicinae 29%. The authors cite several other studies with the same pattern; however, all were from India (see references in Ramesh et al. 2010). Comparable results were also obtained by Marsh (1986) along a climatic gradient in the Namib Desert. However, there are also other examples and these are from West-Africa: Belshaw and Bolton (1993) collected leaf litter ants over several 100 kilometers in forest habitats in Ghana where the Myrmicinae (63%) were followed by the Ponerinae (22%), and then by the Formicinae. The same order was found in the Oumé region (Côte d'Ivoire), where Yéo et al. (2011) studied ant communities in different habitats, comprising primary and secondary forest, tree- and teak plantations, food crops, cocoa plantations, and fallows; 50% of all species belonged to the Myrmicinae, 21% to the Ponerinae and 16% to the Formicinae.

Differences in the land-use practices (site history), **i**n the strength of insolation, or in the original habitat type may possibly explain the reverse order of the Formicinae and Ponerinae. In the studies cited for West Africa, ants were collected either in primary or secondary forests, or in land-use types that were directly derived from forests (Belshaw & Bolton 1993; Yéo et al. 2011). Moreover, Yéo et al. (2011) reported the subfamilies' shares for the whole Oumé region. However, results similar to those of the present study are obtained when calculating the shares for the short-term fallow (2–5 years old) in the Oumé region which was similar to the short-term fallow in the North-Sudan region, where ants were sampled in the second and the fourth year of fallowing. Together, the three subfamilies comprised 84% of all species present in the fallow, like in Burkina Faso or in the Oumé region in total. The subfamilies' shares in the short-term fallow resemble those of the present study: 42% of all species collected in the fallow belonged to the Myrmicinae, 28% to the Formicinae, and 14% to the Ponerinae. Furthermore, Ramesh et al. (2010) who reported of similar ratios sampled ants during the hot dry season; the mean annual rainfall in South India ranges between 200 and 400 mm (www.mapsofindia.com/maps/india/annual rainfall.htm). The studies from West Africa, however, were conducted in regions with higher annual rainfall and higher relative humidity (Belshaw & Bolton 1993; Yéo et al. 2011).

HABITAT PARAMETERS PREDICTING VARIATIONS IN COMMUNITY COMPOSITION

So far, few studies assessed the local or regional termite and ant fauna in semi-arid regions and simultaneously also the abiotic and biotic habitat parameters (e.g. Gillison et al. 2003; Jones et al. 2003; Luke 2010). However, several studies compared termite and ant communities of different land-use types.

Unfortunately, in both regions, only a reduced number of the collected species could be included in the ordinations. Since only common species should be considered in a canonical cluster analysis (CCA), only the species present in three or four habitats were taken into account, i.e. only between 9 and 13 termite and ant species (Fig. 5-12 to Fig. 5-15). The reduced number of included termite and ant species together with the relatively small number of study sites do not favor a completely robust analysis, results obtained should therefore be interpreted very cautiously. Furthermore, due to this low species and habitat number it did not make sense to additionally conduct the ordinations separately for the different functional groups. Nevertheless, the ordinations revealed a series of very consistent trends between certain environmental and termite/ant parameters.

Termites

A great part of the variations in the composition of termite communities along the successional cross-section of the Zaï system was significantly explained by changes in the habitats' crown-cover percentages (Fig. 5-14). The absence of a canopy and concomitant effects on soil microclimate are not only known to reduce the diversity of soil-feeders but also of termites in general (Eggleton et al. 1997). Several studies revealed higher termite diversity and abundance in habitats with a closed or near-complete canopy like in the old Zaï forest of the present study (e.g. Dibog et al. 1999; Eggleton et al. 2002; Eggleton et al. 1997; Jones 2000; Jones & Prasetyo 2002). Similarly in the North-Sudan region, the greatest part of the variations was significantly correlated with changes in the total area covered with tree trunks (Fig. 5-15), another measure for the stock of trees present in a habitat. In the Zaï stages, all parameters related to the tree stock (crown cover percentages, plant species richness, number of tree individuals, mean tree height and cumulated woody plant basal area) were increasing with increasing restoration, i.e. they had all the same trend (Chapter 4, Table 4-4). The difference in the North-Sudan region was that the crown-cover percentages in the reserve were lower than in the pasture although all the other parameters were higher (i.e. they had the same trend and were decreasing with increasing intensification) (Chapter 4, Table 4-6). The present findings are further congruent with those of Jones et al. (2003) and Gillison et al. (2003) where the diversity of termites was found to be strongly correlated with the cumulated woody plant basal area. Adverse changes in environmental factors such as microclimate, vegetation structure, as well as loss of microhabitats or increasing soil bulk density, appear to be most consistently reflected by changes in canopy cover and woody plant basal area, parameters which can be readily determined in the field (Gillison et al. 2003).

Other parameters identified to exert causal influence on the composition of termite communities along the North-Sudanese disturbance gradient, were the median clay-content and the median organic matter content in the upper soil horizon (Fig. 5-15). Termites require well-structured soils rich in organic material for colony building and feeding (Eggleton et al. 1997). In the Zaï succession stages, the diversity of termites was further found to be strongly correlated with the sand content in the upper soil horizon and the availability of litter in the transect sections (Fig. 5-14). The amount of dead wood and leaf litter seemed to be also especially influential for termite communities studied by Jones et al. (2003), Davies et al. (1999), Attignon et al. (2005) and Luke (2010). The correlation of community composition variation with litter availability suggests its importance as a source of food or shelter for the termite species that were present. For example, a higher termite density in an agrisilvicultural system in southern Cameroon was mainly attributed to greater litter inputs around palms (Dibog et al. 1999). Similarly, termite diversity in southern Cameroon recovered more rapidly when dead wood was left on the ground following perturbation (Davies et al. 1999), and Roy-Noël (1978) recorded increases in *Trinervitermes* species in man-modified habitats in a southern Guinea savanna where management practices increased the supplies of dead wood and grass. One of the most important management practices recommended by Jones et al. (2003) to help mitigate the loss of termites was leaving dead wood to decay in situ. The importance of soil type shown for termites in both study regions may reflect differences between the species' nesting and feeding strategies, as was also the assumption of Luke (2010). For instance, especially fungus-growing Macrotermitinae like *Macrotermes* spp. are known to prefer soil rich in clay particles to construct their nests and mounds (Sileshi et al. 2010). A study undertaken in the Lama Forest Reserve in Benin (West Africa) revealed the soils' water content as significant predictors of termite community composition (Attignon et al. 2005). Unfortunately, I did not measure soil water content during the diversity assessment; however, parameters like the soils' clay- or sand-content and the soils' organic matter content are known to significantly influence the soils' water holding capacity and thus also the soil water content.

The present findings appear to reflect the response of termite communities to progressing simplification of the habitat's physical structure, leading to an alteration in canopy openness, microclimate, and the loss of feeding and nesting sites. Habitat heterogeneity and stability as affected by human interference did seem to account for inter-habitat variability in species richness in several studies (e.g. Attignon et al. 2005; Bignell & Eggleton 2000; Deblauwe et al. 2008). Gillison et al. (2003) found that plant-based heterogeneity and aboveground habitat structure may predict termite diversity response to disturbance. However, neither the total abundance of fungus-growers in the Lamto reserve (Côte d'Ivoire) nor that of the dominant fungus-growing species[7] was strongly affected by habitat variability; the high ecological plasticity of fungus-growers was assumed to be the reason (Dosso et al. 2010b).

Ants

The environmental parameters identified as significant predictors of variations in the composition of ant communities were similar to those identified for termites. A great part of the variations in the composition of ant communities along the successional cross-section of the Zaï system was significantly explained by changes in the height of trees, followed by the air humidity and the clay content in the topsoil (Fig. 5-12). Similarly in the North-Sudan region, the greatest part of the variations was significantly correlated with changes in the habitats' crown-cover percentages, probably because of the greater diurnal temperature and moisture fluctuations in ecosystems with low crown-cover percentages as already stated above (Fig. 5-13). Additional predictor variables were the quantity of litter and again the height of trees (Fig. 5-13). The importance of the litter quantity is assumed to reflect differences between the ant species' nesting and feeding strategies. The leaf litter cover was also found to predict variations in ant communities in Malaysia (Luke 2010). Similar findings as in the present study were furthermore obtained by Teodoro et al. (2010) in coffee agroforests of different shade and tree diversity levels in Ecuador; relative humidity had the highest independent contribution to explain variations of ant species richness, followed by temperature, their combined effect, and crown-cover (Teodoro et al. 2010). Accordingly, a survey of ant communities along an altitudinal gradient in Peru revealed that local and regional variations were significantly correlated with temperature, relative humidity, and again their combined effect (Delgado et al. 2008). Presumably due to the close vicinity of the study sites to each other, temperature variations were not strong within a study region; moreover, in the North-Sudan region none of the habitats had a closed canopy. The finding that the height of trees appeared to be important for ants in both study regions, may also reflect differences in the habitats' physical structural complexity, and therefore presumably in the number of potential feeding and nesting sites.

Correlation between Ants and Termites

Interactions between ants and termites and their variation across a forest disturbance gradient in Malaysia were studied by Luke (2010). Ant-termite interactions appeared to play a significant role in structuring ant and termite communities at a smaller scale (in her study

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[7] *Ancistrotermes cavithorax, Microtermes toumodiensis* and *Pseudacanthotermes militaris.*

in quadrats of 16 m^2) and these interactions seemed to be altered by habitat change. Luke (2010) concluded that changes in inter-species relationships may cause declines of assemblages in human-altered habitats – in addition to the influence of changes in environmental variables. Lower predation pressure by ants on termites in teak plantations in the vicinity of the Lama Forest Reserve in Benin (West Africa) were already assumed to have contributed to the high abundance of termites (Attignon et al. 2005).

Additional insights in termite- and ant communities could also be gained via the application of our newly revised combined RAP-protocol (Chapter 3.1). In future studies, it would therefore be interesting to statistically analyse correlations between ant and termite taxa with regard to their relative abundances and their species richness across the disturbance gradients. However, some similarities can also be noticed in the findings of present study, for instance: *Anochetus sedilloti* Emery, 1884 (Ponerinae) occurred in each Zaï succession stage – however, in greater numbers only in the two Zaï forests (Table 5-3). In the North-Sudan zone, the species was only found once in the near-natural savanna (Table 5-4). *A. sedilloti* was classified as 'specialist predator[8]' (Longhurst 1977), a group comprising medium-sized to large species that are specialized to predate on other arthropods (Andersen 2000). Except for direct predation, they tend to have little interaction with other ants owing to their specialized diet and typically low population densities (Andersen 2000). In fact, in Burkina Faso, *A. sedilloti* was a medium-sized species with low to medium relative abundances. In a southern Guinea savanna in Nigeria, Longhurst (1977) observed *A. sedilloti* predating on following termite species: *Macrotermes bellicosus, Ancistrotermes cavithorax*, several *Odontotermes* and *Microtermes* species as well as wood-feeding *Microcerotermes* species. When comparing the presence of these species and genera along the two disturbance gradients of the present study, *M. bellicosus*, *Microtermes havilandi* and *Microtermes subhyalinus* were also (and almost exclusively) present in higher frequencies in those sites where *A. sedilloti* was found – and in lower frequencies also *A. cavithorax, Amitermes evuncifer* and *Amitermes guineensis* (Table 5-5, Table 5-6).

5.5 CONCLUSIONS

The combined rapid assessment protocol RAP as well as the application of only one of the two protocol-components apart (ant- or termite-transect) turned out to be very effective to representatively characterize, statistically compare, and monitor the termite and ant fauna in the near-natural savannas and agroecosystems selected in semi-arid Burkina Faso. The insights in termite- and ant communities gained via the application of this newly revised protocol are greater than the sum of insight obtained by the application of the two protocol-components (termite transect, ant transect) apart. Additional information can also be gained concerning the interaction of termites and ants, together representing the most important soil arthropods in the semi-arid tropics.

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[8] Specialist predators include solitary foragers (e.g. *Pachycondyla* species) as well as group raiders (e.g. *Leptogenys* species) (Andersen 2000).

Possible optimization of the protocol: For ants, one sampling unit generally comprises one pitfall trap (PF), one 'Winkler-site' (W), and one transect section. However, since eight ant sampling stations (each comprising one PF and one W) were installed per termite transect of 50 m length, two sampling units were identical to only one transect section. To overcome this problem in future studies, the number should be increased to 10 ant sampling stations per transect.

Plant-based heterogeneity and aboveground habitat structure may predict termite and ant diversity response to increasing land-use intensification. For rapid surveys of termites and ants, logistic efficiency may be achieved by the use of particular, readily observable plant indicators such as woody plant basal area, crown cover percentages and tree height. The quantity or availability of litter and the soil type appeared to influence the composition of both termite and ant communities.

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6. PHYSICAL ECOSYSTEM ENGINEERING – AN INTRODUCTION

The present chapter introduces Chapter 7 and Chapter 8 in which I assessed different aspects of the role of ants and (most notably fungus-growing) termites as allogenic engineers in different agro-ecosystems studied in semi-arid Burkina Faso. In order to judge the relative importance of ants and termites for soil turn-over, a standard protocol was followed to rapidly assess the quantity of soil these taxa bioturbated – without direct human intervention – to construct their epigeal soil structures (Chapter 7). In the four succession stages of the traditional restoration system Zaï in Ouahigouya (sub-Sahel region, northern Burkina Faso), a split plot design was chosen to actively attract termites with different locally available organic materials and to induce their foraging activity, aiming to quantify: i) the soil-masses bioturbated to construct sheetings when food is not a limiting resource, ii) their effect on local soil properties and iii) the effect of foraging-holes on water infiltration capacity (Chapter 8).

Agricultural processes are particularly affecting ecosystems and have been a leading cause of global biodiversity loss (Green et al. 2005) and land degradation (Bai et al. 2008). This problem will even increase in the future: Until 2050 crop production will have to increase by 70%–100% to meet the growing food and feed demand driven by human population growth (FAO 2009; Godfray et al. 2010). The combined effect of overgrazing, increasingly shorter fallow periods or even continuous cultivation, over-exploitation of natural resources and the decrease in rainfall during the last 30 to 40 years has led to a steep increase of unproductive, entirely barren land. Brady (1990) estimated that 65% of the agricultural land in sub-Saharan Africa is degraded and according to the UNEP Atlas of Desertification (UNEP 1997) almost 30% of the Sahel is affected by human-induced soil degradation. However, the opinions about the accuracy of these numbers vary greatly. For example, Somé et al. (1992) estimated that as much as 75% of Burkina Faso was suffering from important to very severe land degradation. Reich et al. (2001) estimated that 38% of the total area in Burkina Faso is moderately and 50% highly to very highly vulnerable to desertification. Mazzucato and Niemeijer (2001), on the other hand, doubted the correctness of the methodology followed to assess the global and local status of degradation and called for improved scaling-up methods. The authors urged the experts not to underestimate the abilities of local farmers and the soil and water conservation (SWC) techniques traditionally applied in Burkina Faso.

Degraded land is characterized by a tremendous loss of water through runoff due to the unvegetated, crusted soil surface which impedes water infiltration and root growth, by nutrient imbalance and reduced biodiversity causing very low to zero primary production (Maatman et al. 1998; Mando et al. 1999).

The quest for diversified, self-sustaining, low-input and energy-efficient agricultural systems with a high but sustainable level of productivity is therefore a growing concern of many farmers, researchers and policymakers worldwide (Altieri 1999; Balakrishna 2007) and calls for in-depth knowledge of biological regulations in ecosystems, and for the integration of traditional agricultural knowledge held by local farmers (Malézieux 2011). Especially in the Sudano-Sahelian areas where technical possibilities are limited and where farmers face the urgent need to increase soil fertility and the sustainability of agricultural production, it is essential to study and improve the techniques traditionally used for soil restoration and the management of agro-ecosystems.

The sustainable use of water and nutrients are of crucial importance in sustainable agriculture (Pretty et al. 2010). SWC-practices are therefore an important aspect to consider when it comes to environmental sustainability (Mazzucato & Niemeijer 2001). SWC practices refer to mechanical practices such as stone bunds and grass strips and to agronomic and biological practices such as mulching, selective clearing and adapted plant spacing. In Burkina Faso, the first mentioned mechanical practices are used on 10% of the plots according to a national survey[1] conducted in 1993; the agronomic and biological SWC practices are used throughout the country (Mazzucato & Niemeijer 2001). The challenge is to develop agricultural production systems that prevent soil degradation and simultaneously also enhance soil health (Balakrishna 2007). Doran and Zeiss (2000) defined 'soil health' as "the capacity of soil to function as a vital living system, within ecosystem and land use boundaries, to sustain plant and animal production, maintain or enhance water and air quality, and promote plant and animal health". The biological component of the soil system has a high dependence on the chemical and physical soil properties (Balakrishna 2007). Below-ground biological diversity in soils is dramatically reduced when agricultural land-use is intensified (TSBF-CIAT 2007). This can lead to a decreasing productivity and an increasing vulnerability to climatic events, erosion, pests, disease and other threats (TSBF-CIAT 2007).

Soil organisms provide services that are essential for the functioning of all ecosystems and they represent important resources for the sustainable management of agricultural systems (TSBF-CIAT 2007). Darwin already stated in 1881 that "worms have played a more important role in the history of the world than most persons would at first suppose" (Darwin 1881). With his book he laid the foundation to the scientific concept of 'bioturbation', defined as the "biological reworking of soils and sediments by all kinds of organisms including microbes, rooting plants and burrowing animals" (Kutschera & Elliott 2010). He further laid the

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[1] MARA (1996) Enquête nationale de statistiques agricoles E.N.S.A. 1993: Rapport général. Direction des Statistiques Agro-Pastorales, Ministère de l'Agriculture et des Ressources Animales, Ouagadougou.

foundation to the concept of ‘ecosystem engineering’ defined as the "modification, maintenance or creation of habitats" (Jones et al. 1994; Jones et al. 1997). Please see chapter 1.2 for examples of ecosystem engineering species.

In the tropics and sub-tropics, termites (Isoptera) and ants (Hymenoptera, Formicidae) are major examples of ‘allogenic ecosystem engineers’ (sensu Jones et al. 1997) whose activity alter the habitat and they appear to replace earthworms as soil engineers in drylands (Evans et al. 2011; Lee & Foster 1991). In sub-Saharan Africa, termites and ants represent the only active quantitatively remarkable soil macrofauna during the seven months dry season (Rouland et al. 2003; Schuurman 2006), and in the sub-Sahel zone in northern Burkina Faso termites are even the only active decomposers all year round (Mando & Brussaard 1999). They modify habitats to create an environment suitable for their own purposes. In doing so, they move through the soil and build different organo-mineral structures, so-called ‘biogenic structures’ (e.g. mounds, nests, soil-sheetings, galleries, foraging holes) (Lavelle et al. 1997).

Through soil turn-over (also called pedoturbation or bioturbation) during the construction of these biogenic structures, ants and to an even greater extent termites bioturbate huge amounts of soil masses and massively affect the soil structure, thereby essentially and positively influencing the soils’ porosity and aeration, the absorption and storage of water in soils, as well as carbon fluxes and storage (see following reviews Bignell & Eggleton 2000; Del Toro et al. 2012; Folgarait 1998; Hölldobler & Wilson 1990; Lal 1988; Lavelle et al. 1997; Lee & Wood 1971; Lobry de Bruyn & Conacher 1990; Sileshi et al. 2010; Wood 1988). According to Lavelle et al. (1997), in most tropical soils surface horizons are mainly composed of an accumulation of these biogenic structures. The biogenic structures of termites (sheetings, epigeal mounds) consist of countless agglutinated spherical or oval ‘pellets’ – depending on the constructing species with a diameter ranging between 50 µm and 1,000 µm (1 mm) (Eschenbrenner 1986). These ‘pellets’ are constructed by termite workers from exogenous material like wood and mineral soil particles (taken from subsoil or topsoil) transported by the mandibles, and organic material in the form of saliva[2] and faeces. Macrotermitinae use faeces only to construct fungus combs; in other termites faeces and exogenous particles are used in varying proportions (Noirot & Darlington 2000). As particles over 2 mm are not carried by the termites, the coarse fragments gradually concentrate at the bottom of the worked zone. Nye (1955) therefore stated that stonelines in sedentary tropical soils are generally attributed to the activity of termites.

The impact termites and ants exert via their foraging structures (sheetings, galleries, macropores) appears to be greatest in hot and seasonally dry climates (Lal 1988; Lobry de Bruyn & Conacher 1990) – similar to that prevailing in the sub-Sahel zone of Burkina Faso. In such conditions where water is a limiting resource for plant growth in non-irrigated agriculture, soil surface properties are the main parameters controlling the hydrological behavior of the soils (Casenave & Valentin 1992; Rouland et al. 2003). The manipulation and translocation of soil particles (Bagine 1984; Jouquet et al. 2002b), as well as the collection

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[2] Glycoproteins secreted with the saliva of termites cement particles together.

and procession of live and dead plant material to feed themselves (Ohiagu 1979), strongly influences the water-holding capacity and nutrient availability to nearby vegetation, thereby significantly modulating vegetation patterns (e.g. Abe et al. 2012; Del Toro et al. 2012; Jouquet et al. 2004; Konaté et al. 1999; Siegle 2009; Sileshi et al. 2010; Traoré et al. 2008). Each termite and ant species or functional group produces biogenic structures with specific properties regarding their size, texture and stability (Lavelle et al. 1997). Their impact on soil functioning is therefore very diverse and depends e.g. on the type and the total amount of the structures, its persistence over time, the engineers' diet, and the soil type (e.g. Bayen 2010; Brossard et al. 2007; Graiff 2009; Grohmann 2010; Konaté et al. 1999; Korb & Linsenmair 1999; Lee & Wood 1971; Siegle 2009). Although ants produce similar structures, most of the following description and examples will be given for termites – especially for the fungus-growing Macrotermitinae (genera *Odontotermes* and *Macrotermes*) as they will be in the focus of Chapter 8.

The nest center (so-called 'hive' or 'habitacle') and associated structures such as soil-covered runways, soil-sheetings and subterranean galleries or chambers, represent a more or less closed system which is constantly modified depending on the needs of the colony and the availability of resources (Wood 1988). Termites spend their entire existence within this nest system – except for some species that forage in the open (e.g. *Trinervitermes* species). Many different types of nests exist with many intermediate forms. Arboreal nests, especially numerous in tropical forests, are attached to tree trunks or branches and are always linked with the soil by covered galleries. Epigeal mounds are built in different shapes and sizes, ranging from a few centimeters up to several meters in height. The large epigeal mounds built by some Macrotermitinae (e.g. *Macrotermes*) are a conspicuous feature of many African savannas (e.g. Holt & Lepage 2000; Korb & Linsenmair 1999; Lee & Wood 1971). Mounds built by *Macrotermes bellicosus* on a highly weathered Ultisol of a Nigerian savanna had a total clay stock of 2,874 ± 781 kg ha^{-1} which corresponded to 2.52% of the stock in the surface horizon and an estimated clay turn-over rate of 169 kg ha^{-1} yr^{-1} (Abe et al. 2012). Other species build subterranean nests, either diffuse nests consisting of few isolated chambers only (e.g. *Microtermes*) or concentrated ones which can reach diameters of up to several meters (e.g. *Odontotermes*) (Konaté et al. 1999; Lee & Wood 1971).

Mounds and nests form a significant bank of nutrients that are temporarily withheld from plant growth. Additionally, the contents in inorganic nutrients are greater in subsoil than in topsoil, and the organic compounds of the mounds' soil are further mineralized by bacteria and fungi which are present in the mound wall (Holt & Lepage 2000). In a meta-analysis, Sileshi et al. (2010) demonstrated that – compared to the surrounding savanna soil – mounds of *Ancistrotermes*, *Macrotermes*, *Odontotermes* (family Macrotermitinae), *Cubitermes* (family Termitinae) and *Trinervitermes* (Nasutitermitinae) are significantly enriched in clay (75%), carbon (16%), total nitrogen (42%), calcium (232%), potassium (306%) and magnesium (154%). The time for release depends on their longevity and the degree of erosion. Mounds may persist in the landscape for more than two decades

(Grohmann 2010; Lobry de Bruyn & Conacher 1990; Rouland et al. 2003), some authors even suppose *Macrotermes* mounds to persist for a century (Lavelle et al. 1997).

Various types of galleries and runways are associated with nests or mounds. Subterranean galleries (also called 'tunnels') often form a dense network just beneath the soil surface. Some are vertical galleries descending down to sources of moisture in order to maintain humidity in the nest, but most are subterranean foraging galleries (Lee & Wood 1971). Foraging galleries lead the workers to the food source (wood, grass, dung, etc.) on the surface which is accessed via foraging holes ('macropores') from beneath. An example: in an area of 8,000 m^2, a single mound of *Macrotermes michaelseni* (Sjöstedt) was associated with 6 km of subterranean galleries and 72,000 storage pits (Darlington 1982) and Yakushev (1968) reported of vertical galleries descending down to a depths of 70 m. Epigeal soil-covered runways are mostly the continuation of subterranean galleries. Wood feeders in Africa (e.g. *Nasutitermes, Fulleritermes* and *Microcerotermes*) construct long, covered runways over dead wood and standing trees by mixing soil and wood with faeces (resulting in a material called 'carton'). Soil-sheetings are constructed by most termites around the food source to protect themselves against direct sun-radiation, desiccation and predation during foraging. Their construction was vividly described by Drummond (1888). Especially the fungus-growing Macrotermitinae can build large quantities of soil-sheetings within a short time; they use salivary secretions to cement (Bagine 1984) the soil particles taken from the topsoil (Jouquet et al. 2002a).

In contrast to mounds which can persist for decades, soil-sheetings erode easily and are often replaced thereby directly influencing the local physico-chemical soil properties (Bagine 1984; Holt & Lepage 2000; Wood 1988). They were therefore assumed to have a more important impact on the soil (turn-over and soil properties) than the nests (Rouland et al. 2003). In a semi-arid savanna in Senegal receiving an annual rainfall of 440 mm, nearly 47 tons per hectare were constructed after five months dry season. Lepage (1974) estimated the amount of *Macrotermes subhyalinus* soil-sheetings to range from 675–900 kg ha^{-1} yr^{-1} in a savanna in Senegal with 750 mm rain annually. More than 1.000 kg ha^{-1} yr^{-1} were recorded in Kenya (Bagine 1984; Kooyman & Onck 1987) and 2.600 kg ha^{-1} in the Chihuahuan desert (Mackay & Whitford 1988). However, in spite of the enormous amounts of soil-masses moved to construct sheetings, only few studies assessed their impact on local physico-chemical soil properties (Jouquet et al. 2005; Jouquet et al. 2002a; Ndiaye et al. 2004; Rouland et al. 2003; Siegle 2009). *Odontotermes* sheetings were found to contain more nutrients; especially the content of carbon and exchangeable cations was higher than in the surrounding soil (Jouquet et al. 2002a). And in a semi-arid savanna in Senegal increased contents in NH^{4+} and NO^{3-} were found in soil sheetings of *Macrotermes* and *Odontotermes* species thereby increasing the availability of nitrogen to plants (Ndiaye et al. 2004).

Contrary to termites, ants do not cement the dug-out subsoil material together and they neither mould it into cohesive mounds (Nye 1955). Soil material excavated by ants is therefore easily eroded by rain and wind. However, even though ants occur in exceptionally high densities, to my knowledge, there are still no data available to draw any substantial conclusions regarding the amount of soil turn-over (Lal 1988).

In spite of the wide range of services provided, surprisingly few studies have been reported on the utilization of termite and ant activity for the management of soil fertility in agro-ecosystems or for the rehabilitation of degraded soils. Most of the literature regarding the effect biogenic structures exert on local soil properties refer to epigeal mounds or subterranean nests. Numerous publications are discussing the accumulation of nutrients in termite mounds and surrounding soils (e.g. Black & Okwakol 1997; Brossard et al. 2007; Grohmann 2010; Holt & Lepage 2000; Lavelle et al. 1994; Lee & Wood 1971; Lobry de Bruyn & Conacher 1990; López-Hernández 2001; Sileshi et al. 2010).

Since the mid-70s, researchers pointed out the possibility of using termite mound debris as soil amendments in cropped savanna soils in low-input agricultural systems (Watson 1977). Due to the high nutrient contents accumulated in the large mounds of *Macrotermes* species, Watson (1977) and Dangerfield et al. (1998) have recommended the use of mound material as fertilizer in nutrient-deficient African soils. It is already described that indigenous people use such agricultural practices of improving calcium fertility by adding termite mound materials (Milne, 1947). However, to my knowledge, no study scientifically analyzed the management of ant and termite activity to increase soil fertility. It has been shown that in principle, the manipulation of soil ecosystem engineers such as earthworms can increase soil fertility and supports the restoration of degraded soils (Lavelle et al. 1997).

A very promising example for a traditional soil restoration method in semi-arid West Africa, which is making use of the positive effects termites exert on soil properties, is the Zaï practice. Zaï is a very complex soil restoration system using organic matter localization, termites to bore channels in the crusted soils, runoff capture in microwatersheds, and seed-hole cropping of sorghum or millet (David 2003; Kaboré & Reij 2004a, b; Laguemvare 2003; Reij 2012; Reij et al. 2009a, b; Roose et al. 1999; Spielman & Pandya-Lorch 2009). Recurrent droughts and repeated harvest failures in the early 1980s provoked some farmers in the sub-Sahel region of Burkina Faso to resurrect and to improve this ancient cultivation and restoration technique (Kaboré & Reij 2004b). While SWC practices usually produce benefits in the medium or long-term, the advantage of the Zaï practice is that it produces a yield already in the first year (Kaboré & Reij 2004b). A very good overview of the emergence of the improved planting pits (Zaï practice) as well as their advantages, disadvantages and impact is given in the discussion paper of Kaboré and Reij (2004b). Presently, Zaï is – despite its high efficiency and very positive short- and long-term effects – still only applied in north-western Burkina Faso. And a comparable technique called 'Tassa' is used in some regions of Niger and Mali (Slingerland & Sork 2000). Surprisingly no studies were conducted how to optimise the system by manipulating the biological component, the termite fauna – e.g. by selective attraction of specific species (or functional groups) or by fastening the successional dynamic.

6.1 ASSUMPTIONS

In the following applied part of the present thesis, I aimed at testing several assumptions.

6.1.1 Chapter 7: Relative importance of termite and ant structures for soil turn-over

1) The amount of soil naturally[3] bioturbated by termites and ants to construct their epigeal biogenic structures (nests, mounds, sheetings) will differ between the two taxa, between the two study regions (sub-Sahelian and North-Sudanese zone) and between the study sites. Other soil-dwelling macrofauna will be of minor importance for soil bioturbation, especially in the sub-Sahel region. In the more humid North-Sudanese zone, additionally earthworm structures (casts) may be found.

2) In the course of constructing their soil structures termites and ants continuously bring up soil material from deeper horizons to the surface thereby significantly altering the grain-size distribution along the soil profile. In the Zaï system, I attempt to clarify whether differences noted between the four Zaï stages could be attributed to the bioturbation activity performed by termites and ants during the past 30 years.

6.1.2 Chapter 8: Role of termites in the process of soil-restoration with the Zaï practice

3) In order to restore fully degraded soils and to sustain crop production in the sub-Sahel region of Burkina Faso where the soils' surface properties are the main parameters controlling the hydrological behavior into soils, the most interesting macrofauna-group to manage will be termites, especially the fungus-growing genera *Macrotermes* and *Odontotermes.*

4) The foraging activity of termites can be manipulated in order to multiply the amount of biogenic structures (soil sheetings, foraging-holes), e.g. by placing different locally available organic materials (hay, soft-wood, compost) on the soil surface. The magnitude or strength of foraging activity – e.g. measured via the number of foraging-holes created or the amount of sheetings built in a certain time period – will differ between the three food types.

5) The stimulation of their foraging activity will significantly increase soil turn-over (bioturbation) and positively modify the soils' structure: In the degraded land, (subterranean galleries and) foraging holes created to access the food source will break the soil crusts open; in the millet field and the two forested sites they will increase macroporosity (number of foraging-holes). As a result, the soils' water-infiltration capacity, measured by means of double ring infiltrometers (ponded water infiltration), will be significantly increased in all four Zaï stages.

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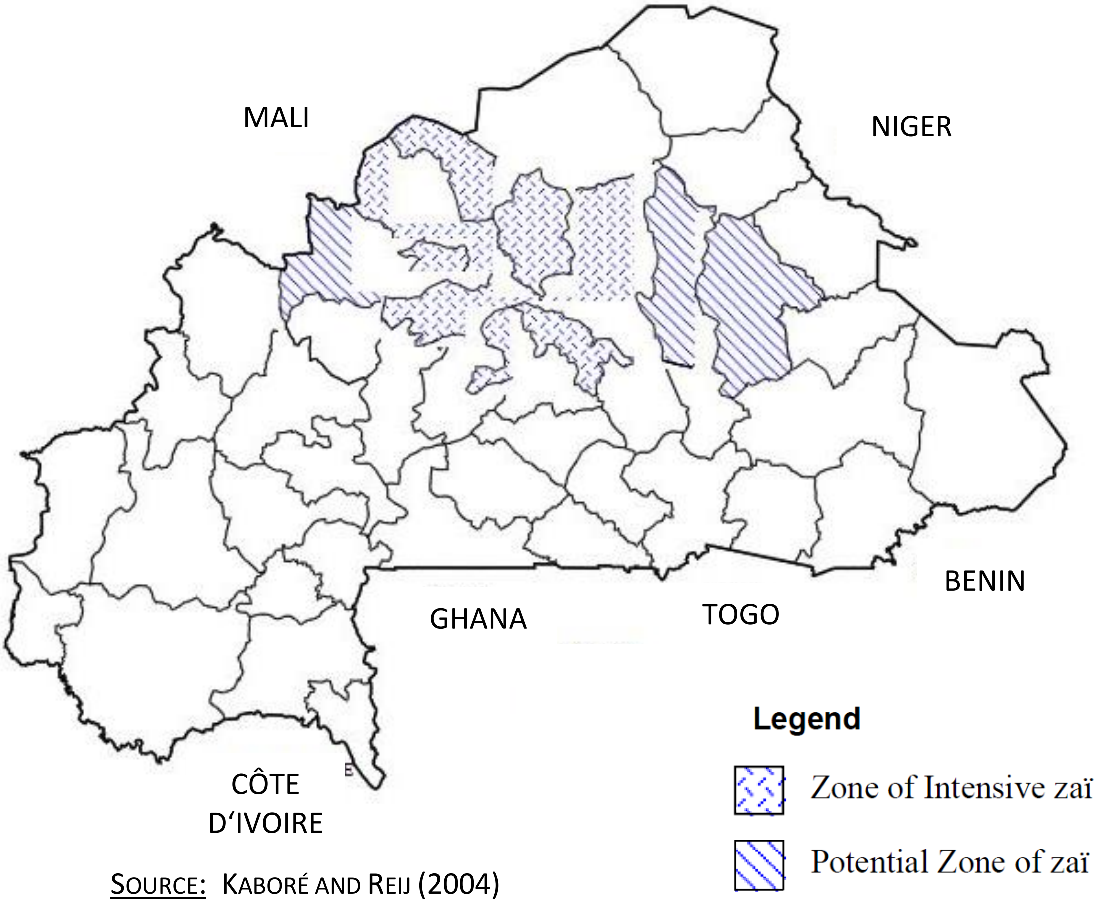
[3] 'Naturally': without human intervention such as the active attraction of termites and ants to baits.

6) The physico-chemical properties of termite-modified soil will significantly differ from the habitats' topsoil. For example, sheeting-soil will have an increased cation exchange capacity and increased nutrient contents, and *Macrotermes*-sheetings will have higher clay-contents.

7) We further assume that although the two genera *Macrotermes* and *Odontotermes* are belonging to the same functional group, the fungus-growers, the properties and quantities of their foraging structures will differ. We also want to determine differences in their foraging pattern, the food preferences, the area-to-weight relation of soil sheetings etc.



SOURCE: KABORÉ AND REIJ (2004)

Fig. 6-1: Distribution of Zaï in Burkina Faso.

6.2 REFERENCES

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7. RELATIVE IMPORTANCE OF TERMITE AND ANT STRUCTURES FOR SOIL TURN-OVER

7.1 MATERIAL & METHODS

A standard protocol was followed to rapidly assess epigeal biogenic structures (BS) of termites and ants (nests/mounds, sheetings, macropores) aiming at judging their relative importance for soil turn-over and macroporosity.

The assessment of these structures was carried out in each habitat of the sub-Sahel as well as the North-Sudan region of Burkina Faso. In 5–10 m intervals, 10–20 quadrats with an area of 1 m^2 were placed along a transect-length of 100 m. A wooden frame of 1 m^2, by means of a rope subdivided into a grid of 100 quadratic meshes (Fig. 7-1), was placed on the ground and all visible epigeal soil structures were first mapped, then collected according to the constructing taxon, genus or functional group, air-dried, and finally weighed. To account for annual climate variations, the assessment was replicated during three dry seasons (2006, 2007, 2009). In the Zaï system, one additional assessment was carried out during the rainy season 2005. The standard protocol will be referred to as 'BS-transect'; some more photos illustrating the working-steps are shown in the Appendix of Chapter 7 (Fig. A7-1 to Fig. A7-3).

Fig. 7-1: Wooden frame of 1-m^2 subdivided into a grid of quadratic meshes of 10 cm^2 area. Every 5–10 m, the frame was placed on the ground and all visible epigeal biogenic soil structures were first mapped, then collected, air-dried and finally weighed according to the taxon, the genus or the functional group affiliation.

The grain size termites are able to transport with their mandibles is restricted by the size of the mandibles; soil particles over 2 mm cannot be carried by any termite species (Eschenbrenner 1986; Nye 1955) (see explanations in Chapter 6). Between the four Zaï stages, differences could be noted in the grain-size distribution along the soil profiles: With increasing habitat restoration, coarse fragments and gravel (grain size > 2 mm) decreased in the upper horizons and became concentrated deeper along the soil profile (see Fig. 4-1 in Chapter 4). In order to verify whether these differences could be mainly attributed to the termites' soil turn-over activity, the mean dry weight of the biogenic structures was taken to roughly calculate the height of the layer possibly accumulated with termite soil since the beginning of the restoration process. In the sub-Sahel region, the rain falls in a unimodal pattern from end-May/June to mid-October; that means about 62% of the year is dry season and 38% is rainy season. The means of the 40 plots sampled in the three dry seasons were therefore taken to calculate soil accumulation for the dry season months (62% of the year), and the means of the 10 plots sampled in the rainy season 2005 to calculate the soil accumulation for the rest of the year (38%).

The following time periods were considered for the calculation:

According to the farmer, the areas of both Zaï forests were first cultivated with the Zaï technique for the duration of four years and were then left fallow – the area of the young forest for the last 16 years, the area of the old forest for the last 26 years (site history and climate see Chapter 2). For the young forest, the total height of the layer accumulated until 2009 was calculated by multiplying the annual growth (dry season plus rainy season shares) of the millet field with 4 (years of millet cultivation), and by multiplying the annual growth of the young forest with 16 (years of fallow). Accordingly, the height of the layer in the old forest was calculated by multiplying the annual growth of the millet field with 4 (years of cultivation), by multiplying the annual growth of the young forest with 16 (first years of fallow until the area of the old forest had reached a stage resembling the present stage of the young forest), and by multiplying the annual growth of the old forest with 10 (last years of fallow).

By doing so, I overestimated the amount of soil accumulated in the different time periods (4 years cultivation, 16 years fallow, etc.). For example, at the time of the BS-transects, the millet field was in the 7th, 8th, and 11th year of Zaï cultivation; however, for the two forests the means were taken to calculate soil accumulation during the first four years. Since soil turn-over increased with increasing habitat restoration, it can be assumed that soil accumulation in the millet field was lower in the first cultivation years. However, there are more reasons why this calculation should be regarded as a very rough estimation only. For instance, soil turn-over during the rainy season was only assessed once in 2005. By assuming these values for the rainy season shares of all the years between the beginning of the restoration process and 2009, the quantity might be both largely over- or underestimated. Moreover, included are only termite structures without taking into account e.g. wind-blown soil material (both out of and into the habitat), the quantity of tree litter forming humus layer, or biogenic structures of ants. Furthermore, in the two Zaï forests no *Macrotermes* mound was located in any of the 1 m^2-plots assessed along the BS-transects.

7.2 RESULTS

Epigeal soil structures were found throughout the years and in all land-use types. For each season and year, the mean dry weight of these structures was calculated in tons of soil bioturbated per hectare and month. The means for three dry seasons are illustrated as boxplots in Fig. 7-2 and Fig. 7-3 for the sub-Sahel and the North-Sudan region of Burkina Faso, respectively. Each assessment, including the one conducted during the rainy season, is also shown separately as bar plot in Appendix 7 (Fig. A7-4, Fig. A7-5). For the sub-Sahel region, termites are differentiated into the fungus-growing genera *Odontotermes* and *Macrotermes* and the grass-feeding genus *Trinervitermes*; for the North-Sudan region, they are just differentiated into fungus-growers and grass-feeders.

7.2.1 Disturbance gradient in the sub-Sahel region of Burkina Faso

In the heavily degraded soils of the Zaï system in Ouahigouya, biogenic structures of termites were found in all age stages (Fig. 7-2). Especially soil-sheetings built by the fungus-growing termite genera *Odontotermes* and *Macrotermes* during foraging seem to have an enormous influence on soil turn-over (Fig. A7-4). The mass of soil bioturbated in the course of foraging increased strongly in both seasons and all investigated years from the degraded, barren towards the most rehabilitated site, the 30 years old Zaï forest (Fig. 7-2, Fig. A7-4). The means for the dry season increase from about 1.5 kg of soil per hectare and month in the degraded area (*Odontotermes*) up to about 4 tons of soil in the old Zaï forest (*Macrotermes* and *Odontotermes*) (Fig. 7-2, Fig. A7-4). The corresponding values for the rainy season 2005 amount to 0 kg and 11.5 tons, respectively (Fig. A7-4).

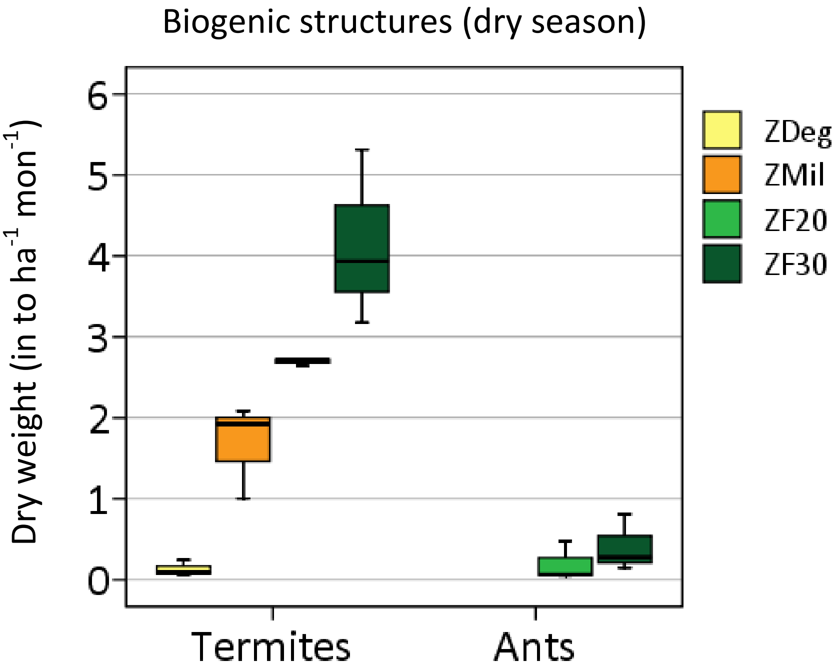

Fig. 7-2: Mean dry weight of epigeal biogenic structures (in tons per hectare and month) constructed by termites and ants during three dry seasons (2006, 2007, 2009) in 40 plots (each 1-m^2) per site. Zaï stages are ZDeg: degraded area, ZMil: millet field, ZF20: young Zaï forest, ZF30: old Zaï forest.

Ant structures, in contrast, were rare and no traces of other macroscopic soil-living organisms (e.g. earthworms) could be found. Structures of ants were only found later in the succession in the reforested sites (Fig. 7-2). The dry season means for the old Zaï forest amount to about 400 kg per hectare and month. The only biogenic structures found in the degraded bare soil originated from the fungus-growing termite genus *Odontotermes* (Fig. A7-4).

For each Zaï stage, the means were taken to calculate the annual growth of the soil layer accumulated with termite structures (mainly consisting of soil-sheetings built by fungus-growers) – on a pro rata basis for the dry season months and the rainy season months (Table A7-1). The resulting annual growth values were then used to calculate the height of the soil layer possibly accumulated between the beginning of the restoration process and 2009 (Table A7-1):

- 1.42 cm in the millet field,
- 5.46 cm in the young forest,
- 10.66 cm in the old Zaï forest.

Caution has to be exercised in the interpretation of these data; as already stressed above, this calculation contains a considerable error probability and should only be regarded as a very rough estimation.

7.2.2 Disturbance gradient in the North-Sudan region of Burkina Faso

Biogenic structures of termites and ants were found in all land-use types studied around Fada N'Gourma (North-Sudan zone) (Fig. 7-3). The main bioturbators were again fungus-growing termites (*Odontotermes* and *Macrotermes*). However, a significant part of the termite soil originated from epigeal mounds of grass-feeders (Appendix 7, Fig. A7-5).

The total mass of soil termites bioturbated per month and hectare decreased strongly in all investigated years with increasing land-use intensification, that is from the least disturbed habitats reserve and pasture towards the more intensively used habitats, the short-term fallow and cotton fields (Fig. 7-3, Fig. A7-5): The means for the dry season decrease from about 5 tons of soil per hectare and month in the protected reserve (fungus-growers and grass-feeders) down to about 0.5 tons of soil in the most intensively used cotton fields (fungus-growers) (Fig. 7-3, Fig. A7-5).

In the more humid region of Burkina Faso, especially in the protected savanna of the Pama reserve, earthworms contributed significantly to soil turn-over: Around 2 tons of soils were collected in the form of earthworm casts**.** They were also found in the pasture and the short-term fallow, although to a much lesser extent (Fig. 7-3). In relation, ant structures were more important in the disturbed habitats short-term fallow and cotton fields (Fig. 7-3). The short-term fallow had exceptionally many nests of the granivorous ant species *Messor galla*. In August 2004, about 85 nest-entrances were counted in the hectare-plot.

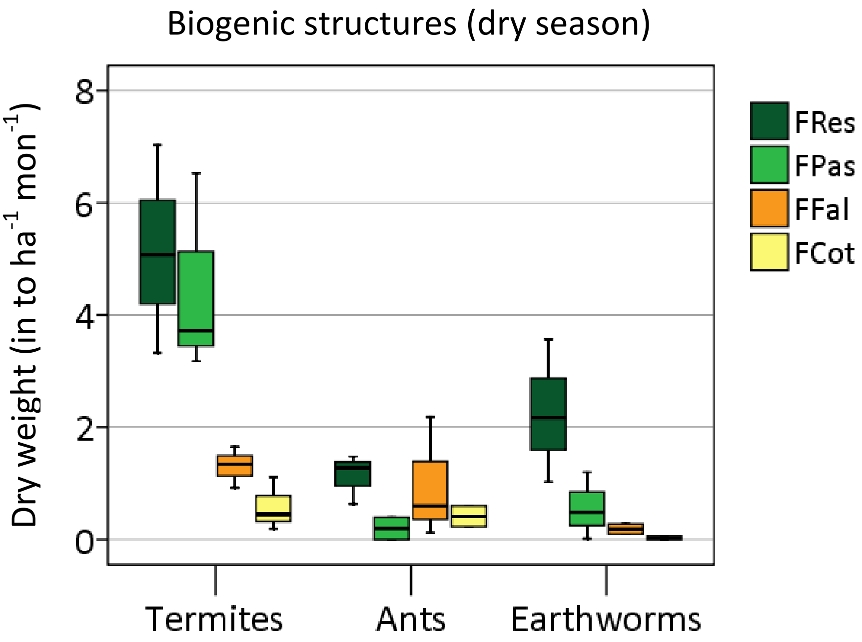

Fig. 7-3: Mean dry weight of epigeal biogenic structures (in tons per hectare and month) constructed by termites, ants and earthworms during three dry seasons (2006, 2007, 2009) in 40 plots (each 1-m^2) per site. Habitats are FRes: Pama reserve, FPas: pasture area, FFal: short-term fallow, FCot: cotton fields.

7.3 SUMMARY AND CONCLUSIONS

The main bioturbators in both regions with an enormous influence on soil turn-over were termites, especially termites belonging to the fungus-growing genera *Odontotermes* and *Macrotermes*. Ant structures seemed to be of minor importance for soil turn-over. In the heavily degraded soils of the Zaï system, no traces of other soil-dwelling macrofauna could be found. The bioturbated soil mass varied between seasons and years; the proportion between the different taxa however, that is their relative importance for soil turn-over, seemed to be fairly constant in both regions (Fig. 7-2 and Fig. 7-3). The findings of the present study confirm impressively that in arid and semi-arid regions as the degraded soils of the Sudano-Sahelian zone of Burkina Faso, termites fully take over the important function of bioturbation.

The dominant role of *Odontotermes* and *Macrotermes* in soil turn-over appears to be characteristic for many semi-arid savanna and agro-ecosystems in West Africa, e.g. Senegal (Lepage 1974; Rouland et al. 2003), Nigeria (Longhurst et al. 1978), and Niger (Léonard & Rajot 2001); in East Africa, e.g. Kenya (Bagine 1984), and in Southern Africa, e.g. Botswana (Schuurman 2006) and Namibia (Grohmann 2010). However, soil turn-over in the present study surpassed the findings of the other studies. In Kenya, about 1.3 tons of sheeting-soil ha^{-1} year^{-1} were accumulated by *Pseudacanthotermes spiniger*, *Microtermes* spp. packed around 80-180 kg soil ha^{-1} year^{-1} in maize stalks (Kooyman & Onck 1987); and *Odontotermes latericius* (Haviland) and *Odontotermes boranicus* Ghidini bioturbated soil at a rate equivalent to 1.06 tons ha^{-1} year^{-1} to construct soil-sheetings (Bagine 1984). In a Sahelian savanna of Senegal, termites translocated 675–900 kg soil ha^{-1} year^{-1} (Lepage 1974), and 2.6 tons ha^{-1} year^{-1} are reported from the Chihuahuan desert (Mackay & Whitford 1988). There are other examples in the literature (e.g. see review of Wood 1988), however, the reported soil masses were mostly lower.

Termites do not prefer special grain sizes but use the bulk soil for the construction of foraging structures (Jouquet et al. 2002a; Jouquet et al. 2002b). However, there is an upper limit for their transportation ability of about 1,000 µm, and in gravely soils distinct gravel-free soil layers may be formed upon gravel rich horizons (e.g. as seen in Awadzi et al. 2004; Christiansen & Awadzi 2000; Kooyman & Onck 1987; Nye 1955). The soil profiles in the Zaï system (Fig. 4-1 in Chapter 4) appear to illustrate this process. The study of Kooyman and Onck (1987) further revealed that pellets occurred as backfill material in tunnels and cavities, but most of all as matrix material in the soil. The authors estimated that in areas with large termite populations, the area fraction of termite pedofeatures accounts for about 20% of the soil matrix[1] (Kooyman & Onck 1987). The estimated heights of the layers possibly accumulated with termite sheetings since the beginning of the restoration process seem to support the findings of Kooyman and Onck (1987).

The higher values of soil turn-over obtained in the present study might possibly be due to the study region, the foraging termite species, more appropriate soil structures or soil depths (Nash et al. 1999), the food type (Rouland et al. 2003), the time of the year when sampling took place, the habitat type or habitat mosaic, local or regional species pools, the absence of competition with other decomposers, or more advantageous positions of subterranean nests or mounds.

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8. THE ROLE OF TERMITES IN THE PROCESS OF SOIL RESTORATION

8.1 MATERIAL AND METHODS

8.1.1 Study sites and study seasons

The role of termites as ecosystem engineers (sensu Jones et al. 1994) in the process of soil restoration was studied in a temporal cross-section of the traditional Zaï system in northern Burkina Faso (Ouahigouya, 13°32'N, -2°22'E, Yatenga province, sub-Sahel zone, mean annual rainfall about 600 mm). Zaï, a traditional soil water conservation technique to restore fully degraded, heavily encrusted lands, exists in two forms today – the agricultural and the forestry Zaï variant. To quantify soil turn-over via soil-sheetings constructed by foraging termites and to assess the effect of termite foraging-holes on water infiltration capacity, two representative age stages were chosen for each Zaï variant. A degraded, barren area (ZDeg; Fig. 8-1) was selected to represent the initial habitat form and millet fields (ZMil; Fig. 8-2) were chosen for the agricultural variant. For the forestry Zaï variant, a young forest with an age of about 20 years (ZF20; Fig. 8-3) and an old one with about 30 years (ZF30; Fig. 8-4) were selected. Please refer to Chapter 2 for a general description of the region, the Zaï technique and the habitats, and to Chapter 4 for the biotic and abiotic parameters used to characterize each Zaï stage. An overview of the general site characteristics is given in Table 8-1.

In each study site, nine experimental blocks each comprising four sub-quadrats of one square meter surface area, were used to attract termites with different, locally available organic materials and to stimulate their foraging activity. The experiment was conducted twice for the duration of four weeks – at the end of the rainy season 2005 (9.9.–10.10.05) and in the dry season 2006 (18.3.–22.4.06).

8.1.2 Biological material

The indigenous termite fauna in each of the Zaï stages has been described extensively in Chapter 5 (for the rapid assessment protocol see Chapter 5). Individuals of eight indigenous termite genera were collected in the different organic materials used to induce termite activity in the experimental plots: *Macrotermes*, *Odontotermes*, *Microtermes* and *Ancistrotermes* (all belonging to the sub-family Macrotermitinae, fungus-growing termites), *Trinervitermes* (sub-family Nasutitermitinae), *Amitermes* and *Microcerotermes* (sub-family Amitermitinae), and *Cubitermes* (sub-family Termitinae). Fungus-growing termites dominated the assemblage in all plots. The main soil bioturbators in both seasons and therefore in the focus of attention were the fungus growing termite species of the genera *Odontotermes* and *Macrotermes*.

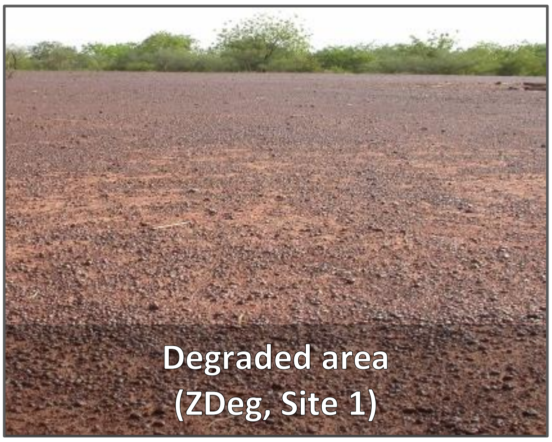


Fig. 8-1: (left) Degraded, barren land (ZDeg), almost devoid of any vegetation, representing the initial stage of Zaï restoration. **Fig. 8-2: (right)** Millet field (ZMil), representing the agricultural Zaï variant resulting from the Zaï-cultivation method and termite actions during the first years. In contrast to the Zaï forests (site 3 and 4), the farmer continued to cultivate the field after four years – in 2009, the field was in the 11th year of Zaï cultivation.

Four succession stages of the Zaï system in Ouahigouya (13°32’N, -2°22’E, Yatenga province, sub-Sahel region of Burkina Faso) chosen to determine the role of foraging termites in the process of soil restoration. Together, the sites were representing a temporal cross-section of the traditional rehabilitation technique Zaï.

Fig. 8-3: **(left)** Young Zaï forest (ZF20) and first representative for the forestry Zaï variant. **Fig. 8-4**: **(right)** Old Zaï forest (ZF30) and second representative for the forestry Zaï. The old forest was representing the last stage of Zaï restoration. About ten years of succession separated the two forests: both were first cultivated with the Zaï-method for the duration of four years and were then left as fallow, the young forest for the last 16 years, the old one for the last 26 years.

Table 8-1: General characteristics of four succession stages studied in the Zaï system in Ouahigouya, sub-Sahel region, Burkina Faso.

Short-cut	Study sites, age in 2009	Latitude Longitude	Type and history of land-use since initial degraded stage	Relative land-use intensity
First land-use intensification gradient (LUI-1), four age stages of the Zaï system in Ouahigouya, sub-Sahel region of Burkina Faso Altitude: 329 m a.s.l.; climate means for period 1998–2008: annual rainfall 660 mm, monthly temperature 19.1–39.1°C				
ZDeg 2 plots	Degraded land ≥ 30-yrs old	13°32’36”N 2°22’59”W	Habitat represents the initial stage of all Zaï stages; lateritic infertile soil; barren, crusted and impermeable soil surface; almost devoid of any vegetation; soil type ‘sandy loam’(1); 70% stones in soil samples.	highest
ZMil 2 plots	Millet field (agricultural Zaï) 11-yrs old	13°32’28”N 2°23’07”W	Agricultural fields of millet or Sorghum combined with nitrogen-fixing green beans, cultivated with the Zaï method. During the last decade, the farmer started to cultivate his fields longer than before (the Zaï forests laid fallow after four cultivation years): at the time of sampling, the fields were in the 5th, 7th and 8th cultivation year; soil type ‘loam’(1); after the harvest, grazing allowed to the farmers’ own cattle.	high
ZF20 1 plot	Young forest (forestry Zaï) 20-yrs old	13°32’35”N 2°22’54”W	First cultivated with Zaï for 4 years, followed by 16 years fallow; diverse woody and herbaceous vegetation; few areas with thin, closed canopy; degraded areas; areas with thin grass cover and isolated trees or bushes; soil type ‘loam’(1); some stone lines present. In the dry season, grazing allowed to the farmers’ own cattle and wood collection allowed to the women of the farmers’ own family.	medium
ZF30 1 plot	Old forest (forestry Zaï) 30-yrs old	13°32’25”N 2°22’56”W	First cultivated with the Zaï-method for 4 years, followed by 26 years fallow; diverse woody and herbaceous vegetation, mostly with thin but closed canopy; very few degraded areas; areas with dense and with thin grass cover; soil type ‘sandy loam’(1); some stone lines present; no wood collection or grazing allowed during the last 10 years (before as in ZF20).	low

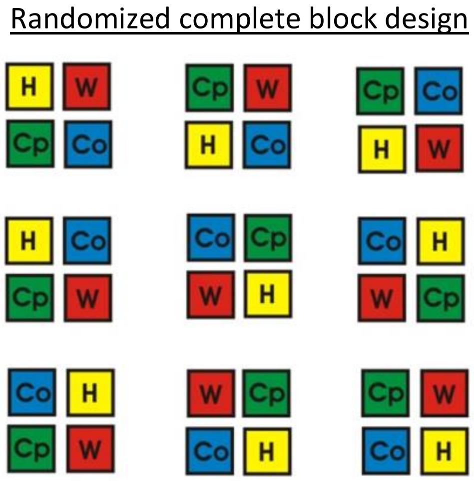
(1) Mean of all topsoil-samples taken in the habitat (0–10 cm); please refer to Chapter 4.3 for the biotic and abiotic habitat parameters.

Fungus-growing termites construct elaborate foraging tunnel networks and either large epigeal mounds (*Macrotermes*) or subterranean nests (*Odontotermes*), mostly within 25–50 cm of the soil surface (Black & Wood 1989; Jouquet et al. 2004), but frequently venture to deeper horizons to gather clay-rich material used to construct the complex, self-supporting nest structures (Holt & Lepage 2000; Lee & Wood 1971). They collect large quantities of plant material from different origins to cultivate fungal crops (genus *Termitomyces*, Basidiomycotina). The fungus grows enclosed in chambers within the termite nest on so-called fungus combs, structures built by the termites consisting of harvested plant litter (e.g. Aanen & Eggleton 2005; Aanen et al. 2002; Koné et al. 2011; Rouland-Lefèvre 2000; Rouland-Lefevre et al. 2002). *Termitomyces* is found as mycelium in the fungus comb and as round white asexual structures (mycotêtes) on the comb surface (De Fine Licht et al. 2005). The fungus combs are continuously provided with plant substrates whereas older parts that have been well degraded by the fungus are consumed (De Fine Licht et al. 2005; Hyodo et al. 2000). The termite nests are constructed to offer optimal growth conditions for the fungus, for example in the case of *Macrotermes bellicosus* in the Côte d'Ivoire: all year-round a constant nest temperature of about 30°C and humidity near saturation (Korb & Linsenmair 1998a, b). The agricultural symbiosis between termites and fungi is one of the most spectacular examples of mutualistic symbiosis and is pivotal to the success of the Macrotermitinae. Cultivating fungi has allowed fungus-growing termites to become one of the most important decomposer groups in the Old World tropics (Visser 2011). In areas of low annual rainfall as in the study area, they even represent the predominant decomposer organisms (Aanen & Eggleton 2005; Mando & Brussaard 1999). Please refer to Appendix 4B for photos of epigeal mounds built by fungus-growing termites of the genus *Macrotermes* and their internal architecture (Fig. A4-6 to Fig. A4-11).

Taxonomic identification: All collected termite samples were taxonomically identified to the level of species or morphospecies by Tra-Bi Crouland (Université de Cocody-Abidjan UCA, Station d´Écologie Tropicale de Lamto, Côte d'Ivoire). Please refer to Chapter 3 ('General Methods') for further information.

8.1.3 Experimental design to attract termites and to stimulate their foraging activity

The experiment was conducted twice for the duration of four weeks, once in the rainy season 2005 and once in the dry season 2006. A randomized complete block design was used as experimental design. For each run, nine blocks of about 4 x 4 m were randomly distributed in each of the four Zaï stages (Fig. 8-5, Fig. 8-6). Each block comprised four sub-quadrats of one square meter surface area where different, locally available organic materials were applied to attract foraging termites: 1.5 kg of *Aristida kerstingii* hay (H), 3 kg of *Bombax costatum* wooden blocks (W), 9 kg compost used by the farmer (Cp) and a control (Co) without any amendment (Fig. 8-5, Fig. 8-6). In total, 144 sub-quadrats were installed – 36 per habitat.


Randomized complete block design

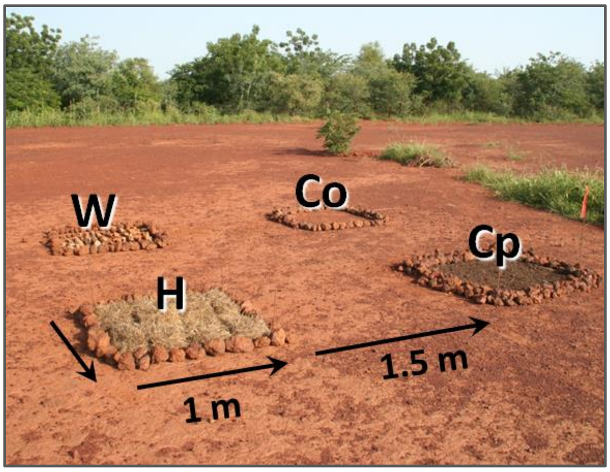


Fig. 8-5: (left) Nine block-replicates were installed in each of the four Zaï stages, each comprising four sub-quadrats with different, locally available organic material: W: *Bombax costatum* wood, H: *Aristida kerstingii* hay, Cp: compost used by the farmer, and a Co: control without any amendment. In total, 144 sub-quadrats were installed (36 per habitat).

Fig. 8-6: (right) One experimental block located in the degraded, barren area (ZDeg).

Since the materials used to attract termites differed in their density (dry weight per volume) and their nutritional value, we decided to take the amount needed to cover the whole quadrat area and to calculate the amount of bioturbated soil per gram organic material afterwards. Before weighing, care was taken that the material was homogeneous with regard to its consistency and humidity.

An area of 1.5 to 2 m was separating the four sub-quadrats from each other to facilitate unhindered inspection on the one hand and to avoid any influencing effects while assuring similar physico-chemical soil properties for the whole block on the other hand. Stone lines were placed around each sub-quadrat as barrier against material loss during rain fall (Fig. 8-6). As stone lines can change the microclimatic conditions for soil-dwelling organisms thereby possibly influencing their foraging behavior, they were also placed during the dry season run. However, due to freely grazing cattle during the dry season, it was necessary to additionally protect the hay quadrats by barriers made of spiny branches (e.g. *Acacia* spp., *Balanites aegyptiaca*). Please refer to Appendix 8 for more photos of the experimental plots (Fig. A8-1).

To determine the potential production capacity of soil-sheetings in the four sites when food is not a limiting resource, all organic amendments were offered in excess. The availability of the organic materials in the sub-quadrats was checked daily. In case of complete consumption of the offered hay, new material was added throughout the experimental 4-week duration. Especially during the dry season, some of the hay quadrats in the two forest sites had to be replaced in short intervals – in extreme cases even daily.

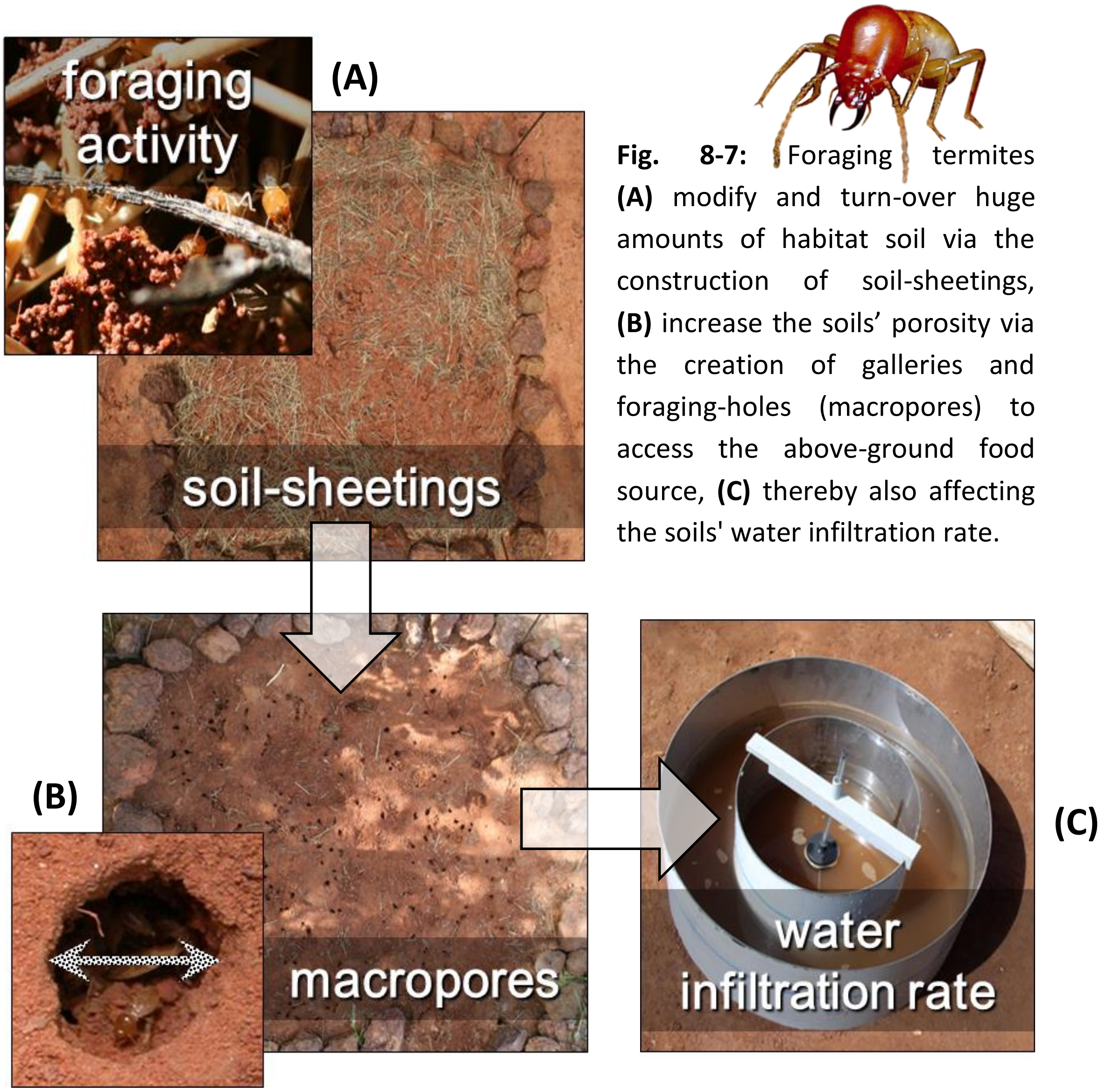


Fig. 8-7: Foraging termites **(A)** modify and turn-over huge amounts of habitat soil via the construction of soil-sheetings, **(B)** increase the soils' porosity via the creation of galleries and foraging-holes (macropores) to access the above-ground food source, **(C)** thereby also affecting the soils' water infiltration rate.

To summarize, the experiment was designed to determine the effect of termites on:

➢ Soil turn-over *via* soil-sheetings	(Fig. 8-7 A)
➢ Soil porosity *via* foraging-holes (macropores)	(Fig. 8-7 B)
➢ Ponded soil water infiltration	(Fig. 8-7 C)
➢ Physico-chemical soil parameters	

While paying attention to potential influences of the following parameters:

- Season
- Zaï stage
- Organic material
- Termite genus

8.1.4 Parameters assessed throughout and at the end of the experimental duration

As measure of foraging activity and to quantify the soil bioturbation activity, the increase of the area covered by sheetings was chronologically followed: all visible sheetings were mapped on millimeter paper and – due to easily recognizable granular structure – assigned to the respective termite genus (Fig. 8-8). The differences between the granular structure of soil-sheetings built by *Odontotermes* and *Macrotermes* are shown in Appendix 8 (Fig. A8-2; Fig. A8-3). A wooden frame with an area of 1 m^2 was placed on top of the quadrats. To facilitate the mapping process, the frame was subdivided in 100 units of 10 x 10 cm with a rope.

The quadrats were checked for foraging termites; specimens of all species encountered were stored in 90% ethanol for later identification. When all sub-quadrats in the four sites had been mapped, a new ‘control-cycle’ was started. In the rainy season, ending the control of all plots during a cycle was often hindered by rainfalls which destroyed most of the soil sheetings. Rain events always required the start of a new control-cycle. In the dry season on the other hand, several control-cycles could be completed during which all sub-quadrats in the four sites were mapped at least once.

The surface area of the mapped sheetings was determined afterwards in the program ArcView GIS 3.2a (ESRI, Environmental Systems Research Institute Inc.).

<u>After four weeks all blocks were ended:</u>

1. All sheeting soil was collected, air dried and weighed according to the different termite genera; samples of the sheetings were taken and stored for later analysis in the laboratory (Fig. 8-7 A).
2. The foraging-holes were counted and their diameter measured (Fig. 8-7 B).
3. Samples of the topsoil (0–10 cm) were taken from each sub-quadrat, air dried and stored for laboratory analysis.
4. Additionally, soil water infiltration was measured in selected quadrats (with less than 600 macropores per m^2) with double ring infiltrometers (Fig. 8-7 C).

Before adding new hay to a quadrat in case of complete consumption, the same procedure (step 1 and 2) was followed – all soil-sheetings were collected and the macropores counted.

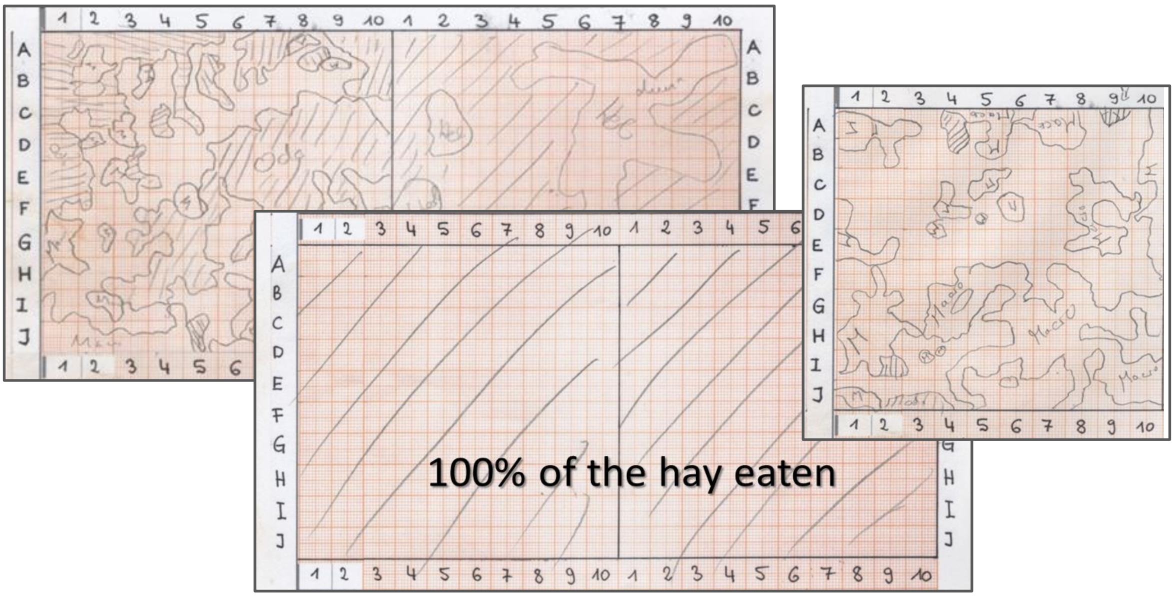


Fig. 8-8: In each sub-quadrat, the increase of the area covered by soil-sheetings was chronologically followed: all visible sheetings were mapped on millimeter paper and, due to easily recognizable granular structure, assigned to the respective termite genus. Differences between the granular structure of soil-sheetings built by *Odontotermes* and *Macrotermes* are shown in Appendix 8 (Fig. A8-2, Fig. A8-3).

8.1.5 Sample preparation and analysis of the organic materials used to attract termites

The hay-sample (*Aristida kerstingii*) was grinded twice by means of an Ultra Centrifugal Mill type ZM 1 (ring sieve with 2.0 and 0.2 mm perforation; Co. Retsch, Haan, Germany). The compost-sample (dry, earthy-structure with parts of animal feces with Ø 0.5 cm) was crushed for 10 min with a micro-mortar grinder (Retsch, Haan, Germany) and was then sieved through a 2 mm-screen. The residue was discarded. A Forstner-drill was used to produce chips from the wood-samples (*Bombax costatum*). The chips were grinded by means of an Ultra Centrifugal Mill type ZM 1 (Co. Retsch, Haan, Germany). Soil-samples were mixed thoroughly and any remaining hay-particles within the samples were sorted out. Sub-quantities were then taken with a spatula.

For a detailed description of the physico-chemical parameters analyzed and the methods used in the laboratory, please refer to Chapter 4.2.

8.1.6 Measuring soil water infiltration with double ring infiltrometers

The double ring infiltrometer is a simple instrument used to determine the rate of infiltration of water into the soil and consists of an inner and outer ring; both inserted about 5 to 10 cm into the ground (Fig. 8-7, Fig. 8-9). A number of soil hydrological features can be determined (per soil layer), namely the Infiltration capacity, the near-saturated hydraulic conductivity, the infiltration curve and the cumulative infiltration over a certain period.

The term soil water infiltration refers to the downward entry of water into the immediate surface of soil. The infiltration rate is determined as the amount of water per surface area and time unit that penetrates the soil. The infiltration rate can be calculated on the basis of the measuring results and the Law of Darcy and is limited by the capacity of the soil and the rate at which water is applied to the surface (http://en.eijkelkamp. com). The maximum rate at which water can infiltrate into a soil under a given set of conditions is termed 'infiltration capacity'. Water infiltration decreases with time due to changes in surface and subsurface conditions and, overtime as the matrix potential decreases and gravity forces dominate, thereby causing a reduction in the infiltration rate. Soil factors that control the infiltration rate are the soils' porosity and permeability, the vegetative cover, root development and organic content, its moisture content, the texture and structure, bulk density and compaction as well as the topography (slope, position in the landscape).

Therefore, to assess the influence of the foraging-holes on water infiltration, measurements had to be taken simultaneously in sub-plots with recent foraging activity (hay-, wood-, compost-plots) and without (control-plot) (Fig. A8-4 in Appendix 8). The difference between the two sub-plots was then assigned to the newly established macropores.

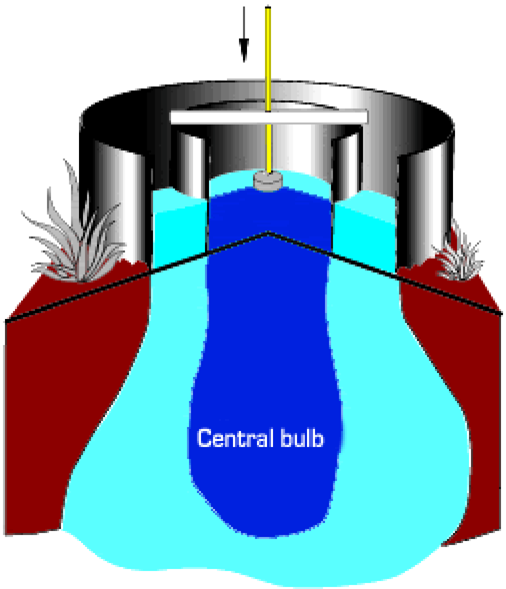


Fig. 8-9: Schematic diagram showing the vertical flow that is generated from the inner ring (http://en.eijkelkamp.com).

Once the double rings were set in position and knocked into the ground, water was filled up in the rings without disturbing the soil surface – first in the outer, then the inner ring. As vertically infiltrated water also runs away to the sides, the outer ring serves as a separation accounting for all the lateral flow. By allowing water in the inner ring to flow nearly exclusively straight down, the outer ring virtually turns a 3-dimensional single ringed system of looking at infiltration into a one-dimensional. The schematic diagram in Fig. 8-9 illustrates this one-dimensional, vertical flow of water that is generated from the inner ring. If water is flowing in one-dimension at steady state condition, the infiltration rate is approximately equal to the saturated hydraulic conductivity.

All measurements exclusively take place in the inner ring. To fill the inner ring, the water was poured over the hand which was removed quickly once the desired level of water was reached. At this point, the time and the water level were recorded as the start of the infiltration measurement. The rate of infiltration is determined by the amount of water that infiltrates into the soils per surface area (parameters of the inner ring) per unit of time. The volume of water needed to maintain a specified level and the time factors were recorded. The information was then converted into the specific infiltration rate by using a data sheet that was provided with the rings. These data points were plotted in a graph of infiltration versus time. The rate, at which water penetrates the surface of the soil, is commonly expressed in millimeter or centimeter per hour (mm hr^{-1} or cm hr^{-1}).

As soon as the water in the outer ring started to leak sideward at the rings' base, *Macrotermes* mound-soil was used to seal the base of the outer ring. In most infiltration runs, the clayey mound-soil had to be applied at some point of the measurement. Therefore, before the start of the infiltration runs, soil of dead *Macrotermes*-mounds was collected, thoroughly grinded and filled in plastic bags (see Fig. A8-4 in Appendix 8).

Stopping-rule

An infiltration measurement process was stopped, when a steady state was reached and the infiltration rate had reached a constant value. That is, when the variation of the infiltration rate was smaller than 10% for the last 3 to 5 measurements. Depending on the type of soil this may occur within 2 hours or after a day. In the Zaï system sites, most of the infiltration runs took between 4 and 8 hours and 200 to 400 liters water, in extreme cases even 600 liters.

The water from the well of the community was filled in 200 liter barrels and was then transported to the field with donkey carts. There the water was filled in 20 liter plastic-canisters which were used to pour water into the rings (see Fig. A8-4).

Problems related to the use of infiltrometers are:

1. Pounding of the infiltrometer into the ground can deform the soil causing cracks and increasing the measured infiltration capacity.
2. Natural rainfall reaches terminal velocity. Also natural droplet sizes differ with different types of storms. Pouring water from a canister however loses this momentum and variance.
3. The method is very time consuming, requires permanent attention, either by recording measurements or by maintaining equilibrium in the height between the rings.

4. The infiltration rate varies with different soil types, which can affect the accuracy of the results. (Source: www.sdec-france.com; http://en.eijkelkamp.com).

8.1.7 Statistical analysis

A two-way between-groups analysis of variance (SPSS 15.0) was conducted to explore the impact of Zaï stage and food type on the dry weight of sheetings per square centimeter area. Post-hoc comparisons were performed with the Tukey HSD test. Correlation tests were carried out to determine the relationship between the different foraging parameters. Shapiro-Wilk test was used to assess whether the data of physico-chemical soil-parameters were normally distributed. Except very few cases, all data were normally distributed. Homogeneity of variances was tested using Levene's test. Levene's test was non-significant thereby indicating that the variances of the sheeting or topsoil data were equal. As the assumptions for parametric tests were met, paired-samples *t* tests were performed to compare the different sample-types. The non-parametric Wilcoxon test was used for the few non-normal distributions.

All statistical tests were performed at the 0.05 significance level and were carried out using SPSS 15.0 for Windows. All Zaï stages were included in the analysis.

8.2 RESULTS

The foraging activity on the experimental plots was monitored twice for the duration of four weeks – in the rainy season 2005 (09.09.–10.10.) and in the dry season 2006 (18.03.–22.04.).

In the dry season run, seven 'control-cycles' could be completed during which the blocks in all sites (144 sub-quadrats) were mapped at least once. Each block was thus surveyed every 4–5 days. Some of the hay quadrats which had to be replaced following their complete consumption were mapped in shorter intervals, in extreme cases even daily. In the rainy season, however, rain events often hindered the completion of a mapping cycle as most of the soil-sheetings were – at least partly – destroyed afterwards. As a result, sheetings could not always be allocated to the constructing termite genus. Furthermore, although the erosion process could be slowed down by surrounding the quadrats with stone lines, unknown quantities of sheeting-soil were lost. Most of the following analyses were therefore exclusively made with data from the dry season run. The effect of termites on physico-chemical soil properties and on the water infiltration capacity, however, was analysed for both seasons.

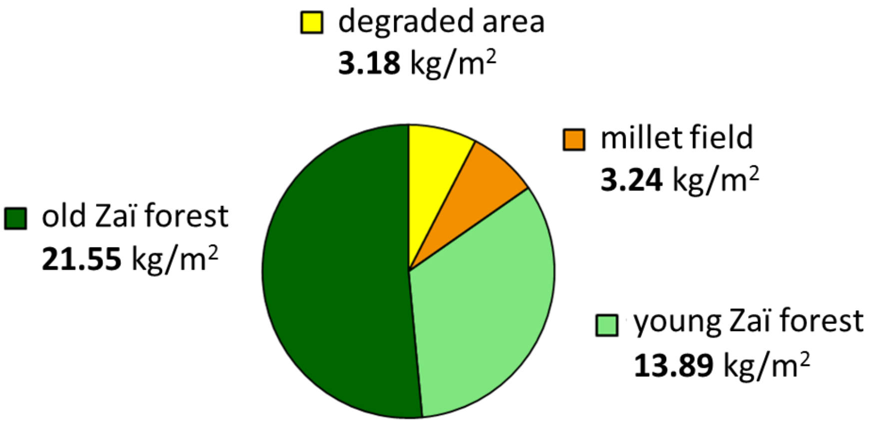


Fig. 8-10: Cumulated soil-sheeting dry weight in kilogram and square meter after four weeks. In each Zaï stage, all 36 sub-quadrats and termite genera were combined.

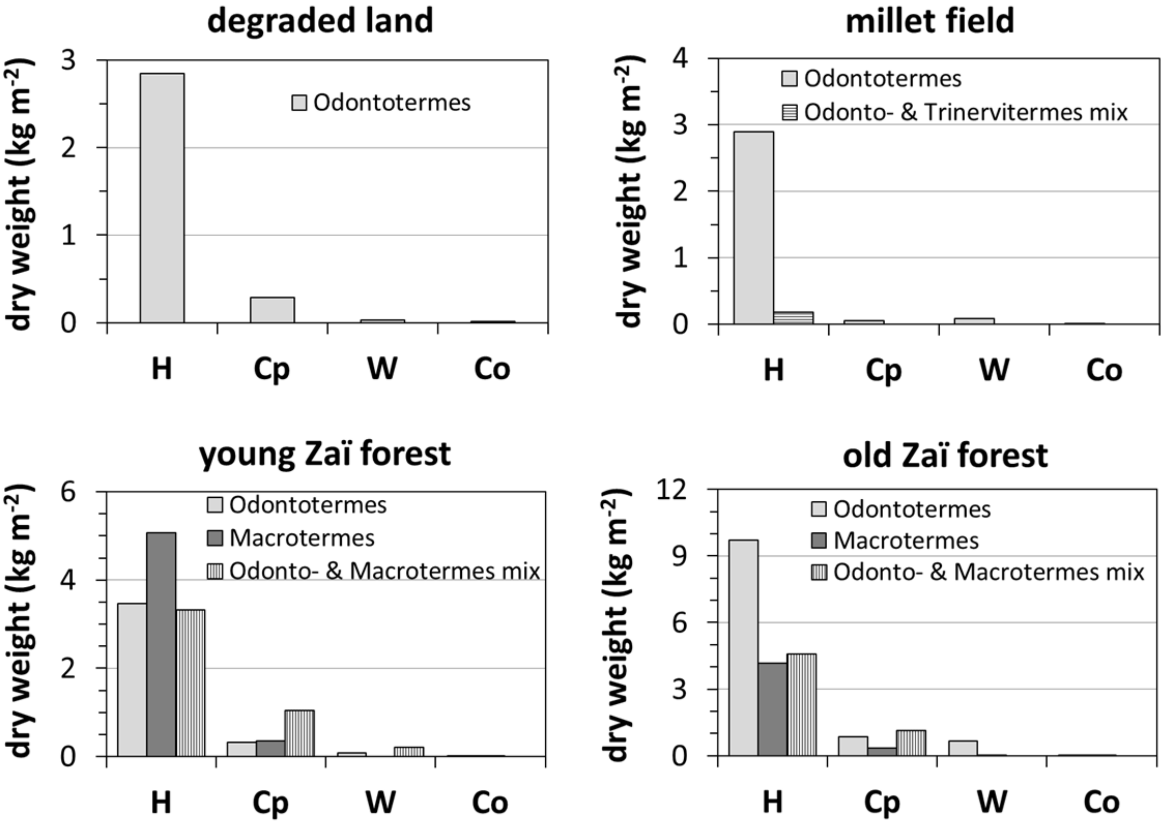


Fig. 8-11: Cumulated soil-sheeting dry weight (in kg m^{-2}) after 4 weeks, shown per Zaï stage according to the different organic materials and termite genera.

Organic materials are hay (H), compost (Cp), wood (W), and control (Co).

8.2.1 Soil turn-over *via* soil-sheetings

8.2.1.1 Quantity of soil brought to the ground surface by foraging termites

After 4 weeks, the total quantity of soil used by termites to construct the protecting soil-sheetings in the experimental blocks was calculated. For each Zaï stage, the cumulated dry weight of sheeting-soil in kilogram per square meter is first shown for all plots and all termites combined (Fig. 8-10) and secondly, differentiated according to the different organic materials and termite genera (Fig. 8-11).

With increasing habitat restoration, an increasing quantity of soil was bioturbated by foraging termites (Fig. 8-10). For example after 4 weeks, the total dry weight of soil-sheetings constructed by termites in 36 sub-quadrats of the degraded area (ZDeg) was 114.48 kg, which is 3.18 kg per square meter. In the millet field (ZMil), the equivalent amount of soil bioturbated per square meter was 3.24 kg. In the young (ZF20) and the old Zaï forest (ZF30), the bioturbated soil amounted to 13.89 kg and 21.55 kg, respectively (Fig. 8-10).

Termites of the genus *Odontotermes* were foraging in all four succession stages; especially high was the activity in hay-quadrats (Fig. 8-11). All termites foraging in the degraded area and except for one quadrat on one day also in the millet field belonged to the genus *Odontotermes* (Fig. 8-11).

Therefore, in the Zaï system studied in Ouahigouya, *Odontotermes* was the pioneer-genus, initiating the restoration process (Fig. 8-11). Termites of the genus *Macrotermes* were foraging in the young and the old forest (Fig. 8-11). Together, the two genera were constructing all of the sheetings that were collected in the two Zaï forests – *Macrotermes* slightly more in the young forest, *Odontotermes* slightly more in the old forest (Fig. 8-11).

8.2.1.2 Soil turn-over per gram foraged material

All sheetings were collected and weighted at the end of the experiment. In the hay-plots, sheetings were collected as soon as the offered quantity of 1.5 kg hay per quadrat was completely consumed. A measure of soil turn-over is obtained when calculating the dry weight of sheetings with regard to the quantity of the organic material eaten.

However, several difficulties were encountered when collecting the compost and wooden blocks that were not eaten until the end of the experiment. Galleries within dead wood were partly filled with sheetings what made the separation extremely difficult. When taking soil samples within compost plots, some of the finer material had been fallen through the macropores into the galleries constructed below the experimental plots. Problematic was also the separation of soil-sheetings and compost rests; some of the sheeting-soil had sometimes been left in the remaining compost. All of these difficulties could potentially have given a false result in terms of the exact quantity of the remaining material. In hay-plots, no significant difficulties occurred. Therefore, for sheetings constructed by the genera

Odontotermes and *Macrotermes* in hay, the dry weight per gram foraged hay is illustrated for each study site (Fig. 8-12).

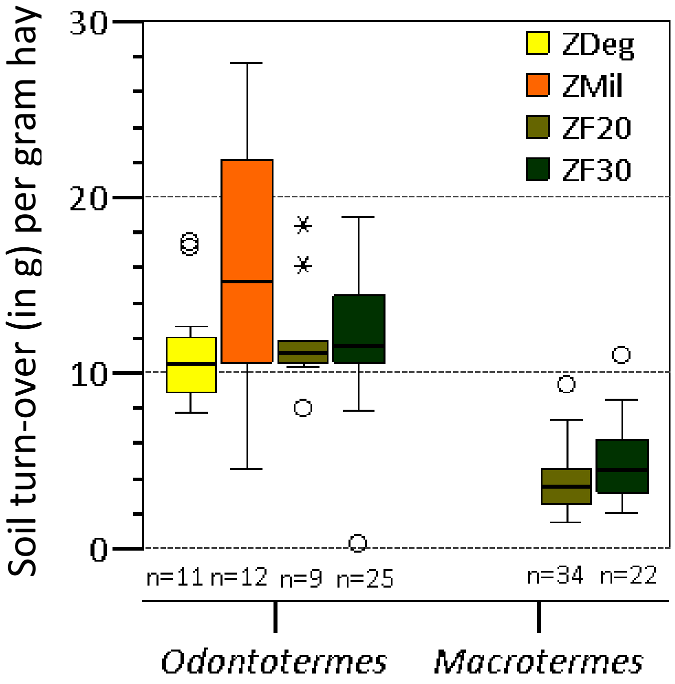


Fig. 8-12: The sheeting dry weight (in g) per gram hay eaten is given for both genera (*Odontotermes*, *Macrotermes*) for all hay-plots per study site (dry season 2006). Study sites are ZDeg: degraded land, ZMil: millet field, ZF20: young Zaï forest, ZF30: old Zaï forest.

Roughly summarized the figure indicates that for 1 g hay that was removed, *Macrotermes* bioturbated around 4 g soil, *Odontotermes* about three times as much i.e. around 12 g soil – irrespective of the study site (Fig. 8-12). Variations for *Odontotermes* were largest in the millet field (ZMil) (Fig. 8-12).

8.2.1.3 Dynamics of foraging and soil-sheeting establishment

The activity in the experimental blocks was checked regularly. As measure of foraging activity, soil-sheetings constructed in the plots were mapped and assigned to the respective termite genus. In the dry season run, seven 'control-cycles' could be completed during which the blocks in all sites (144 sub-quadrats) were mapped at least once.

Soil-sheeting establishment in single hay-plots

Since *Macrotermes* foraged only in the two Zaï forests, I will describe the dynamics of soil-sheeting establishment for the nine hay-plots in these forested sites. During the 4-weeks of the dry season run in the young forest, *Odontotermes* foraged alone in four hay-quadrats, *Macrotermes* in one. In two hay-plots, *Odontotermes* started to forage alone in the beginning and was then replaced by *Macrotermes* in one plot, in the other one both genera fed together after the arrival of *Macrotermes*. In the last two hay-quadrats of the young forest, both genera started to forage together but in one plot, *Macrotermes* displaced *Odontotermes* after a while and fed alone thereupon for the rest for the experiment. Correspondingly, the hay-quadrats of the old Zaï forest: In one hay-plot, each genus fed alone for the whole experimental duration. In two plots, both genera foraged together in the beginning and *Macrotermes* displaced *Odontotermes* after a while. In four hay-plots, *Odontotermes* started to forage alone in the beginning and both genera fed together upon the arrival of *Macrotermes* – in three of these four plots, it took 2–3 weeks until *Macrotermes* located the food source; in the fourth hay-quadrat, *Macrotermes* arrived early, foraged together with *Odontotermes* for a while, displaced *Odontotermes* in the end and foraged alone thereupon. Only in one plot, *Macrotermes* foraged alone most of the experimental duration and simultaneously with *Odontotermes* after their arrival. Examples for the increasing dry weight and area of sheetings constructed during the 4-weeks are shown for three single hay-plots in Appendix 8 (Fig. A8-5 to Fig. A8-10). The cumulated quantity of hay consumed during this time is shown in the figures illustrating the cumulated dry weight, the number of macropores created in those illustrating the sheeting-area.

Cumulated soil-sheeting establishment in all replicate plots

To give an overview over the whole bioturbation activity during the experimental duration according to food type (wood, hay, compost, control) and restoration stage (ZDeg, ZMil, ZF20, ZF30), the sheeting-area of all replicate plots was cumulated for each control-cycle. Replicate plots are all sub-quadrats within a study site that are covered with the same food type (*N* = 9). The dynamics of sheeting establishment is first illustrated for both genera in total (Fig. 8-13 to Fig. 8-15), then separately for *Odontotermes* (Fig. 8-17 to Fig. 8-19) and *Macrotermes* (Fig. 8-21 to Fig. 8-23). Equivalent figures for all soil-sheetings built by *Odontotermes* and *Macrotermes* together (sheeting-mix), which could not be separated into sheetings built by *Macrotermes* and sheetings built by *Odontotermes,* are shown in Appendix 8 (Fig. A8-11 to Fig. A8-14). These latter sheetings which could not be separated into the constructing taxa will be called ‘sheeting-mix’ henceforth. The restoration stages in Fig. 8-13 to Fig. 8-23 are differently colored: Sheetings constructed in the degraded area (ZDeg) are in yellow, those in the millet fields (ZMil) in orange, sheetings in the young and the old Zaï forest (ZF20, ZF30) in light green and dark green, respectively.

The total sheeting-area as well as the dynamics of their construction in wood, hay and compost when cumulating all sheetings constructed by the two genera, was similar in the two Zaï forests (Fig. 8-13 to Fig. 8-15). However, when looking at the genera separately, the dynamics and the size of the area covered differs clearly (Fig. 8-17 to Fig. 8-23). *Macrotermes* foraged only in the forests (Fig. 8-21 to Fig. 8-23). The areas covered by sheetings in the first two succession stages (ZDeg, ZMil) are thus identical in the figures illustrating all sheetings in total (Fig. 8-13 to Fig. 8-15) and those of *Odontotermes* alone (Fig. 8-17 to Fig. 8-19). The total area *Odontotermes* covered with sheetings increased with increasing habitat restoration (Fig. 8-17 to Fig. 8-19).

Only during the last week, the cumulated area in the hay- and control-plots of the millet field surpassed those of the young forest (Fig. 8-17, Fig. 8-19). In the hay- and compost-plots of the old forest, *Odontotermes* workers covered about twice of the area they covered in the young forest (Fig. 8-17, Fig. 8-19); in wood, the area was about one third larger in the old forest (Fig. 8-17). During the first week of the experiment, the total area covered by *Macrotermes* in the hay-plots had the same size in both forests; in the following three weeks, the cumulated area in the old forest was increasingly larger (Fig. 8-21). The total sheeting-area *Macrotermes* constructed in the compost-plots of the young and the old forest had the same size during the first two weeks of the experiment; however, in the remaining two weeks, the cumulated area was increasingly larger in the young forest (Fig. 8-23). It took almost three weeks before *Macrotermes* started to construct sheetings in the wood-plots of the young forest (Fig. 8-21).

The cumulated soil turn-over within a site was always highest in hay, followed by compost, then by wood and in the end control (Fig. 8-13 to Fig. 8-23). For example in the old forest, when looking at both genera in total, sheetings in hay covered about two-times the area than those built in compost and ten times the area than those built in wood (Fig. 8-13 to Fig. 8-15). The cumulated area covered by *Odontotermes*-sheetings in the old forest was four times larger in hay than in wood and still one third larger in hay than in compost (Fig. 8-17 to Fig. 8-19). The sheeting-area constructed by *Macrotermes* in all hay-plots was even 25 times larger than the area constructed in wood and still more than three times larger than the area constructed in compost (Fig. 8-21 to Fig. 8-23). Furthermore, in all food types that were offered, the activity of *Odontotermes* started fastest in the two forests. And, except for the compost-quadrats, it took always longer in the degraded area than in the millet field. In the degraded land, it took almost 3 weeks until *Odontotermes* started to construct sheetings in wood-plots at all (Fig. 8-17).

To facilitate the direct comparison of the foraging activity between the two fungus-growing genera within a Zaï stage, the cumulated increase in sheeting-area constructed during the 4-weeks duration is additionally shown per sheeting-type (*Macrotermes*, *Odontotermes*, sheeting-mix and in total) – for each food type offered in the young and in the old Zaï forest (Fig. A8-15 to Fig. A8-22; Appendix 8). In these figures, different grey-scales are used for each sheeting-type: Sheetings of *Odontotermes* and *Macrotermes* in total are dark grey, the ‘sheeting-mix’ is white; sheetings of *Odontotermes* and *Macrotermes* have grey scales in between.

To summarize, at any time and in all food types offered in the old forest, the cumulated sheeting-area constructed by *Odontotermes* was always larger than the area built by *Macrotermes*. Least differences between the two genera were noted in hay (A8-15 to Fig. A8-18). In the young forest, the cumulated area covered with *Macrotermes*-sheetings in hay surpassed the cumulated area covered with *Odontotermes*-sheetings (Fig. A8-19 to Fig. A8-22).

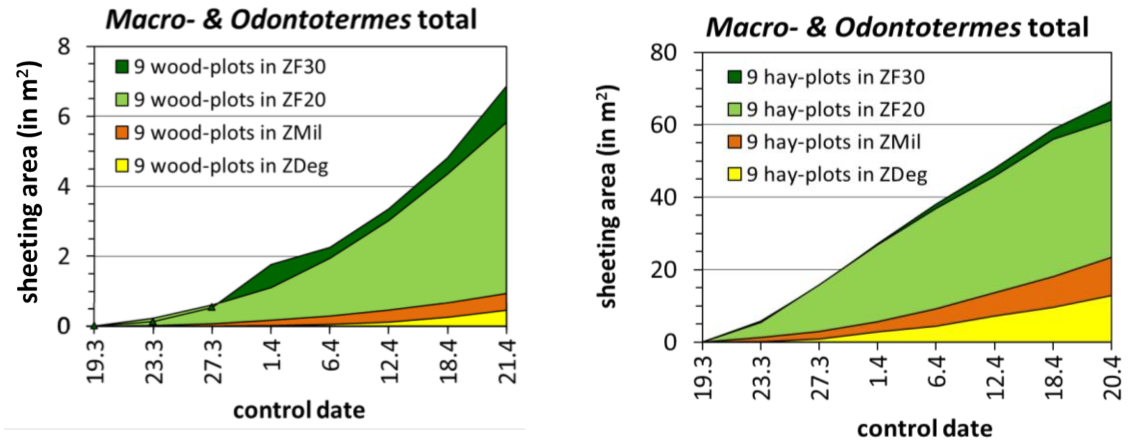


Fig. 8-13: The cumulated increase in sheeting-area constructed by *Odontotermes* and *Macrotermes* during the experimental 4-weeks duration in total is shown per Zaï stage for all wood-quadrats combined; and in **Fig. 8-14:** for all hay-quadrats combined (dry season 2006).

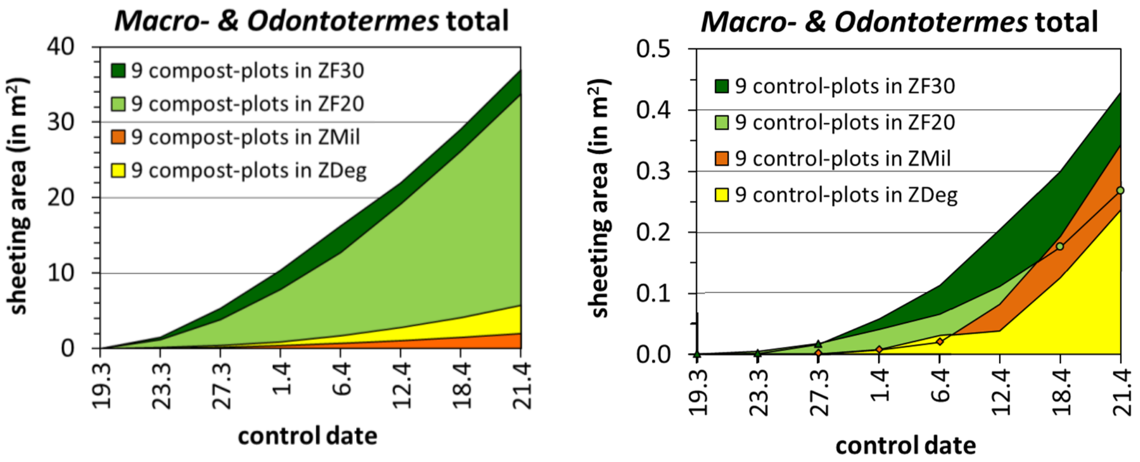


Fig. 8-15: The cumulated increase in sheeting-area constructed by *Odontotermes* and *Macrotermes* during the experimental 4-weeks duration in total is shown per Zaï stage for all compost-quadrats combined; and in **Fig. 8-16:** for all control-quadrats combined (dry season 2006).

Study sites are ZDeg: degraded land, ZMil: millet field, ZF20: young Zaï forest, ZF30: old Zaï forest.

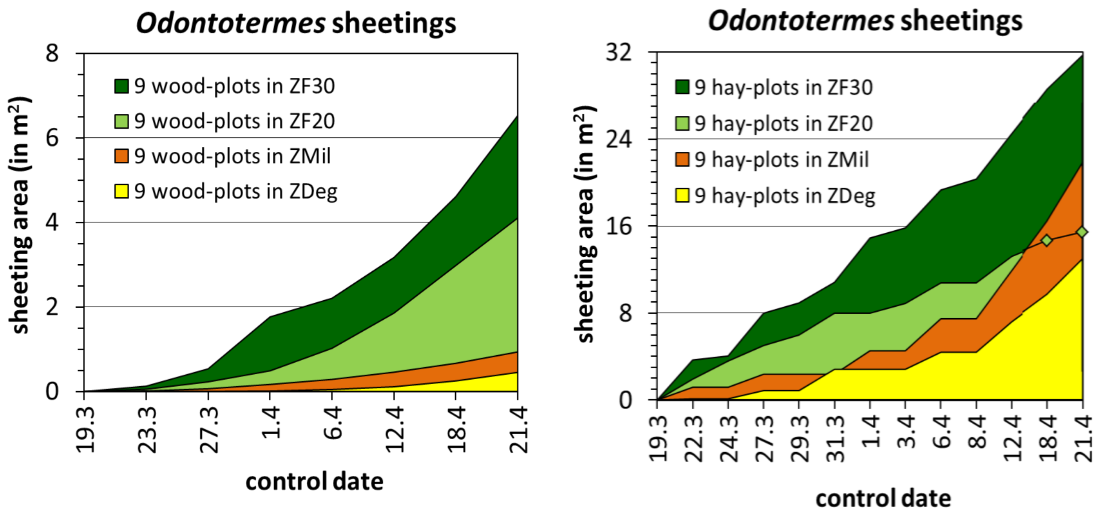


Fig. 8-17: The cumulated increase in sheeting-area constructed by *Odontotermes* during the experimental 4-weeks duration is shown per Zaï stage for all wood-quadrats combined; and in **Fig. 8-18:** for all hay-quadrats combined (dry season 2006).

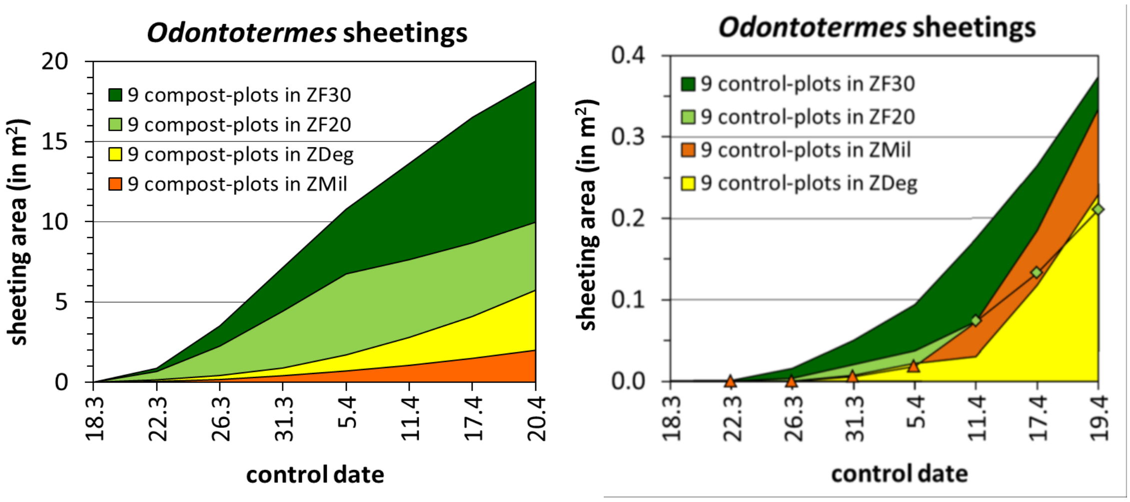


Fig. 8-19: The cumulated increase in sheeting-area constructed by *Odontotermes* during the experimental 4-weeks duration is shown per Zaï stage for all compost-quadrats combined; and in **Fig. 8-20:** for all control-quadrats combined (dry season 2006).

Study sites are ZDeg: degraded land, ZMil: millet field, ZF20: young Zaï forest, ZF30: old Zaï forest.

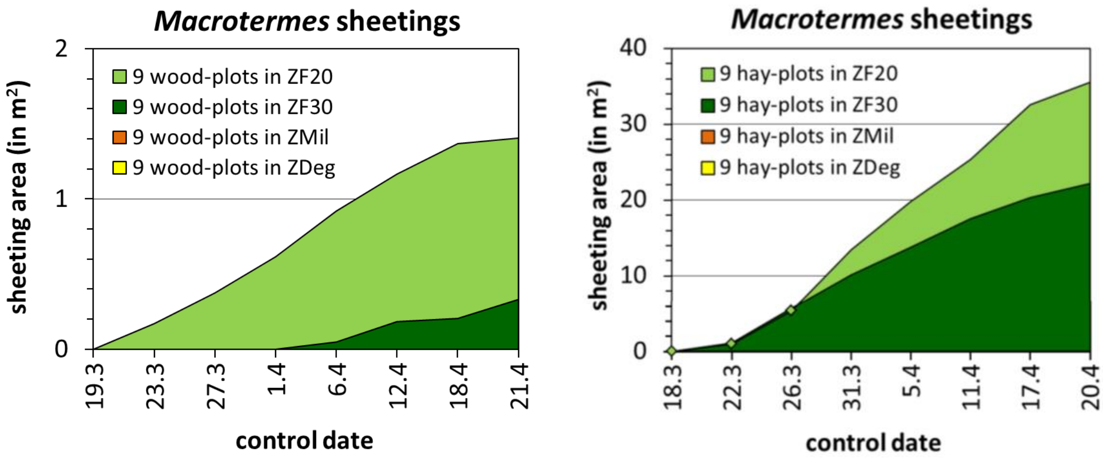


Fig. 8-21: The cumulated increase in sheeting-area constructed by *Macrotermes* during the experimental 4-weeks duration is shown per Zaï stage for all wood-quadrats combined; and in **Fig. 8-22:** for all hay-quadrats combined (dry season 2006).

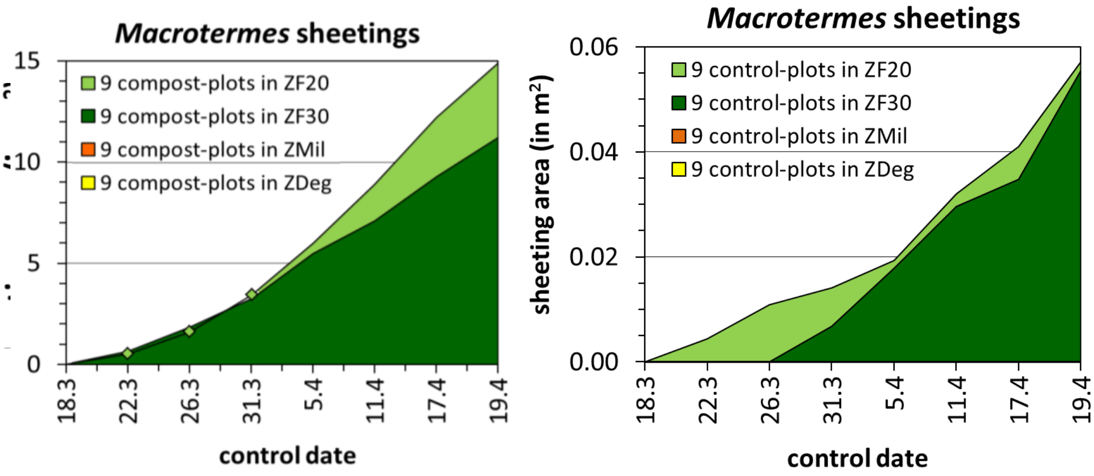


Fig. 8-23: The cumulated increase in sheeting-area constructed by *Macrotermes* during the experimental 4-weeks duration is shown per Zaï stage for all compost-quadrats combined; and in **Fig. 8-24:** for all control-quadrats combined (dry season 2006).

Study sites are ZDeg: degraded land, ZMil: millet field, ZF20: young Zaï forest, ZF30: old Zaï forest.

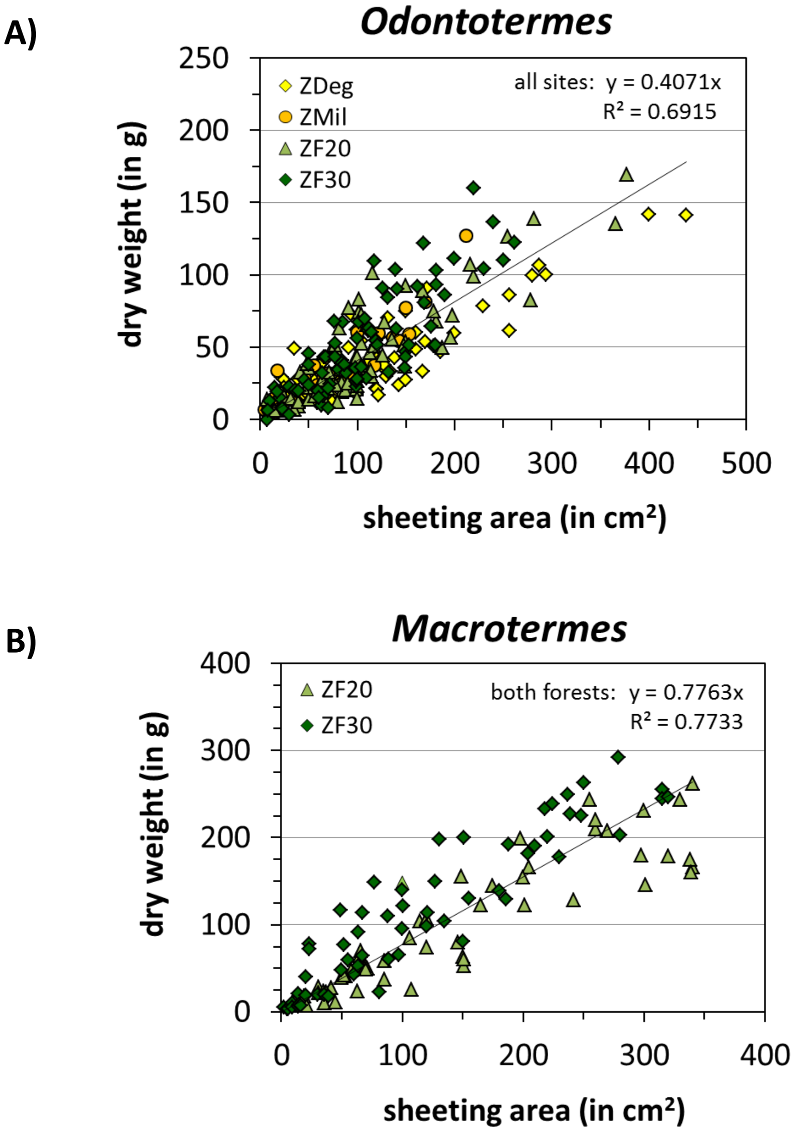
8.2.1.4 Correlation between sheeting-weight and sheeting-area

In Appendix 8, the correlation between the dry weight and the area of sheetings built by termites of the genera *Odontotermes* and *Macrotermes* is shown for all hay-plots of the dry season 2006 (Fig. A8-23 A, B). The data were collected either at the end of the experiment or throughout the four weeks when replacing sheetings with new hay. For both genera, the correlation-equations were calculated 1) for all Zaï sites combined, and 2) for each Zaï stage separately; the respective equations are shown for 1) in the scatter plots, for 2) beside the scatter plots.

The coefficients of the correlation-equations (1 and 2) indicate that sheetings of *Odontotermes* were heavier than those of *Macrotermes* (Appendix 8, Fig. A8-23 A, B). For *Odontotermes,* the dry weight of sheetings built in all Zaï stages in hay could be calculated by multiplying the sheeting-area with 14.8 (Fig. A8-23 A); in the case of *Macrotermes*-sheetings built in hay, the dry weight could be calculated by multiplying the area with 5.8 (Fig. A8-23 B).

These results contradict, however, the in-situ observations. When comparing small areas of sheetings built by *Odontotermes* with sheetings built by *Macrotermes* (e.g. 10 x 10 cm), some differences were especially striking. The pellets of sheetings built by *Macrotermes* had at least twice the diameter of the pellets in *Odontotermes*-sheetings. *Macrotermes*-sheetings had a stable consistency; with some care they could be lifted without crumbling. *Odontotermes*-sheetings with the same area could not be lifted without crumbling; due to the smaller pellet-size, they were lighter and far more fragile. A difference between the two genera could also be noted in their ‘sheeting construction-behavior’ in hay-quadrats. When foraging in hay, *Odontotermes* started from below and built then, from bottom to top, several layers of sheetings sometimes resulting in a height of more than 10 cm. *Macrotermes*, on the other hand, usually built just one thick layer of sheetings with a height of only few centimeters (between 0.5 cm and a maximum of 4–5 cm). Differences were even greater during the dry season when *Macrotermes* was especially active during night-time. In night-time, sheetings did not need to protect the termites against direct sunlight and desiccation. Hay-quadrats where *Macrotermes* was foraging during the night were often not even covered with a continuous sheeting-layer. In Appendix 8, photos are illustrating the granular structure of *Macrotermes*- and *Odontotermes*-sheetings and show differences in the termites’ sheeting construction-behavior (Fig. A8-2; Fig. A8-3).

The height of sheetings, however, was not measured when collecting the sheeting-soil from quadrats. In order to examine whether the height of sheetings accounted for the higher coefficient-values in the correlation-equations calculated for *Odontotermes*-sheetings (Fig. A8-23), smaller sections with varying dimension but comparable heights were collected from sheetings constructed by both genera in the wood-, hay- and compost-plots. Before collecting the soil, the dimensions were measured and recorded. These smaller sections will be referred to as ‘sheeting-sections’. All samples were sun-dried and weighed. In total, 115 sheeting-sections were collected for *Macrotermes* and 254 for *Odontotermes*. The correlation between the dry weight and the area is shown for these sheeting-sections in Fig. 8-25 A and Fig. 8-25 B for sheetings built by *Odontotermes* and *Macrotermes*, respectively.



ZDeg: $y = 0.3367x$
$R^2 = 0.7477$

ZMil: $y = 0.4657x$
$R^2 = 0.8461$

ZF20: $y = 0.416x$
$R^2 = 0.7402$

ZF30: $y = 0.484x$
$R^2 = 0.6962$

ZF20: $y = 0.6687x$
$R^2 = 0.815$

ZF30: $y = 0.9165x$
$R^2 = 0.8484$

Fig. 8-25: Illustrated is the correlation between the dry weight (in g) and the area (in cm^2) of 'sheeting-sections' constructed in hay-, wood- and compost-plots by *Odontotermes* (A) (*N* = 254) and by *Macrotermes* (B) (*N* = 115).

Zaï stages are ZDeg: degraded area, ZMil: millet field, ZF20 / ZF30: young / old forest.

Correlation-equations were again calculated 1) for all Zaï sites combined, and 2) for each Zaï stage separately. The respective equations are shown for 1) in the scatter plots and for 2) beside the scatter plots (Fig. 8-25 A, B).

When comparing the coefficients of the correlation-equations calculated for these sheeting-sections (1 and 2), *Macrotermes* built heavier sheetings than *Odontotermes*. For sheetings of *Odontotermes* – again without distinguishing the sites –, the dry weight could be calculated by multiplying the area with 0.41 (Fig. 8-25 A), for *Macrotermes* with 0.78 (Fig. 8-25 B)

A two-way between-groups analysis of variance was conducted for both termite genera to explore the impact of Zaï stage and food type on the dry weight of sheetings per square centimeter area – as measured by the smaller sheeting-sections. For *Macrotermes*-sheetings, the interaction effect between study site and organic material was not statistically significant, *F* (2, 108) = 1.22, *p* = 0.30. There was a statistically significant main effect for study site, *F* (1, 108) = 12.12, *p* = 0.001 (large effect size, partial eta squared = 0.10 or 10%). The main effect for food type did not reach statistical significance, *F* (2, 108) = 0.94, *p* = 0.39. That means, the dry weight of *Macrotermes*-sheetings differed between the two Zaï forests; the food source, however, was not decisive.

For the sheeting-sections built by *Odontotermes*, the interaction effect between study site and food type was statistically significant, *F* (6, 241) = 3.27, *p* = 0.004. Therefore, the interpretation of the following main effects has to be treated with caution. There was a statistically significant main effect for food type, *F* (2, 241) = 7.33, *p* = 0.001 (medium effect size, partial eta squared = 0.06 or 6%). Post-hoc comparisons using the Tukey HSD test indicated that the mean score for hay (*M* = 0.43, *SD* = 0.22) was significantly different from compost (*M* = 0.54, *SD* = 0.33), and that the mean score for compost (*M* = 0.54, *SD* = 0.33) was significantly different from wood (*M* = 0.544, *SD* = 0.19). However, wood was not significantly different from hay. The main effect for study site alone did not reach statistical significance, *F* (3, 241) = 0.15, *p* = 0.07. Post-hoc comparisons using the Tukey HSD test indicated that the mean score for ZMil (*M* = 0.60, *SD* = 0.37) was significantly different from ZDeg (*M* = 0.41, *SD* = 0.24) and from ZF20 (*M* = 0.45, *SD* = 0.25); the mean score of the other sites did not differ significantly from each other.

Again for the sheeting-sections collected in the experimental plots, an overview is given over the dry weight in gram per square centimeter when differentiating the food type (hay, compost, wood) in which they were constructed (Fig. 8-26). The Zaï stage is indicated by the color, the food type by the pattern of the boxes. To summarize, differences between the two genera are quite obvious: One square centimeter sheetings built by *Macrotermes* had almost twice the weight of those built by *Odontotermes* (Fig. 8-26).

8.2.1.5 Termite associations

Another observation was made in the experimental plots: *Odontotermes* was frequently observed to forage simultaneously with termites of the genera *Macrotermes, Microtermes,* and *Ancistrotermes* in the same plot; *Macrotermes,* on the other hand, was only observed feeding simultaneously with *Odontotermes* but never with one of the other genera.

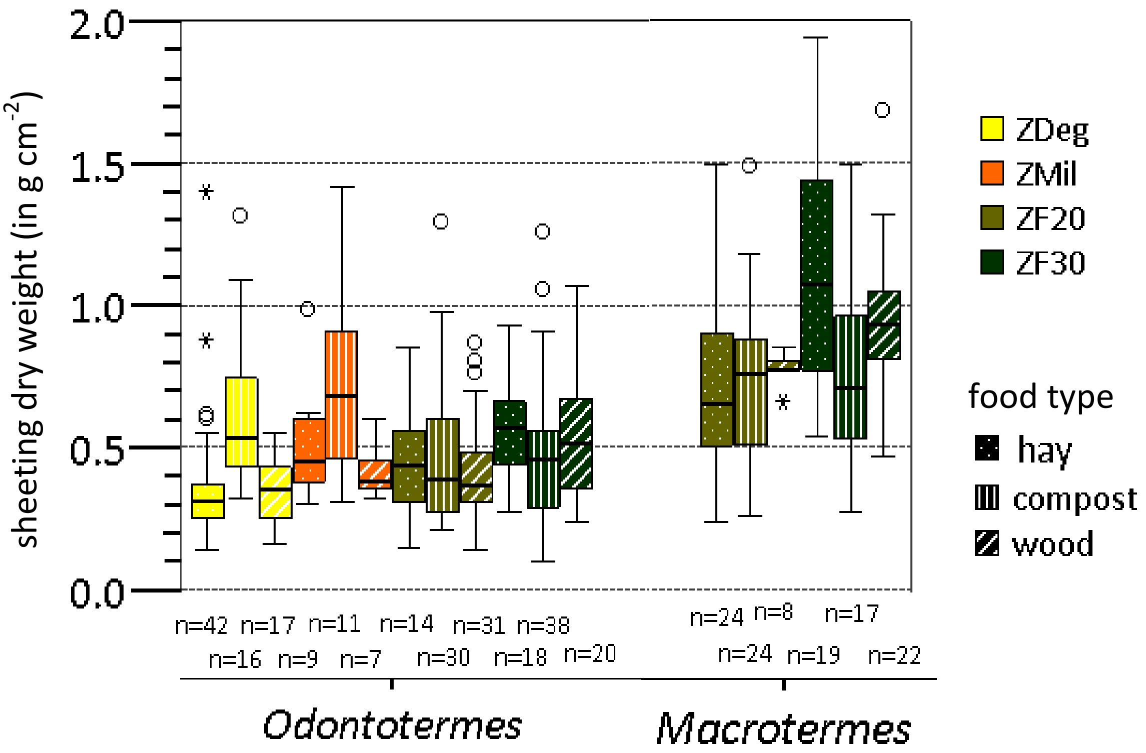


Fig. 8-26: The sheeting dry weight (in g cm^{-2}) is given for both genera (*Odontotermes*, *Macrotermes*) per study site and food type. Illustrated are small areas of the sheetings collected during the dry season 2006 ('sheeting-sections'). These sections had comparable heights and were collected to calculate the correlation between dry weight and area.

Study sites are ZDeg: degraded area, ZMil: millet field, ZF20: young Zaï forest, ZF30: old Zaï forest.

8.2.2 Soil-porosity *via* foraging-holes

All macropores within the sub-plots (each 1 m^2 area) were assessed at the end of the experiment, i.e. after 4 weeks foraging activity. Each boxplot in Fig. 8-27 comprises the numbers counted in the nine replicate-plots per Zaï stage which had the same organic amendment. In some cases, indicated by the reduced number (*N*), counting was hindered e.g. due to cattle walking through the plot.

As indicated in Fig. 8-27, an increasing number of foraging-holes were counted with increasing restoration stage. Within each site, the number of macropores increased in the following order: control < wood < compost < hay. That means the highest numbers were assessed in hay-plots, the lowest in control-plots (Fig. 8-27).

The diameter of macropores was measured whenever possible and is illustrated in the appendix for those quadrats where either *Macrotermes* or *Odontotermes* were foraging (Fig. A8-24, Appendix 8). The median diameter of 508 macropores measured for *Macrotermes* was 8 mm (*SD* = 3.4), the median of 483 macropores of *Odontotermes* was 4 mm (*SD* = 1.2) (Fig. A8-24, Appendix 8).

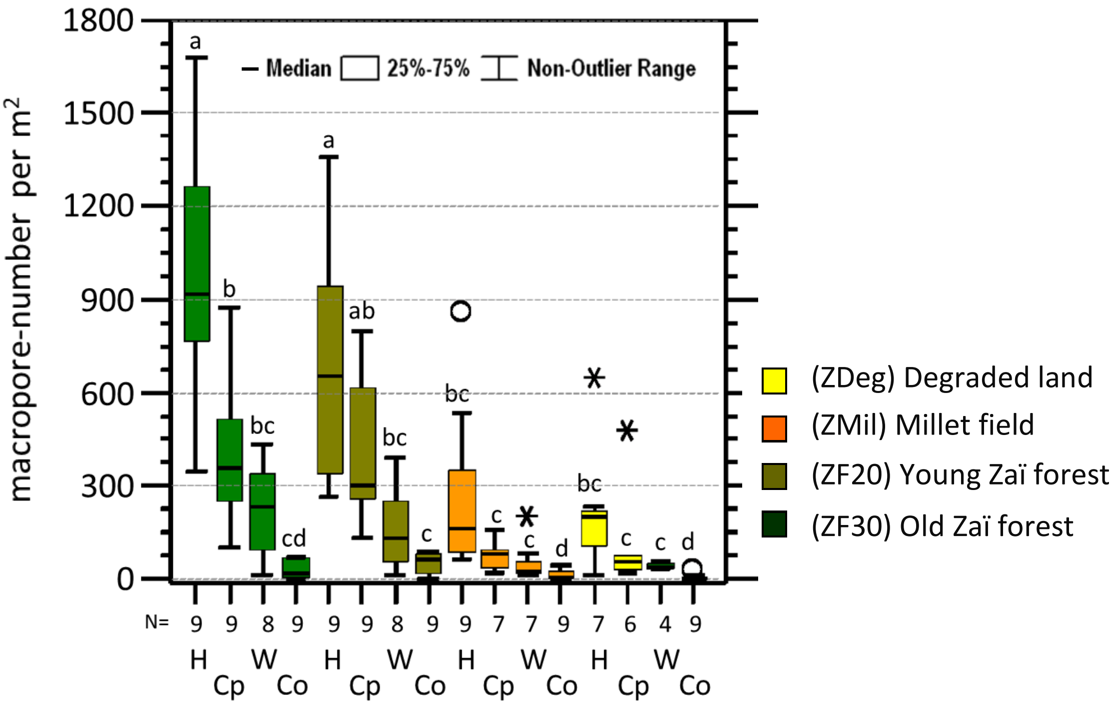


Fig. 8-27: Macropore-number per square meter after 4 weeks foraging activity (shown per food type and Zaï stage. Values with the same letter (a, b, c, d) are not significantly different at p<.05 level (Kruskal-Wallis).

Food types are H: hay, Cp: compost, W: wood, Co: control.

8.2.3 Effect of foraging-holes on ponded soil water infiltration

Ponded soil water infiltration was measured in selected quadrats at the end of the experiment (double ring infiltration). Water infiltration was measured until the variation of the infiltration rate was smaller than 10% for the last 3-5 measurements (steady state). In order to assess the influence of foraging-holes on water infiltration, measurements were taken in a sub-plot with recent foraging activity (hay-, wood- or compost-plots) and simultaneously in the respective control-plot. The difference between the two sub-plots was then assigned to the newly established macropores.

One example of two simultaneous infiltration-runs, conducted in the degraded site in a hay-plot with 201 and the respective control-plot with 9 visible macropores of *Odontotermes*, is illustrated in Fig. 8-28. The steady state in hay was reached after 6 hours at an infiltration rate between 230-240 mm/h. In the control, the infiltration rate noted after more than 7 hours at steady state was about 110 mm/h (Fig. 8-28). The foraging activity thus increased the infiltration rate by more than 100%. Although the infiltration process in the hay-plot was ended one hour earlier than in the control, water had to be filled in twice as often (Fig. 8-28). Most of the infiltrations in the Zaï system took 4–8 hours and 200–400 liters water; in extreme cases 600 liters had to be filled into the rings.

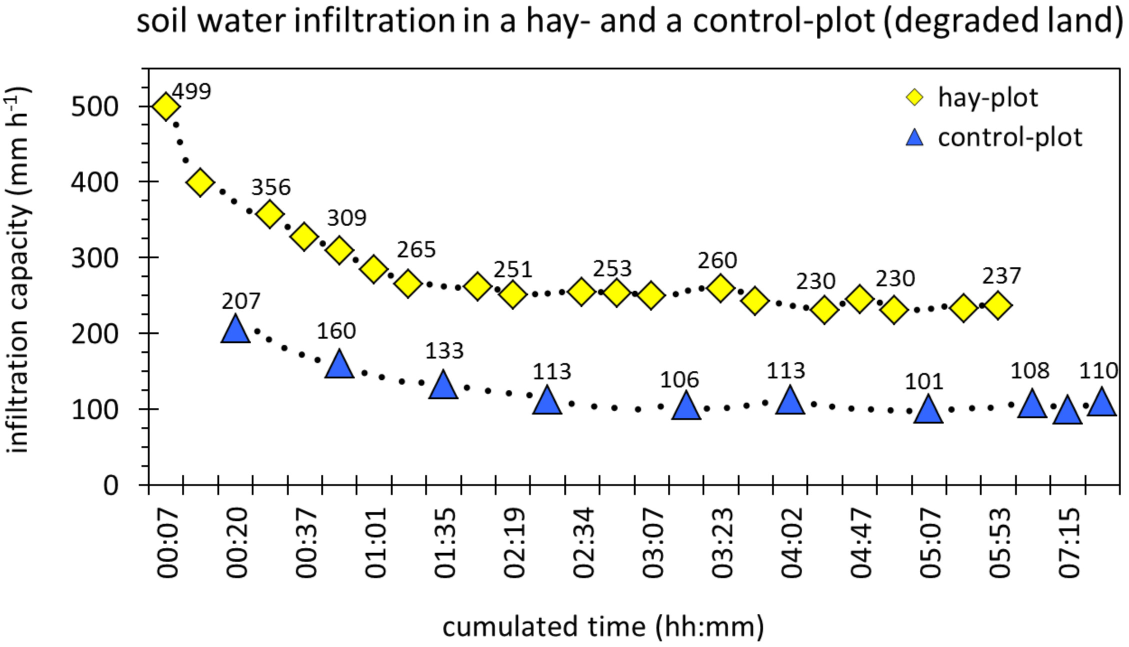


Fig. 8-28: Example of soil water infiltration (in mm h^{-1}) after 4 weeks – measured simultaneously in a hay-plot and the respective control-plot (double ring infiltration).

The increase of water infiltration capacity (in %) in 33 plots with recent foraging activity, compared to the respective control-plots, is illustrated in Fig. 8-29. Included are all infiltration measurements without distinguishing the season, the Zaï stage or the organic material; differences between these parameters were not significant at $p < .05$ level (Kruskal-Wallis test).

The figure highlights, that the enormous increase in surface pore-space following one month of induced foraging activity significantly increased the water infiltration capacity between 2–4 times (Fig. 8-29). However, this is a conservative number because infiltration was not measured in quadrats with more than 500–600 macropores or in plots where *Macrotermes* was foraging alone. The water consumption in these cases was exaggerated to such an extent that was neither justifiable nor workable. In extreme cases that were just workable, the infiltration rate in the activity-plots was increased up to 8 times.

To summarize the most important findings so far (Chapter 8.2.1, 8.2.2 and 8.2.3)

- Hay is the most attractive bait in all stages of the succession, inducing the highest quantity of soil turn-over and the creation of the greatest number of foraging-holes.
- The main bioturbators are the fungus-growing termite species of the genera *Odontotermes* and *Macrotermes*.
- *Odontotermes* is the decisive primary physical ecosystem engineer in the Zaï system, initializing the restoration process.
- The mass of soil bioturbated increased strongly from the degraded, barren towards the most rehabilitated, reforested site.
- The enormous increase in surface pore space after one month of induced foraging significantly increased the water infiltration rate (between 2 and 4 times)

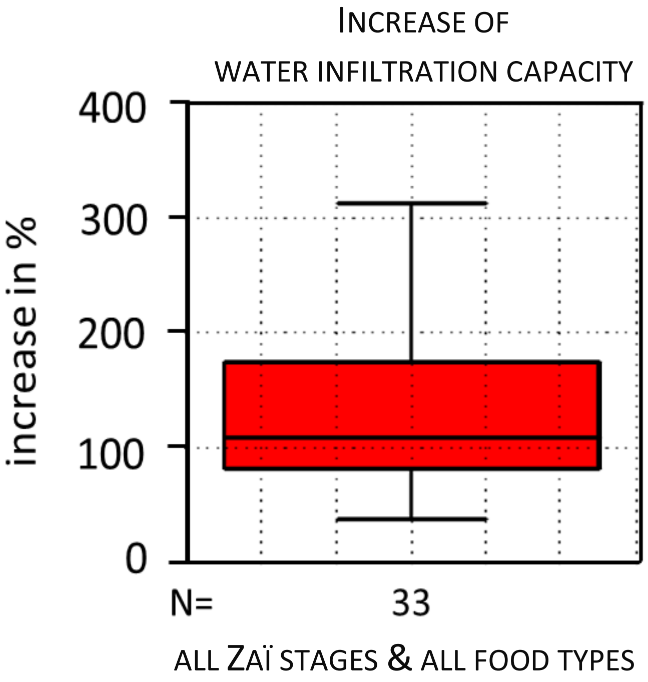


Fig. 8-29: Increase of water infiltration capacity (in %) in 33 plots with termite activity compared to the respective control plots. Included are infiltration measurements run in both the dry and the rainy season, in all Zaï stages and in all food types (hay, wood, and compost).

8.2.4 Physico-chemical parameters of soil-sheetings and their effect on habitat soil

One aim of the experiment was to determine the physico-chemical parameters of soil-sheetings and their effect on the habitat soil while paying attention to potential influences of the season, the Zaï stage, the food type and the termite genus. When sheetings allocated to a single termite genus were collected, samples were taken for later analysis. Additionally, topsoil samples (0–10 cm) were taken from each sub-plot at the end of the experiment. To decide whether the fungus-growing termite genera *Odontotermes* and *Macrotermes* significantly modify the soils' physico-chemical properties when constructing their protective soil-sheetings, comparisons were made with the topsoil samples of the respective control-plots. We further evaluated whether the soil-modifications were different for the two termite genera. Shapiro-Wilk test indicated that – except for very few cases – all data were normally distributed. Levene's test was non-significant thereby indicating that the variances of the sheeting or topsoil data were equal. Paired-samples *t* tests were performed at the 0.05 significance level to compare the different sample-types. The outcome of the comparisons with the paired-samples *t* test – that is mean values (*M*) with standard deviations (*SD*) for each sample type, the mean difference (Δ) between the sample-pairs, the 95% confidence interval of the mean difference and the *p*-value – is given for all physico-chemical parameters (Table A8-1 to Table A8-8). All Zaï stages were included in the following analysis.

Results for the carbon to nitrogen ratio (CN-ratio), the soil organic matter content (SOM), the pH (pH_{KCl}), the total nitrogen (N total) and the total phosphorous content (P total) are shown in Table A8-1 for samples of the rainy season and in Table A8-2 for those of the dry season-experiment. The electrical conductivity (EC), the grain sizes coarse, middle and fine sand as well as the total sand content are compared in Table A8-3 for the rainy season and in Table A8-4 for the dry season run. The distribution of the grain sizes coarse, middle and fine silt, the total silt and the total clay content are shown in Table A8-5 and Table A8-6 for the rainy and dry season samples, respectively. The chemical parameters plant-available phosphorous (P_CAL), plant-available potassium (K_CAL), base saturation (BS) and potential cation exchange capacity at pH 8.1 ($CEC_{pH\ 8.1}$) are solely compared for the dry season samples (Table A8-7), as are the cations sodium (Na^+), potassium (K^+), magnesium (Mg^{2+}) and calcium (Ca^{2+}) (Table A8-8).

Additional remark: Mean values and standard deviations given for one and the same parameter and sample type can differ slightly between the sample-pairs depending on which experimental plots were included in the comparisons. For example, the mean carbon to nitrogen ratio measured for the control-plots is 9.3 ± 2.7, 9.7 ± 2.2 and 9.7 ± 2.8 for comparisons with sheetings built by *Odontotermes* on compost, hay and wood, respectively (Table A8-1). These differences result from the small-scale heterogeneity of soil properties. When comparing control-soil with sheeting-soil, the selection of the samples (i.e. sub-quadrats) which were included per Zaï stage to calculate the means depended on the plots in which the soil-sheetings (here: *Odontotermes*) were constructed. An example: In the young forest, *Odontotermes* constructed sheetings in four of nine compost-plots (plot-number 3, 4, 7, 9) and in five of nine wood-plots (plot-number 2, 3, 5, 6, 8). The means for the control-soil were thus also calculated only from the composite-samples taken in the control-plots of those experimental blocks: for the sample-pair 'Control with *Odontotermes*-sheetings in Cp', means for the young forest, were calculated from control-samples of plot 3, 4, 7 and 9; and, for the sample-pair 'Control with *Odontotermes*-sheetings in W', means were calculated from control-samples of plot 2, 3, 5, 6, and 8. The samples included from the other three Zaï-stages were selected in the same way. *Macrotermes* only foraged in the two Zaï forests. Therefore, for the comparisons with *Macrotermes*-sheetings, only samples of the two Zaï forests were included for the control-soil.

During foraging, fungus-growing termites of the genera *Odontotermes* and *Macrotermes* significantly modified several of the soils' physico-chemical parameters when constructing their protective soil-sheetings (Table A8-1 to Table A8-8). The comparison of the sheeting-soil built in compost, hay and wood with adjacent, recently un-modified topsoil revealed significant differences for samples of the rainy season experiment in 2005 and of the dry season experiment in 2006 (Table A8-1 to Table A8-8). However, for both genera no clear pattern could be detected in the soil modifications; the direction (lower or higher content of nutrients) and the magnitude of soil modifications differed between the three food-types and between the two seasons. Quite uniform was only the direction of soil-modifications by *Odontotermes* during the dry season experiment: All *Odontotermes*-sheetings – whether they were collected in compost, hay or wood – had a higher pH, higher electrical conductivity (EC), a higher base saturation, higher contents in soil organic matter, total nitrogen, plant-available phosphorous and clay, as well as higher contents of the cations sodium, potassium and magnesium. And except for the sheetings collected in wood, a higher potential cation exchange capacity and higher contents in plant-available potassium and calcium-cations were measured in the sheetings *Odontotermes* constructed during the dry season experiment. However, a comparable pattern to that found for the dry season-samples could not be detected in sheetings constructed by *Odontotermes* during the rainy season experiment.

Some 'trends' were detectable for the soil-parameters that were analysed in both seasons:

- Soil-modifications were different for the two termite genera; *Odontotermes* significantly modified more of the soils' physico-chemical parameters in the soil-sheetings (Table A8-1 to Table A8-8).
- For both genera, least seasonal differences in the direction of significant soil-modifications were noted in the sheetings constructed in compost (Table A8-1 to Table A8-6).
- Both genera significantly modified more physico-chemical parameters in sheetings they constructed during the dry season experiment (Table A8-1 to Table A8-6).
- In both seasons and for both genera, nutrient contents and the significance of modifications were highest in sheetings constructed in compost; and, with very few exceptions, the weakest significance in modifications of the soils' chemical parameters was observed for sheetings constructed in wood (Table A8-1 to Table A8-8).

- The electrical conductivity (EC) was significantly higher in all soil-sheetings in whatever season or food type they were constructed by *Odontotermes* and *Macrotermes* (Table A8-3; Table A8-4).

Some examples for these trends:

- EC-values of sheetings built in the rainy season in compost were 15-times higher and 10-times higher for *Odontotermes* and *Macrotermes*, respectively (Table A8-3).
- EC-values of dry season-sheetings built in compost were even 21-times higher and 25-times higher for *Odontotermes* and *Macrotermes*, respectively (Table A8-4).

Macrotermes:

- Soil-sheetings constructed by *Macrotermes* during the rainy season in compost had a higher pH, and higher contents in soil organic matter, total nitrogen and total phosphorous, while those constructed in wood differed significantly only in their EC; sheetings constructed in hay had a significantly lower nitrogen content and the C:N ratio was higher as well (Table A8-1; Table A8-3).
- Soil-sheetings constructed by *Macrotermes* during the dry season in compost had a higher pH, and higher contents in soil organic matter, total nitrogen and total phosphorous, while sheetings constructed in hay and wood had just significantly higher contents in soil organic matter and total nitrogen (Table A8-2).

8.2.5 Summary of soil-modifications by *Odontotermes* and *Macrotermes*

In contrast to epigeal termite mounds, soil-sheetings erode easily and are distributed fast. Even small rain events or trampling by cattle already destroyed sheetings at least partly. Their effect on the physico-chemical parameters of habitat soil is thus more direct. Table 8-2 is summarizing the modifications of the soils' physico-chemical properties in sheetings built by *Odontotermes* and *Macrotermes* during the rainy and the dry season in compost, hay and wood relative to the adjacent, recently un-modified control-topsoil.

In Appendix 8, all physico-chemical soil parameters that were significantly modified in sheetings constructed by *Odontotermes* and/or *Macrotermes* in compost and hay are plotted against the same parameter of the respective control-topsoil (Fig. A8-25 to Fig. A8-28; Appendix 8). Scatter-plots of the rainy and the dry season illustrating the same parameter are thereby arranged next to each other whenever the modification was significant in samples of both seasons (Fig. A8-25 to Fig. A8-28).

Table 8-2: Differences between the physico-chemical parameters of sheeting-soil and recently un-modified (adjacent) topsoil.

Dry season 2006	*Odontotermes*-sheetings on			*Macrotermes*-sheetings on		
	compost	hay	wood	compost	hay	wood
CN-ratio	similar	similar	similar	similar	higher	similar
SOM	higher	higher	higher	higher	higher	higher
pH	higher	higher	higher	higher	similar	similar
N total	higher	higher	higher	higher	higher	higher
P total	higher	similar	similar	higher	similar	similar
Sand total	similar	similar	similar	similar	similar	similar
Silt total	similar	lower	lower	similar	similar	similar
Clay total	higher	higher	higher	higher	higher	similar
EC	higher	higher	higher	higher	higher	higher
P_CAL	higher	higher	similar	higher	higher	similar
K_CAL	higher	higher	higher	higher	higher	similar
CEC	higher	higher	similar	higher	higher	higher
BS	higher	higher	higher	higher	similar	similar
Na^+	higher	higher	higher	higher	similar	similar
K^+	higher	higher	higher	higher	higher	higher
Mg^{2+}	higher	higher	higher	higher	higher	similar
Ca^{2+}	higher	higher	similar	higher	similar	higher

Rainy season 2005	*Odontotermes*-sheetings on			*Macrotermes*-sheetings on		
	compost	hay	wood	compost	hay	wood
CN-ratio	similar	higher	similar	similar	higher	similar
SOM	higher	higher	similar	higher	similar	similar
pH	higher	higher	higher	higher	similar	similar
N total	higher	similar	similar	higher	lower	similar
P total	higher	similar	similar	higher	similar	similar
Sand total	lower	higher	lower	higher	higher	similar
Silt total	similar	similar	similar	similar	similar	similar
Clay total	similar	similar	higher	similar	similar	similar
EC	higher	higher	higher	higher	higher	higher

Similar: no significant differences ($p > 0.05$); higher, lower: significant differences ($p < 0.05$)

8.2.6 Chemical properties of the three offered food types (hay, compost and wood)

The three organic materials that were applied on the experimental plots to attract termites and to induce their foraging activity were analyzed in the laboratory of the University of Marburg (Germany). Their chemical properties are shown in Table 8-3.

Table 8-3: Chemical properties of three organic materials used to attract termites.

Organic materials	*Bombax costatum* W		*Aristida kerstingii* H		Compost of farmer Cp	
	Rainy season	Dry season	Rainy season	Dry season	Rainy season	Dry season
SOC (g kg^{-1})	413.0	523.0	266.0	266.0	206.0	206.0
SOM (g kg^{-1})	712.0	901.7	458.6	458.6	355.1	355.1
N total (g kg^{-1})	37.0	22.0	34.0	34.0	204.0	204.0
P total (g kg^{-1})	0.20	0.00	0.20	0.20	2.20	2.20
CN-ratio	11.2	23.8	7.8	7.8	1.0	1.0

8.3 DISCUSSION

The present study revealed very promising findings for the management of low-input farming systems in the sub-Sahel zone of West Africa. Placing different locally available organic materials (*Aristida kerstingii* hay, *Bombax costatum* wooden blocks, and compost) on the soil surface in different Zaï stages attracted fungus-growing termites in a short time and induced their foraging and soil bioturbation activity. This is consistent with Mando et al. (1999) who found that placing mulch on crusted soil in northern Burkina Faso resulted in the colonization of this soil by termites.

FUNGUS-GROWING TERMITES IN THE ZAÏ SYSTEM

Fungus-growing termites of four genera dominated soil turn-over in the Zaï system (Fig. 5-3). *Microtermes* and *Ancistrotermes* species did not construct sheetings in the strict sense but rather fed inside millet stalks or dead wood; they were therefore not considered in the present study. *Odontotermes* and *Macrotermes* (*Macrotermes bellicosus*, *Macrotermes subhyalinus*) were the main soil bioturbators year-round as was also observed during the rapid assessment of biogenic structures (BS) conducted to assess the relative importance of ants and termites for soil turn-over (BS transects in Chapter 7). The two genera also constructed the majority of the soil-structures collected in the North-Sudan region; however, due to the higher annual rainfalls in this zone, earthworms contributed significantly to soil bioturbation (Fig. 7-3). *Odontotermes* was the only genus to be attracted by organic material in the initial habitat stage (ZDeg). The same observation was made by Siegle (2009) in a heavily crusted, barren area located around 2 km south-east of my study sites. Therefore, *Odontotermes* appears to be the decisive primary physical ecosystem engineer in the Zaï system initiating the restoration process. *Macrotermes* was neither encountered in the millet fields, in contrast to other studies where different *Macrotermes* species caused agricultural damage to several crop species (e.g. Bandiya et al. 2012; Collins 1981; Cowie et al. 1990; Lepage 1981; Pearce et al. 1995; Togola et al. 2012). *M. bellicosus* was found in the young and the old Zaï forest, *M. subhyalinus* only in the old one (Table 5-5). Construction of soil-sheetings of the fungus-growing termites *Macrotermes subhyalinus* and *Odontotermes nilensis* was also one of the main soil translocation processes in a Sahelian savanna of Senegal in an experiment conducted to assess the effect of litter quality on the foraging pattern of fungus-growing termites (Ndiaye et al. 2004; Rouland et al. 2003).

FORAGING PARAMETERS

The best surrogates for the foraging and bioturbation activity were i) the dry weight of soil bioturbated to construct soil-sheetings, and ii) the increasing plot-area covered with sheetings. The dry weight of the sheeting-soil could be assessed more rapidly as it required only the collection, drying and weighing of the sheeting-soil. Measuring the increasing sheeting-areas, on the other hand, turned out to be a complex and time-consuming process as it required i) mapping of the individual sheeting-areas on millimeter paper, ii) importing the scanned sheets (maps) into the computer program ArcView GIS 3.2a (ESRI), iii) tracing the margins of each individual sheeting-area (these areas could comprise numerous little sheeting-spots scattered over the 1 m^2-plot-area, especially in compost-plots), before iv) the surface-calculations (exact size of the individual sheeting-areas) could be computed. The determination of the surface-area was only simple in hay-plots (mainly in the two forests) where one genus was foraging alone and where the applied 1.5 kg hay was fully consumed. In these cases, the sheeting-area corresponded mostly with the plot-area; only in those plots where *Macrotermes* was foraging extensively during the night, it could be smaller than the plot-area. The number of macropores created in the experimental plots did not prove to be quantitatively as good as the other two measures. Moreover, the feasibility of counting them depended greatly on the topography and the soil type; the gravelly and uneven surface in the millet field complicated the assessment of macropores immense – if it was possible at all.

A surrogate for the sheeting-area proved to be a measure of termite activity in the experiment in Senegal (Rouland et al. 2003): In each experimental plot, the two diagonals were marked with a rope; the rope-sections with soil-sheetings underneath were measured and summed up. The cumulated length of these sections was then used as a surrogate for the total sheeting-area constructed in the respective plot.

SOIL TURN-OVER VIA SOIL-SHEETINGS

The impact of foraging termites on soil formation is substantial. Huge amounts of soil were moved to construct sheetings in the experimental plots. In both seasons, soil turn-over was increasing with increasing habitat restoration from the degraded, barren towards the most rehabilitated 30 years old Zaï forest (Fig. 8-10). In contrast to the dry season run, however, it was not possible to determine the total quantity of soil bioturbated to construct sheetings in the rainy season run. Although stonelines were placed around each plot to halt the erosion of sheeting-soil during rainfalls (Fig. A8-1), I had to abstain from the collection of all soil-sheetings since an indeterminable amount was lost through gaps between the stones.

When combining all 36 sub-plots per Zaï stage, 31.8 tons of soil per hectare and month were translocated in the degraded area to construct sheetings, 32.4 tons ha^{-1} mon^{-1} in the millet fields, 138.9 tons ha^{-1} mon^{-1} in the young and even 215.5 tons ha^{-1} mon^{-1} in the old Zaï forest. Similar high values of soil turn-over were only reported by Mando and Miedema (1997) in northern Burkina Faso; after two weeks mulching with a mixture of *Pennisetum pedicellatum* straw and *Pterocarpus lucens* wood, *Odontotermes smeathmani* (Fuller) and *Microtermes lepidus* (Sjöst) dug out 20 tons ha^{-1} mon^{-1} from the soil and reworked it into sheetings. Control plots without organic matter showed no traces of recently-made termite structures – like in the study of Mando and Miedema (1997). Lower quantities were reported by Rouland et al. (2003) from Senegal (mean annual rainfall 440 mm); in plots where Macrotermitine termites foraged strongly, they moved around 9.4 tons soil ha^{-1} mon^{-1} from lower horizons to construct their soil-sheetings.

FORAGING-BEHAVIOR AND DYNAMICS OF SOIL-SHEETING ESTABLISHMENT

The experiment was very time-consuming but allowed detailed information to be gathered on the termites' foraging behavior which differed in several aspects, for instance:

SOIL TURN-OVER PER GRAM FORAGED HAY

A strong linear relationship was observed between hay removal and soil accumulation at the surface. Irrespective of the habitat type, *Macrotermes* translocated around 4 g soil per gram hay removed, *Odontotermes* about three times as much (Fig. 8-12). In a seasonally dry Costa Rican pasture, about 2 g soil for each gram of dung removed was accumulated by *Amitermes beaumontii* and *Hoplotermes* species (Herrick & Lal 1996).

FOOD LOCATION

The temporal comparison of sheeting-establishment in the Zaï forests revealed that *Odontotermes* species located the food sources in most cases faster than *Macrotermes* species (Fig. A8-15 to Fig. A8-22, Appendix 8). This was also observed by Siegle (2009) during a food choice experiment in the young forest. Moreover, *Odontotermes* located experimental plots mostly faster in the forests than in the millet field and the degraded area (Fig. 8-17 to Fig. 8-19). Once it was located, *Macrotermes* exploited the organic material often faster than *Odontotermes*. Similarly, in Botswana *Macrotermes michaelseni* was more likely to come to a bait after *Odontotermes* sp. than vice versa (Schuurman 2006) and in Senegal, *Macrotermes subhyalinus* delayed its foraging activity compared to *Odontotermes nilensis* and exploited the material in an extensive way upon its discovery (Rouland et al. 2003). Siegle (2009) observed rarely that *Macrotermes* built their sheetings on top of existing *Odontotermes*-sheetings; in the present study the opposite was the case (8.2.1.3). After the arrival of *Macrotermes* in the forest plots either both species foraged together simultaneously or *Macrotermes* exploited the food source alone. Differences in the plot-size may have accounted for these contrasting findings in the same study site. The areas Siegle (2009) covered with organic material were only 10 x 30 cm that is rather small compared to the plots of the present study; once it was located, the organic material was depleted in a short time. An explanation for the faster food location might be that *Odontotermes* species put more effort and energy resources into the exploration of new feeding sites compared to *Macrotermes* species. A strongly exploratory behavior of *Odontotermes* was indeed reported by Buxton (1981). However, I did not find any studies comparing the effort both genera put into food exploration.

SOIL TURN-OVER ACTIVITY WITH INCREASING HABITAT RESTORATION

The foraging and soil turn-over activity of *Odontotermes* was steadily increasing with increasing habitat restoration (Fig. 8-11; Fig. 8-17 to Fig. 8-19); in contrast, more *Macrotermes*-sheetings were constructed in the young than in the old forest (Fig. 8-11; Fig. 8-21 to Fig. 8-23). The increasing bioturbation activity of *Odontotermes* is assumed to be explained by an increasingly higher nest density with increasing habitat restoration. A higher nest density would then imply that the subterranean nests could have had more advantageous positions within the habitat area, closer to the experimental plots. This would also explain why *Odontotermes* located experimental plots faster in the forests than in the first two succession stages. Another explanation for the faster food location might be that the number of *Odontotermes* colonies surpassed the number of *Macrotermes* colonies what again may lead to more advantageous positions within the habitat area. Unfortunately, I was not able to map the locations of *Odontotermes* colonies during the assessment of epigeal termite mounds in 2008 (Fig. A4-4). Except for foraging structures, no epigeal traces of *Odontotermes* colonies could be found in the Zaï system; in contrast to the North-Sudan region where *Odontotermes* exhibited the ‘classical’ nest structure (according to Darlington 1997) characterized by a distinctly raised surface devoid of any vegetation (Fig. A2-12 C in Appendix 2; Fig. A4-5 in Appendix 4). Since more *Macrotermes*-sheetings were collected in the young than in the old forest (Fig. 8-11), it would be conceivable that the number of *Macrotermes* mounds was higher in the young forest. However, the opposite was the case: during the assessment of mounds in 2008, eight live mounds were counted in the old forest and two in the young forest (Fig. A4-4). These numbers, however, are only apparently contradictory as six of the live mounds in the old forest were still in a juvenile stage; they had not been recorded during the diversity assessment (2004–2007). The two mounds in the young forest were about 80 cm high, two in the old forest around 40 cm and the juvenile ones less. *Macrotermes* species search in the immediate surroundings of their nest for food, thereby constructing a network of underground passages (Jmhasly & Leuthold 1999) which is representing their feeding territory (Kettler & Leuthold 1995). Foraging tunnels around mature *Macrotermes* colonies can radiate for 50 m or more into surrounding soils (Turner

2006); two adult colonies may thus easily span a hectare (area of each Zaï stage) what might explain the higher activity in the young forest.

Moreover, during the diversity assessment, *Macrotermes bellicosus* was found in both forests, *Macrotermes subhyalinus* only in the old forest (Table 5-5). Intra- and interspecific aggressions between neighboring *Macrotermes* colonies may have inhibited the enlargement of their feeding territories in the old forest thereby accounting for the lower bioturbation activity. In laboratory studies, feeding territories with inter- and intraspecific aggression were reported for *M. subhyalinus* (Kettler & Leuthold 1995), and Sugio (1995) observed in Thailand that the less *Macrotermes* species foraged above ground, the larger was the proportion of this subterranean network relative to the whole foraged area. Moreover, Kettler and Leuthold (1995) discovered a pile of dry head capsules of termite soldiers at the territory border between two nests of *M. subhyalinus* and *M. bellicosus*, and Darlington (1982) found dry head capsules and dead termite bodies in between two neighboring nests of *M. michaelseni* in Kenya.

TERMITE ASSOCIATIONS

Interspecific aggressions might also explain why *Macrotermes* never foraged simultaneously with termites of other genera except for *Odontotermes*. This assumption is supported by the following findings: *Microtermes* workers were aggressive towards *M. michaelseni* individuals; they foraged more frequently and effectively when *M. michaelseni* numbers had been experimentally reduced (Dangerfield & Schuurman 2000). Moreover, *M. michaelseni* appeared to avoid competition with other fungus-growing species by spatial separation within the savanna habitat in Botswana habitat as well as by limited separation in food selection (Dangerfield & Schuurman 2000). Despite extensive overlaps in distributions of *M. michaelseni, Odontotermes*, *Allodontermes* and *Microtermes* species in Botswana, co-occurrences on baits were significantly less frequent than expected by chance (Schuurman 2006). However, in contrast to my observations, the author noted that the incidence of *M. michaelseni* and *Odontotermes* species in a plot was negatively correlated during the dry season. Similarly, at the beginning of the rainy season when food became limiting in a Guinea savanna in Côte d'Ivoire, Korb and Linsenmair (2001) observed that other termites were more active in the absence of *M. bellicosus* than in its presence; the authors concluded that this complementary activity pattern indicated interspecific competition.

To my knowledge, no evidences for an intra- or interspecific competition have been found for *Odontotermes* species. This is in line with the observation made in the present study that *Odontotermes* species were frequently foraging simultaneously in the same plot with *Macrotermes, Microtermes* and *Ancistrotermes* species. Separated feeding territories in *Macrotermes* and overlapping territories in *Odontotermes* could thus also lead to a faster food location by *Odontotermes* workers.

FOOD PREFERENCES & SHEETING CONSTRUCTION

In the experimental plots, both genera fed on the same food types and no significant seasonal differences were observed. Hay was the most attractive bait in all stages of the succession series. The cumulated soil turn-over within a site was always highest in hay, followed by compost, then by wood and in the end control. Similarly, the foraging activity of *Odontotermes* species in northern Kenya was greater on grass than on wood (Bagine 1984), and no significant differences between the diets of *M. michaelseni* and *Odontotermes* sp. were noted in the Okavango Delta region in Botswana (Schuurman 2006). A preference of *M. michaelseni* for grass litter was further reported by Lepage (1981)[1]. In their review Freymann et al. (2008) compared studies with 12 fungus-growers and 10 non-fungus growers and found that the majority (70%) of non-fungus growers preferred dung, whereas the fungus-growers showed either a preference for alternative plant food items (50%) or no clear preference at all (33%). In contrast, during the food choice experiment in the degraded, barren stage and the young Zaï forest (dry season 2008), *Odontotermes* preferred dung over the other tested organic materials (*Sorghum*, an herbaceous species, wood, leaves) (Siegle 2009). The cost-benefit ratio or effort-effectiveness relationship might possibly explain the different results since the areas Siegle (2009) covered with food were only 10 x 30 cm. This may have influenced the preference for dung which has a more favorable carbon–nitrogen (CN) ratio (Ouédraogo et al. 2004) and a higher weight per volume ratio than the other materials offered by Siegle (2009). The preference for straw despite its very low food quality (CN-ratio) could mean that the symbiotic opportunities available to fungus-growers could overrule for the need to be highly selective in terms of the CN-ratio, as was assumed by Freymann et al. (2008). The authors further hypothesized that this might be a way of avoiding pathogens since microclimatic conditions prevailing within the nests of fungus-growing species (high humidity, stable temperatures) could favor the settlement of entomopathogenic fungi and bacteria which hypothetically could be present in herbivore dung. It might also be more advantageous to forage on one rather than on varying food types (Freymann et al. 2008) since this might help to reduce the number of enzymes the fungal symbiont has to produce in order to degrade organic material (Rouland et al. 1991). A monophagous food choice, however, was not observed in the Zaï system. Sheetings of both genera were collected in all offered food types, only their foraging activity was highest in *A. kerstingii* hay (present study) or in dung (Siegle 2009).

However, although both genera fed on the same food types, limited separation in food selection as a strategy to avoid competition could explain the following observations. In the hay plots of the young forest, the cumulated area covered with *Macrotermes*-sheetings surpassed the area covered with *Odontotermes*-sheetings – and vice versa in the old forest (Fig. A8-16, Fig. A8-20). The same relations were observed with regard to the soil masses

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[1] *M. michaelseni* preferred grass litter on the ground when available but switched to standing crops as the ecosystem became more arid; the author concluded that this observation would explain how *Macrotermes* could become a pest (Lepage 1981).

bioturbated by both genera in hay-plots of the two forests (Fig. 8-11). In the end, sheetings of both genera together covered only a slightly greater area in the old than in the young forest (Fig. 8-13). Comparable observations were made in the compost-plots of both forests (Fig. A8-17, Fig. A8-21; Fig. 8-15), with the difference that most of the sheeting-soil collected in compost-plots was a mixture of both genera (sheetings could not be separated) (Fig. 8-11)

CORRELATION BETWEEN SHEETING-WEIGHT AND SHEETING-AREA

Differences in the area-weight correlation calculated for smaller sections of soil-sheetings[2] constructed by both genera on wood, hay and compost (called 'sheeting-sections') (Fig. 8-25) reflected in-situ observations regarding the sheetings consistency and resistance against crumbling (described in Chapter 8.2.1.4). Soil-sheetings consist of countless spherical or oval 'pellets' constructed from mineral soil particles which are transported with the mandibles and cemented with saliva (Noirot & Darlington 2000). Pellet-diameters are ranging between 50 µm and 1 mm (Eschenbrenner 1986), e.g. 20–50 µm in *Microtermes* and 100–500 µm in *Odontotermes*-sheetings (Kooyman & Onck 1987). Fungus-growers of the genus *Macrotermes* are the largest of all termites. Owing to the larger mandibles, pellets in *Macrotermes*-sheetings had about twice the diameter of pellets in *Odontotermes*-sheetings (Fig. A8-2, Fig. A8-3); and in fact, a square centimeter of sheetings built by *Macrotermes* had almost twice the weight of a square centimeter of *Odontotermes*-sheetings, irrespective of the site or food type covered (Fig. 8-26). Construction with clay as a structural and cementing material is common to many Macrotermitinae (Nye 1955; Wood 1988). Differences in the sheetings' clay content could theoretically also be an explanation for differences observed in their resistance. Dry season sheetings of both genera built on compost and hay had higher clay-contents compared to control soil, but only those of *Odontotermes* on wood (year-round) (Table A8-5, Table A8-6 in Appendix 8). Since all *Odontotermes*-sheetings were more fragile than those of *Macrotermes*, it is more likely that differences noted in the sheetings' resistance resulted from different pellet-diameters. Night-time foraging by *Macrotermes* species and differences in the termites' sheeting construction-behavior (described in Chapter 8.2.1.4) explained why the dry weight of sheetings built by *Odontotermes* in hay-plots (<u>not</u> the sheeting-sections) could be calculated by multiplying the sheeting-area with 14.8, for *Macrotermes* by multiplication with 5.8 (Fig. A8-23). To account for differences in the construction-behavior, additionally the height of sheetings should be measured in future studies.

SOIL-POROSITY VIA FORAGING-HOLES

The foraging activity of fungus-growers led to an increasing surface pore space with increasing habitat restoration. Owing to the termites' body size, foraging-holes (macropores) of *Macrotermes* had about twice the diameter (*Md* 8 ± 3.4 mm) of *Odontotermes*-holes (*Md* 4 ± 1.2 mm) (Fig. A8-24). Almost identical diameters were reported from Niger (Léonard &

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[2] For *Odontotermes*, the dry weight of sheetings could be calculated by multiplying the sheeting-area with 0.41 for *Macrotermes* by multiplying the area with 0.77.

Rajot 2001). Macropores up to 10 mm were measured by Mando and Miedema (1997); with reference to Kooyman and Onck (1987), the authors concluded that these voids were made by *Odontotermes smeathmani* (Fuller). Kooyman and Onck (1987), however, reported that the main foraging tunnels of *Odontotermes* species had diameters of 10–20 mm, but that the smaller secondary foraging tunnels which lead the workers to organic matter on the surface were 2–5 mm (mostly 3–3.5 mm) large.

The example of hay-plots illustrates the enormous effect termites had on macroporosity: The median macropore-number increased from 142 m^{-2} in the degraded, barren site to 163 m^{-2} in the millet field, to 669 m^{-2} in the young forest, and up to 921 m^{-2} in the old Zaï forest (Fig. 8-27). The numbers of foraging-holes in the present study are higher or of the same order of magnitude as in previously released publications where termites were attracted to organic material. For instance, 123 foraging-holes m^{-2} were assessed in Niger (Léonard & Rajot 2001); in a savanna in Senegal macropores reached a density of up to 300 m^{-2}, the mean number was 113 m^{-2} (Rouland et al. 2003)[3]; and in Burkina Faso, Mando and Miedema (1997) counted after two weeks foraging in mulched plots 86 ± 20 macropores m^{-2}. The macropore-number was linearly correlated to the area covered by sheetings, as was also noted by Rouland et al. (2003); however, both the sheeting-area and the dry weight were more accurate measures for termite activity. Moreover, the feasibility of counting foraging-holes depends greatly on the topography and the soil type; for instance, the gravelly and uneven surface millet field complicated the assessment of macropores immense.

EFFECT OF FORAGING-HOLES ON PONDED SOIL WATER INFILTRATION

By creating galleries connected to the soil surface by foraging-holes, termites had a significant influence on ponded water infiltration (Fig. 8-29). Compared to the control plots without recent activity, the infiltration rate with termite activity was increased by a mean factor 2–4 though the variability was quite high; in extreme cases in the dry season, infiltration in termite activity plots was up to 15 times higher (Fig. 8-29). The enormous increase in infiltration capacity may be explained with the findings that the most important factors controlling the hydrological behavior of soils in the arid and semi-arid Sahelian zone are the soil surface properties (Casenave & Valentin 1989), and that water infiltrates quickly through the walls of the gallery into the soil matrix (Léonard & Rajot 2001). The results are consistent with those obtained under similar conditions: In a savanna in Niger (mean rainfall 500 mm $year^{-1}$), foraging termites increased the infiltration rate 2–3 times; even the variability was comparable, increases up to 10 times were measured compared to crusted soil sites (Léonard & Rajot 2001). A termite channel of 0.8 cm diameter on bare Sahelian forest soils in Niger sustained a flow rate of 500–700 ml water min^{-1} for the duration of 30 minutes (Chase & Boudouresque 1987). Termites enhanced water infiltration and retention

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[3] Despite the longer experimental duration (five months dry season), the numbers should be comparable with those obtained in the degraded site or in the millet field since no material was replaced after complete consumption.

of topsoil in a Chihuahuan desert system (Elkins et al. 1986), and termite-made voids significantly increased water infiltration, soil water storage and drainage in northern Burkina Faso (Mando 1997). Some studies, however, revealed seemingly opposing results. For example, Mettrop et al. (2013) found that infiltration rates in the Sanmatenga region in Burkina Faso were significantly slower on plots affected by subterranean termite activity than on reference fields. In Kenya, Kooyman and Onck (1987) recorded increased levels of hydraulic conductivity in plots in which termite activity was obstructed. According to the authors, water flowed through the fine porous soil matrix whereas termite-made tunnels remained air-filled after rainfalls. This cannot be supported by observations in the Zaï stages; ponded infiltration could only be measured in plots with ≤ 600 macropores of *Odontotermes* per square meter. Moreover, in plots where both genera had foraged together or where *Macrotermes* was foraging alone, the subterranean gallery network was so extensive and the macropores that large that the water was infiltrating too fast for the measurements (reading and recording as described in Chapter 8.1.6).

PHYSICO-CHEMICAL PARAMETERS OF THE SHEETING-SOIL

In the present study, sheeting-soil differed strongly from control-soil as well as between the seasons, the food-type covered and the two genera. *Odontotermes*-sheetings differed in more parameters than *Macrotermes*-sheetings (Table 8-2). This is in accordance with previous studies which had shown that sheetings of different species can contain considerable quantities of nutrients (see below). The rate at which nutrients are returned to the surface soil determines the practical significance of the chemical enrichment. In contrast to long-lasting mounds, foraging structures are temporary structures which are easily redistributed by wind, erosion and weathering processes. Although the rate of disappearance has not been studied, it is assumed to be of high magnitude. Especially in semi-arid areas with scanty vegetation cover, sheeting-soil was assumed to exceed the contribution from the erosion of mound-soil (Bagine 1984; Lee & Wood 1971). Soil-sheetings may therefore have an important effect on local soil properties.

Most of the studies that investigated physico-chemical parameters of termite-modified soil analyzed mound-soil, much less considered the fungus-growers' sheeting-soil (Awadzi et al. 2004; Bagine 1984; Grohmann 2010; Jouquet et al. 2002a; Kooyman & Onck 1987; Lobry de Bruyn & Conacher 1990; Mora et al. 2003; Villenave et al. 2009). Ndiaye et al. (2004) concentrated on microbially-mediated nitrogen transformations (nitrification and denitrification) in termite-sheetings. Results obtained with regard to the sheetings' physico-chemical properties compared to control soil differed quite strongly between the studies.

SOIL HORIZON FROM WHERE THE SOIL USED TO CONSTRUCT SOIL-SHEETINGS ORIGINATES

To construct mounds and nests, fungus-growing termites were shown to gather soil from deeper horizons (Abe et al. 2009; Grohmann 2010; Konaté 1998; Kooyman & Onck 1987). However, to minimize energetic resources, it is likely that termites use different strategies to construct biogenic structures depending on whether they are lasting or temporary ones

(Jouquet et al. 2002a). By analyzing the nematofauna in soil-sheetings built by *Ancistrotermes guineensis*, *Odontotermes nilensis* and *Macrotermes subhyalinus* in a Sahelian savanna, Villenave et al. (2009) concluded that the soil used to construct sheetings originated from topsoil, as close as possible to the area where the food source was located. Similar findings are reported by Mora et al. (2003) and Jouquet et al. (2002a). Kooyman and Onck (1987), on the other hand, compared the grain size distribution and the sand-clay ratio in soil-sheetings of *Odontotermes kibarensis* and *Pseudacanthotermes spiniger* in Kenya and inferred that most of the soil was collected at a depth between 20 and 50 cm; the colors of sheetings indicated as well that the material was collected below the topsoil. The same findings are reported by Awadzi et al. (2004) from the moist semi-deciduous forest zone in Ghana; termite-modified soil in dead wood originated from a depth between 10 and 50 cm.

In the Zaï stages, soil profiles were dug to characterize the habitat soil (Fig. 4-2 to Fig. 4-5). Small-scale variations of soil parameters in habitats are known to be considerable (Petersen 2008) what allows direct comparisons only between parameters of sheeting-soil with those measured in the respective control-plot soil. Nevertheless, some trends may be compared. Especially the profiles of the two Zaï forests which had better developed soil horizons illustrate that the upper horizons had higher sand and lower clay-contents – the reverse was true in the lower horizons (Fig. 4-2 – Fig. 4-5). Compared to the adjacent control-soil, dry season-sheetings were composed of a significantly higher clay fraction and a similar sand fraction (Table 8-2); this implies that the soil used to construct sheetings was taken from deeper horizons – at least in parts. Rainy season-sheetings, on the other hand, had similar clay- and either lower or higher sand-fractions what would imply that the sheeting-soil was mainly taken from the topsoil. The differences noted in the clay–sand ratios might theoretically also be a result of clay particle selection by termites – however, it was shown that this is not the case (e.g. Jouquet et al. 2002a; Jouquet et al. 2002b for *Odontotermes pauperans*). It seems therefore more likely, that termites use topsoil and deep-soil in varying mixture-ratios. The admixture of some soil from lower horizons in sheetings built by *M. michaelseni* in Namibia was also assumed by Grohmann (2010). In the laboratory, Jouquet et al. (2002a) demonstrated that *O. pauperans* was able to utilize both top- and deep-soil when building galleries or sheetings but that they preferred the less costly topsoil; the reverse was true when building chamber walls. The use of top- and deep-soil in varying mixture-ratios could also explain the different findings reported in the literature, although care has to be taken since the term ‘topsoil’ is used differently. For instance, Jouquet et al. (2002a) used ‘topsoil’ interchangeable with ‘superficial soil’ for the horizon 15-20 cm, Villenave et al. (2009) and Grohmann (2010) used it for the 0-10 cm horizon like in the present study. The use of top- and deep-soil in varying mixture-ratios might, however, also explain the higher clay content measured in sheetings of the dry season compared to those of the rainy season run (Table 8-2). The present study seems to support another finding of Jouquet et al. (2002a). *Odontotermes* modulated the incorporation of carbon (C) and nitrogen (N) according to the type of the biogenic structure and the nature of the soil used. In foraging structures built with topsoil, less C and N was incorporated than in those built from deep-soil; the reverse was noted in chamber walls (Jouquet et al. 2002a). In the Zaï stages, soil organic matter and carbon (SOM and SOC) as well as N contents were significantly increased in all dry season sheetings, in the rainy season mainly in those built on compost (Table 8-2). Increases in clay and SOM are known to enhance the water-retention capacity, the soils' structural stability as well as the cation exchange capacity (CEC), and to contribute to the availability of nutrients (Dutartre et al. 1993; Jouquet et al. 2007; Mujinya et al. 2010; Tate 1987). Daytime temperature during the dry season can be very high in the sub-Sahel zone of Burkina Faso; increased stability and water retention capacity could thus help to protect foraging termites against desiccation. Accordingly, increased CEC values, higher contents of the agronomically important basic cations, especially potassium and magnesium (K^+, Mg^{2+}), in *Odontotermes*-sheetings mostly also sodium and calcium (Na^+, Ca^{2+}) as well as in plant-available nutrients were characteristic for most of the dry-season sheetings (the latter parameters were solely analyzed for the dry season samples) (Table 8-2; Table A8-7 and Table A8-8 in Appendix 8). Increases were also reported in other studies (e.g. Awadzi et al. 2004; Grohmann 2010; Kooyman & Onck 1987; Mujinya et al. 2010) albeit often to a lesser extent. The basic cations, N and SOM are constituents of plant tissue (Table 8-3) which was often assumed to be the origin of the increased contents in sheeting-soil (Awadzi et al. 2004; Bagine 1984; Lee & Wood 1971); they get probably incorporated into sheetings via salivary materials used by fungus-growers to cement the soil particles (pellets) together. The lesser changes mostly reported in the other studies with regard to the physico-chemical parameters of sheeting-soil compared to the surrounding soil may – apart from differences in the clay–sand ratio – for instance be due to differences in climate, habitat and soil type, the studied termite species, and their ecological requirements.

To summarize, the present study has shown that soil-sheetings can have an important effect on local soil properties and nutrient availability. Degraded, crusted soils are often unproductive because of nutrient imbalance but mostly because of water shortage; they cannot be rehabilitated unless the conditions necessary to reduce runoff from them are created (Mando 1997). Beneficial effects resulting from the termites' tunneling activities, namely soil turn-over (soil-formation), increased macroporosity and water infiltration capacity, as well as the effects resulting from their role as decomposers might therefore be more important for plant-growth.

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CONTENTS OF CHAPTER IX

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9. GENERAL DISCUSSION AND CONCLUSIONS

Many small-scale subsistence farmers in Burkina Faso depend on more or less degraded lands for agricultural production; they may be especially affected if losses of biodiversity lead to changes in ecosystem functioning. To understand how changes in biodiversity influence ecosystem properties and thus functioning requires a profound knowledge of the ‘functional traits’ of the species involved (Hooper et al. 2005). The overall aim of the present thesis consequently was to characterize the functional traits of termites and ants as they are of key ecological importance for a productive and balanced (soil) environment in the study region. They are ‘allogenic ecosystem engineers’ (Jones et al. 1997) whose activity and biogenic structures (e.g. nests, soil-sheetings, foraging holes) alter their abiotic or biotic surroundings. Their impact on soil functioning is very diverse and depends on the engineering species, the type and the total amount of their biogenic structures, its persistence over time, the engineers’ diet, and the soil type (e.g. Konaté et al. 1999; Lee & Wood 1971; Lobry de Bruyn & Conacher 1990). So far, no information was available about the actual diversity or the direction and magnitude of climatic- or anthropogenic-induced changes in the composition of termite and ant communities in Burkina Faso. The first objective of the present thesis consequently was the assessment of the invertebrate’s diversity under different land-use regimes, and the investigation of their response to changing habitat parameters resulting from increasing human impact (‘functional response traits’) (Chapter 3 – Chapter 5).

Two traditional agricultural systems were chosen in Burkina Faso; each represented a land-use intensification gradient comprising four distinct habitats that differed in the magnitude of human intervention. The first was located in northern Burkina Faso (Ouahigouya, sub-Sahel zone) and represented a successional cross-section of the traditional soil restoration technique Zaï, an impressive method used to restore barren, crusted soils and to improve agricultural production in a highly sustainable way; the second was located in the Gourma Province in the Southeast (North-Sudan zone) and represented an agriculture type using crop rotation and fallow as nutrient management techniques. In each habitat, I simultaneously assessed the intrinsic parameters of the termite and ant communities according to our newly revised rapid assessment protocol (RAP) (Chapter 3) and also several abiotic and biotic habitat parameters (Chapter 4). The RAP-protocol combines two widely accepted standard protocols designed to collect termites in tropical forests (Jones & Eggleton 2000) and ants in the leaf litter (Agosti & Alonso 2000), which were adapted to both the climatic conditions prevailing in semi-arid Burkina Faso and the limited size of the studied agro-ecosystems (each about one hectare). The following hypotheses were tested (Chapter 5): In the Zaï system, habitat heterogeneity and crown-cover percentage steadily increase with decreasing intensity and duration of anthropogenic impact. I therefore assumed that species richness and the diversity of termites and ants would increase from the degraded, barren land to the millet-fields, to the young forest, and then to the most rehabilitated stage, the old Zaï forest. In the agricultural system in the North-Sudan zone, the physical structure of the habitat simplifies progressively with increasing intensity of anthropogenic impact, and tillage during the cropping seasons was constantly disturbing the soil profile in the agricultural sites. Hence, I assumed that species richness and the diversity of the focal arthropods would decrease with increasing land-use intensity, i.e. from the near-natural savanna, to the pasture, the short-term fallow, and then the cotton fields with recent pesticide application.

To allow for the identification of those habitat parameters which exert significant influence on the composition of termite and ant communities (‘predictor variables’), two conditions had to be met in the site selection: All land-use types belonging to the same gradient originally had the same initial stage (vegetation, soil, species pool), and their history of exploitation since the initial stage had to be known. The RAP-protocol proved to be very effective to representatively characterize, compare and monitor the termite and ant fauna in the land-use types selected in semi-arid Burkina Faso. Together in both regions, 65 ant species (25 genera) and 39 termite species (13 genera) were collected. In the Zaï system, 41 ant species and 33 termite species were collected; in the agricultural system of the North-Sudan region, 53 ant species and 31 termite species (Chapter 5). To my knowledge, these findings represent the first records for Burkina Faso. Direct comparisons with other studies are hampered due to differences in e.g. the soil type, the annual rainfall, or the intensity of agricultural activity. However, visible trends are compared and discussed in Chapter 5.

The results indicate a high sensitivity of termites and ants to land-use intensification. The strongly decreasing termite diversity with increasing anthropogenic impact in the North-Sudan region confirmed the hypothesis, and is in accordance with other regions where termite communities were consistently found to be less diverse in disturbed habitats (e.g. Davies et al. 1999; Donovan et al. 2007; Gathorne-Hardy et al. 2006; Vaessen et al. 2011) and where crops and plantations hosted less species than nearby natural vegetation (Black & Okwakol 1997). Likewise, the ants’ species richness clearly decreased from the savanna towards the cotton fields, similar to the observations in other regions (e.g. Lobry de Bruyn 1999; Majer & Beeston 1996; Yéo et al. 2011). Promising results concerning the recovery potential of the soil-arthropods’ diversity were gathered in the Zaï system. The data collected are consistent with my assumptions; species richness and diversity of both taxa strongly increased with increasing habitat rehabilitation. It appears that the massive loss of diversity in termite and ant communities with increasing anthropogenic pressure (as in the North-Sudan zone) seems to be reversible with the Zaï technique. The recovery potential of termite communities has already been studied in Australia (Gathorne-Hardy et al. 2002) and the Amazon region (Dibog et al. 1999). However, to my knowledge, no study investigated the recovery potential of termite and ant communities in fully degraded, barren and crusted soils. Therefore, clearly more studies are needed that focus on techniques that support or fasten the recovery of termite and ant communities in previously highly degraded or intensified systems – in other arid and semi-arid regions, but also in regions with higher precipitation, for instance in regions where the cultivation of cash crops (e.g. cotton, coffee, sugar cane, oil palm) left behind highly contaminated or devastated land. Future studies should also address the question how distant the source for the arthropods' resettlement can be.

The relative abundance of termite and ant species and functional groups differed significantly along the gradients. Fungus-growing termites showed the greatest adaptability to different management practices; they dominated the communities in all habitats supporting findings in other studies and regions (e.g. Bignell & Eggleton 2000; Schuurman 2006; Turner 2006). The greatest variations between the habitats in the present study were observed in soil and grass-feeding termites. The findings agree with other authors who found that soil feeders are more vulnerable to cultivation than other functional groups (e.g. Bandeira & Vasconcellos 2002; DeSouza & Brown 1994; Eggleton et al. 1997). The results demonstrate clearly that whole functional groups are missing in heavily impacted habitats[1]. Comparable observations were made e.g. by Gathorne-Hardy et al. (2002) who studied termites in different habitats in Borneo and Sumatra; in the most disturbed habitats, a grassland covered with *Imperata cylindrica* and a cassava field, only two functional groups based on the classification of Donovan et al. (2001) remained: Macrotermitinae and *Amitermes*-group (feeding group II; wood and litter feeders) and *Termes–Capritermes* group (feeding group III/IV; soil-wood interface feeders).

A canonical correspondence analysis was conducted to identify the aforementioned predictor variables. Although the results should be interpreted cautiously due to strongly a reduced number of species considered in the analysis and the lack of plot replicates for most land-use types, the results mainly indicate the importance of the habitats' structural complexity (vegetation structure) and concomitant effects on diurnal temperature and moisture fluctuations, the availability of food sources, and the soil-structure (also affecting soil moisture): The diversity of termites in the sub-Sahel region was strongly correlated with the habitats' crown-cover percentages, the sand content in the topsoil, and the availability of litter in the sections of the RAP-transects. The parameters identified in the North-Sudan region are the cumulated woody plant basal area, the topsoils' clay- and organic matter-content. The predictor variables identified for ant communities in the sub-Sahel region were the height of trees, the topsoils' clay content and the air humidity; a great part of the variations assessed in the North-Sudan region could be explained by changes in the habitats' crown-cover percentages, the quantity of litter, and again the height of trees. Most of the few studies that simultaneously assessed the local or regional termite and/or ant fauna and

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[1] Soil and grass-feeders were absent in the cotton fields and neither soil, nor grass-, nor wood-feeders were present in the degraded barren site in the sub-Sahel zone.

also the abiotic and biotic habitat parameters were undertaken in humid regions of Asia and Africa, mostly in forest habitats. Nevertheless, the predictor variables identified generally agree with those obtained for termite communities (Dibog et al. 1999; Eggleton et al. 2002; Eggleton et al. 1997; Jones 2000; Jones & Prasetyo 2002) and ant communities (Delgado et al. 2008; Luke 2010; Teodoro et al. 2010). Due to the close vicinity of the study sites within a study region, air temperature did not differ significantly and was therefore not influential as in some of these previous studies.

To summarize, definitely much work remains to be done on environmental parameters shaping the composition of termite and ant communities – particularly in arid and semi-arid tropical regions – before one can reliably predict the response of these important ecosystem engineers to different scenarios.

The first part serves as a baseline study for the second thesis part (Chapter 6 to Chapter 8) where I addressed the impact of the biogenic structures built by the focal invertebrates ('functional effect traits'). I followed two approaches to investigate the arthropods' bioturbation activity. In the first one, I rapidly assessed the (natural) variations in soil turn-over in all study sites to judge the relative importance of termite and ant structures for soil turn-over (without attracting them with organic material as in the experiment) (Chapter 7); the second approach was based on a field experiment where termites were actively attracted to organic materials (Chapter 8).

The first approach illustrated impressively that in the Sudano-Sahelian zone of Burkina Faso, termites are the main bioturbators while ant structures seemed of minor importance for soil turn-over. The dominance of Macrotermitinae which was observed during the diversity assessment was even more pronounced in terms of soil turn-over. In the sub-Sahel zone, fungus-growing *Odontotermes* and *Macrotermes* species fully take over the important function of bioturbation. The results further suggested that the bioturbation activity of termites may account for the differences observed between the soil profiles of the four Zaï stages (Fig. 4.1, Chapter 4) – with increasing habitat restoration, coarse fragments decreased in the upper horizons and became concentrated deeper along the soil profile. To verify this assumption, the mean dry weight of biogenic structures (Chapter 7) was taken to estimate the height of the layer possibly accumulated with termite-soil on the surface since the beginning of the restoration process. Although it has to be stressed that the calculation contains to a considerable error probability (see explanations in Chapter 7), the resulting layer for the 30-years old Zaï forest was 10.7 cm; this coincides with Kooyman and Onck (1987) who estimated that termite-soil may account for about 20% of the soil matrix. The few comparable figures in the literature (most studies so far assessed the influence of mounds) are much lower. In an arid savanna in Kenya, about 2,200 kg soil-sheetings ha^{-1} year^{-1}, equivalent to 0.06 cm were built by two *Odontotermes*-species (Bagine 1984), and more than 10,000 kg ha^{-1} year^{-1} (equivalent to 0.27 mm) were reported by Wood (1988) for African savannas and forests.

That termites play an important role in the functioning of the Zaï system was acknowledged by several authors (Kaboré & Reij 2004; Laguemvare 2003; Reij et al. 2009; Roose 1994).

However, to my knowledge, no study was conducted to identify the most influential taxa and the ecosystem services they provide in the different stages of the restoration process. These information, however, are crucial when aiming to manage the biological component of the system in order to fasten or enhance the restoration process. Since it is generally not possible to follow a restoration process during a sufficiently long period, the Zaï system in Ouahigouya provided the perfect place to answer these questions. All succession stages of the restoration process are present (agricultural and forestry Zaï) and could be studied simultaneously, their site history is known and the small-scale farmer and land-owner Yacouba Sawadogo allowed unrestricted access to his land. The few *Macrotermes* mounds in the Zaï forests were small and *Odontotermes* nests are fully subterranean (see Chapter 4). Soil-sheetings, on the other hand, were omnipresent in all succession stages; they were assumed to be responsible for the greatest part of soil turn-over in the Zaï system. To understand the role of termites in the process of soil-restoration, I therefore concentrated on the sheeting-construction behavior of fungus-growers. A split-plot design with 36 experimental plots of 1 m^2 area in each Zaï stage was used to attract termites with locally available hay (*Aristida kerstingii*), wood (*Bombax costatum*), and compost and to test the following assumptions:

- *Macrotermes* and *Odontotermes* species are the most influential ecosystem engineers in the restoration of degraded, barren and crusted soils in the sub-Sahel region;
- their foraging activity can be induced and the amount of foraging structures multiplied;
- the foraging activity differs depending on the food type and the foraging species;
- the increased soil bioturbation rate will positively alter the soils' structure – foraging holes break the soil crusts open and increase the macroporosity in all stages, thereby leading to a significantly increased water-infiltration rate;
- the physico-chemical properties of sheeting-soil will differ from the habitats' topsoil (higher nutrient contents, higher clay-contents, etc.) and between the two genera.

The soil-masses bioturbated to construct sheetings in the experimental plots and the increasing areas covered with sheetings were quantified, the physical-chemical properties of the sheeting-soil were analyzed and the effect of foraging-holes on ponded water infiltration capacity was measured at the end of the experimental 4-weeks duration. The results obtained supported all assumptions and confirmed that *Odontotermes* and *Macrotermes* species are the main soil bioturbators year-round like in other semi-arid savanna and agro-ecosystems in Africa (Lepage 1974; Rouland et al. 2003; Schuurman 2006). *Odontotermes* was the decisive primary physical ecosystem engineer, initializing the Zaï restoration process in the degraded barren stage. In contrast to other studies where *Macrotermes* species caused agricultural damage to crops (e.g. Collins 1981; Lepage 1981; Togola et al. 2012), *Macrotermes* species were only found in the two Zaï forests. *M. bellicosus* was found in both forests, *M. subhyalinus* only in the old one. In the dry season run, *Odontotermes* translocated 31.8 tons of soil per hectare and month in the degraded area, and 32.4 tons ha^{-1} mon^{-1} in the millet fields; and both taxa moved 138.9 tons ha^{-1} mon^{-1} in the young and 215.5 tons ha^{-1} mon^{-1} in the old Zaï forest. The best surrogates for the foraging and bioturbation activity were i) the dry weight of soil bioturbated to construct soil-sheetings and ii) the increasing area covered with sheetings. Few comparable studies were found in the literature; in northern Burkina Faso, both genera constructed 20 tons of sheetings ha^{-1} mon^{-1} after mulching with a straw-wood mixture (Mando & Miedema 1997), and around 10 tons ha^{-1} mon^{-1} were moved in heavily foraged plots in Senegal (Rouland et al. 2003).

Hay was the most attractive bait in both seasons and all stages. Within a site, the cumulated soil turn-over and number of foraging holes created was always highest in hay, followed by compost, then by wood, and in the end control. Similarly, a preference for straw was reported for *Odontotermes* (Bagine 1984), *Macrotermes* (Lepage 1981), or different fungus-growing species (Freymann et al. 2008). Possible explanations for the preference for straw despite its very low food quality (CN-ratio) might be that the symbiotic fungus could overrule for the need to be highly selective in terms of the CN ratio, or it might be a way of avoiding pathogens since microclimatic conditions within the nests could favor the settlement of entomopathogenic fungi theoretically present in herbivore dung (Freymann et al. 2008). A food choice experiment in the same study area revealed opposing findings; *Odontotermes* preferred dung over straw and wood (Siegle 2009). Due to a more favorable carbon-nitrogen (CN) ratio of dung (Ouédraogo et al. 2004), a better effort-effectiveness relationship may explain this contrasting finding, since the areas covered with organic matter were only 10 x 30 cm large (Siegle 2009). Limited separation in food selection as strategy to avoid competition (Dangerfield & Schuurman 2000) could explain why the cumulated dry weight and area of *Macrotermes* sheetings in hay- and compost-plots of the young forest surpassed the area and dry weight of *Odontotermes* sheetings – and vice versa in the old forest.

Odontotermes located the food sources in most cases faster than *Macrotermes*. However, once it was located, *Macrotermes* exploited the organic material often faster than *Odontotermes*. Comparable findings are reported by Siegle (2009), Schuurman (2006), and Rouland et al. (2003). A strongly exploratory behavior of *Odontotermes* (Buxton 1981) could explain the faster food location. It might, however, also be that the number of *Odontotermes* colonies surpassed the number of *Macrotermes* colonies thereby leading to more advantageous positions within the habitat, closer to the experimental plots. Unfortunately, except for the foraging structures no epigeal traces indicated the presence of *Odontotermes* colonies in the Zaï stages, in contrast to the North-Sudan region where *Odontotermes* exhibit the ‘classical’ nest type (Darlington 1997) with a raised surface devoid of vegetation. Intra- and interspecific aggressions between neighboring *Macrotermes* colonies of the same and different *Macrotermes* species (Darlington 1982; Kettler & Leuthold 1995; Sugio 1995) may have inhibited the enlargement of their feeding territories in the old forest, thereby accounting for the lower bioturbation activity in this habitat. The feeding territory of *Macrotermes* species, a network of underground tunnels around the nest (Jmhasly & Leuthold 1999), can radiate for more than 50 m into surrounding soils (Turner 2006). The two adult *Macrotermes* colonies in the young forest may thus easily span the hectare-plot, leading to the higher soil turn-over activity. No evidences for an intra- or interspecific competition have been found for *Odontotermes*, neither in the Zaï system nor in the literature. The faster food location may thus also be a result of overlapping feeding territories in *Odontotermes* and separated territories in *Macrotermes*.

The number of foraging-holes created during the dry season run was higher or of the same order of magnitude as in previously released publications where termites were attracted to organic material (Léonard & Rajot 2001; Mando & Miedema 1997; Rouland et al. 2003): In hay-plots, the median number increased from 142 m^{-2} in the degraded site up to 921 m^{-2} in the old Zaï forest. After the experimental 4-weeks duration, the water infiltration rate was significantly increased by a mean factor 2–4. By creating galleries connected to the soil surface by foraging holes, termites modified the soils' structure and surface properties which are mainly controlling water infiltration in the Sahelian zone (Casenave & Valentin 1989).

Laboratory analyses revealed that sheeting-soil differed significantly from the control soil without recent termite activity as well as between the seasons, the food-type, and the two genera. *Odontotermes*-sheetings differed in more parameters than *Macrotermes*-sheetings, and dry season sheetings differed in more parameters (and more strongly) than rainy season sheetings. For instance, dry season-sheetings had higher clay- and similar sand-contents, an increased electrical conductivity, and they had higher organic matter (OM) and nitrogen (N) contents what implies that the soil used to construct sheetings was taken – at least in parts – from deeper horizons. This conclusion is supported by Jouquet et al. (2002) who showed in laboratory experiments that *Odontotermes pauperans* was able to utilize both top- and deep-soil for their structures and evidenced that the species supplied more or less OM and selected more or less fine particles according to the purpose of the structure. Soil-sheetings are temporary structures used to explore the outside environment whereas mounds are perennial structures that protect the colony. In sheetings, *O. pauperans* preferred the less costly top-soil in which they incorporated less carbon and N than in those built from deep-soil – the reverse was noted in chamber walls (Jouquet et al. 2002). *Macrotermes* species modify the mound-soil and the architecture of their mounds in order to maintain an adequate moisture regime for the termite-fungus symbiosis (Harris 1956; Holt & Lepage 2000; Korb & Linsenmair 1998; Sileshi et al. 2010). Biogenic structures are leading to the decrease of environmental hazards, a better protection against predators and to the optimisation of colony development (Jouquet et al. 2006), and can thus be considered as an extended phenotype (Jones et al. 1997). Increases in clay and OM contents enhance the soils' water-retention capacity, the structural stability and cation exchange capacity (Jouquet et al. 2007; Mujinya et al. 2010; Tate 1987). Daytime temperature in the dry season can be very high in the sub-Sahel zone of Burkina Faso, higher than in the rainy season – the increased stability and water retention capacity could thus help to protect foraging termites against desiccation. The present study therefore confirms that biogenic structures are the reflections of the environmental properties and of the engineers' responses to such properties at a given time (Jouquet et al. 2006). The burrowing activities of termites and ants while constructing their biogenic structures are continuously mixing eroding sheetings with the surrounding soil, in the longer-term leading to surface horizons which are mainly composed of an accumulation of these biogenic structures (Lavelle et al. 1997).

It is difficult to decide which of the services provided by foraging termites are the most important in the restoration process. Their relative importance will differ depending on the stage of Zaï restoration. Of crucial importance in all stages will be the decomposition of organic matter since termites are the only active decomposers in the sub-Sahel zone of Burkina Faso (Mando & Brussaard 1999). Degraded crusted soils are unproductive because of nutrient imbalance, but mostly because of water shortage (Mando 1997). I therefore assume that in the degraded, barren habitat stage, the most important service is the initiation of the restoration process by *Odontotermes* via the construction of subterranean foraging-tunnels and foraging-holes; this allows rainwater to infiltrate, leads to a better oxygen supply and enables root penetration, thereby creating the conditions necessary and sufficient for woody vegetation and herbs to re-establish.

9.1 CONCLUSIONS

The experiment has provided conclusive evidence of the importance of fungus-growing termites (particularly *Odontotermes* and *Macrotermes* species) for the restoration of fully degraded soils and a sustainable agricultural production in the Sahel-Sudanese zone of West Africa. The findings contribute towards a better understanding how restoration efforts can be most effectively partitioned between direct human intervention and natural ecosystem engineers.

Given the importance of the focal arthropods and their biogenic structures for the functioning of (agro-) ecosystems and soil-restoration, one can easily imagine that the enormous loss of taxonomic and functional diversity in heavily impacted habitats may have disastrous consequences for small-scale subsistence farmers, impeding a sustainable agricultural production. A very important and promising finding of this study was therefore the recovery potential of termite and ant communities in fully degraded, barren and crusted soils with the Zaï method. Clearly, more studies are needed that focus on methods that support and fasten the recovery of communities in highly impacted and degraded systems. Future studies should also address the question, how distant an area may be which can act as a reservoir (species pool) for the focal arthropods when conditions improve.

Macrotermitinae termites are generally considered as one homogeneous functional group, particularly regarding their influence on ecosystem functioning (Bignell & Eggleton 2000; Lavelle et al. 1997). However, the assessment of the diversity of termites and ants and of their response to changing environmental conditions resulting from increasing human impact, and the differences noted in the foraging and soil turn-over behavior of *Odontotermes* and *Macrotermes* illustrate clearly that both the functional response and the functional effect traits can differ greatly among species, even when belonging to the same functional group. Services provided by one species cannot be automatically equated with those provided by another species. Therefore, when aiming to predict the influence of termites and ants in a given ecosystem, one has to have a sound picture of the taxonomic composition of their communities and the biological attributes of each species.

From the findings of the present study, several recommendations can be derived how to counteract the great losses and how to maintain a diverse termite fauna. For instance: i) limiting firewood collection, leaving dead wood (also on standing vegetation) and crop residues after the harvest; ii) mulching degraded, barren areas with twigs and dry grass helps to catch wind-blown material (sand, seeds, litter), to induce the termites' foraging activity, to decrease direct sun radiation and soil evaporation, and to protect the soil against erosion; iii) including shady trees in agricultural fields whenever possible; iv) maintaining a landscape matrix with areas which may act as a reservoir (species pool) for the focal arthropods; v) leaving live termite mounds in agro-ecosystems untouched; vi) work-shops for small-scale farmers, e.g. to explain how to make sustainable use of the ecosystem services provided by termites and ants, to point out that diverse communities can strongly increase the habitats resilience to disturbances, to show the most influential taxa, and to convince them not to destroy termite mounds for the use of their soil as fertilizer.

To summarize, the present thesis contributes to a better understanding of the functional response traits of the focal invertebrates, as well as of the functional effect traits of *Odontotermes* and *Macrotermes* species which are of crucial importance when aiming to restore degraded, crusted land in the sub-Sahel zone of Burkina Faso. However, much work remains to be done at different scales of time and space to fully understand and predict the consequences of land-use intensification or climate change on the composition of termite and ant communities and the ecosystem processes they promote.

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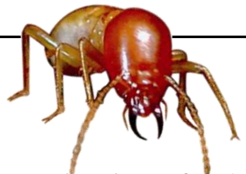

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EHRENWÖRTLICHE ERKLÄRUNG

Gemäß § 4, Absatz 3, Ziffer 3, 3a, 3b, 5 und 8 der Promotionsordnung für die Fakultät für Biologie der Bayerischen Julius-Maximilians-Universität Würzburg vom 15. März 1999, zuletzt geändert durch die zweite Satzung vom 14. November 2013, erkläre ich hiermit ehrenwörtlich, dass ich die vorliegende Dissertation eigenständig und ohne Hilfe einer kommerziellen Promotionsberatung angefertigt habe, und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe. Ferner versichere ich an Eides statt, dass ich die Gelegenheit zum Promotionsvorhaben weder kommerziell vermittelt bekommen habe, noch eine Person oder Organisation eingeschaltet wurde, die gegen Entgelt Betreuer für die Anfertigung der Dissertation gesucht hat. Ich erkläre außerdem, dass ich die Regeln der Universität Würzburg über gute wissenschaftliche Praxis eingehalten habe. Die Dissertation hat keinem anderen Prüfungsverfahren vorgelegen, weder in gleicher noch in ähnlicher Form.

Die Mathematisch-Naturwissenschaftliche Fakultät der Universität in Rostock hat mir am 21.10.2002 den Titel „Diplom-Biologin" verliehen. Weitere akademische Grade habe ich weder erworben noch zu erwerben versucht.

Würzburg, 05. April 2014

Dorkas Kaiser