

**Role of termites for the distribution patterns of carbon and
phosphorus fractions and
the genesis of tropical soils, Brazil**

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Abbreviations

The common abbreviations of chemical elements are not listed.

A	outer nest wall
AAS	flame atomic absorption spectroscopy
ac/al	ratio of acids to aldehydes of the phenolic oxidation products, higher values indicate higher oxidation of the lignin
(ac/al)_S	ratio of acids to aldehydes of the syringyl phenolic oxidation products, higher values indicate higher oxidation of the lignin
(ac/al)_V	ratio of acids to aldehydes of the vanillyl phenolic oxidation products, higher values indicate higher oxidation of the lignin
Al_d	free pedogenic aluminium-oxides, extracted with dithionite-citrate buffer
Al_o	active aluminium-oxides, extracted with acid oxalate solution
ANOVA	Analysis of variance
B	inner nest wall
¹³C/¹²C	ratio of the heavier to the lighter stable carbon isotope
C	central nest part <i>or</i> carbon
C.	<i>Cornitermes</i>
C₃	C ₃ plants use one of three biochemical mechanisms to fix carbon, C ₃ is the dominating photosynthesis pathway occurring in humid areas
C₄	C ₄ plants use one of three biochemical mechanisms to fix carbon, C ₄ is more common in drier areas like savannas
cf.	confer, similar to
C/V	ratio of cinnamyl to vanillyl phenolic oxidation products, higher values indicate higher oxidation of the lignin or a higher proportion of herbaceous lignin
CEC_{pot}	potential cation exchange capacity
δ	the chemical shift of NMR spectroscopy
δ¹³C	¹³ C/ ¹² C ratio in the common notation relative to the international standard
DOC	dissolved organic carbon
Fe_d	free pedogenic iron-oxides, extracted with dithionite-citrate buffer
Fe_o	active iron-oxides, extracted with acid oxalate solution

Abbreviations

FID	flame ionization detector
GC	gas chromatography
HCl_{conc}-P_i	inorganic P occluded in sesquioxides; very stable; extracted with concentrated HCl
HCl_{conc}-P_o	organic P not alkali extractable, but may potentially be bioavailable; extracted with concentrated HCl
HCl_{dil}-P_i	inorganic P bonded in Apatite; extracted with 1 M HCl
ICP-AES	inductively coupled plasma atomic emission spectrometry
MIRS	Mid-infrared spectroscopy
n	number of observations
N.	<i>Nasutitermes</i>
NaHCO₃-P_i	inorganic P bonded to Fe and Al oxides; plant available; extracted with 1 M NaHCO ₃
NaHCO₃-P_o	organic P bonded to Fe and Al oxides; easily mineralizable; extracted with 1 M NaHCO ₃
NaOH-P_i	inorganic P bonded to Fe and Al oxides; moderately labile; extracted with 0.1 M NaOH
NaOH-P_o	organic P bonded to Fe and Al oxides; relatively stable; extracted with 0.1 M NaOH
nd	not detected
NMR	nuclear magnetic resonance
OC	organic carbon
P	significance level
P_i	inorganic phosphorus
P_o	organic phosphorus
P_t	total phosphorus
pH	pondus Hydrogenii, negative decadic logarithmic of the hydrogen ion activity in an aqueous solution
PLSR	partial least squares regression
R²	coefficient of determination
residual-P	comprises highly resistant and occluded P forms; extracted with aqua regia
resin-P_i	inorganic P bonded to surfaces of crystalline compounds; easily plant available; extracted with water and adsorbed to resin strips
RMSECV	root mean square error of cross validation
RPD	relative percent deviation

<i>sp.</i>	species, abbreviated when only the genus is known
S/V	ratio of syringyl to vanillyl phenolic oxidation products, lower values indicate higher oxidation of the lignin
v/v	volume/volume
VSC	sum of vanillyl, syringyl, and cinnamyl phenolic oxidation products
VSC-lignin	lignin determined by the CuO oxidation method and summing the phenolic oxidation products
w/v	weight/volume

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Summary

Tropical soil fertility is limited by low phosphorus (P) availability, limited accumulation of organic matter and by advanced stages of pedogenesis. Termites are well-known soil-engineers, which accumulate clay, organic matter and many nutrients inside their nests. However, the differences between the effects of various termite feeding guilds on soil properties, the influence of termite activities on the properties and genesis of surrounding soil, and the persistence of the termite-induced changes in soils are largely unknown. The aim of the present work was, therefore, (i) to study the effect of different termite feeding guilds on P forms in termite nests across seven tropical ecosystems of Brazil, (ii) to elucidate the spatial and temporal effects of the termites dominant in Cerrado pastures on P distribution patterns and soil genesis, (iii) to use lignin, which is not digested by termites, as a tracer of their influence on soil organic matter accumulation, and finally, (iv) to decipher the impact of the Cerrado termites on nutrients in water drained from termite mounds.

To achieve these objectives I characterized termite nests and transects of surrounding soils by sequential P analyses, ^{31}P NMR spectroscopy, and detection of the contents of organic carbon (OC), nitrogen and lignin-derived phenols. Due to the large sample size, mid-infrared spectroscopy followed by partial least squares regression helped in screening these soil properties for the first time also in the matrix of tropical soils.

The P contents were higher in nests and exceeded those of the surrounding soil by up to 3650%. Especially the wood-feeding termites changed the P availability to more labile forms; whereas the soil/wood interface-feeder termites enriched also mineral-bound P in their nests. For the *Cornitermes silvestrii* of the Cerrado, higher contents of labile soil P were documented vertically down to 30 cm below the lower nest border, and to a lateral distance of 60 cm away from it. Similar patterns were found for OC and lignin, whereas the enrichment and the spatial extension of those constituents were smaller below older, secondarily inhabited mounds. Hence, the lignin was initially accumulated in younger mounds, but it was oxidized and decomposed in older nests. The volume of draining water was reduced below both the younger and the older termite mounds in comparison to the soil, but five times lower dissolved organic carbon fluxes, and three times higher nitrate concentrations were only recorded under older mounds. Also the effect of termites on the physical composition of the soil was only significant below older mounds. There, the argic horizon disappeared, thus changing the soil type from Alisols and Acrisols to Umbrisols or Regosols.

In summary, my data show that wood-feeding termites of Brazil enhance the availability of P, and that the termites of the Cerrado transport clay upwards and accumulate labile P as well as lignin inside their mounds and the adjacent soil in comparison to reference soils. Such elevated contents are, to a lesser degree, also persistent below older mounds, as are the changed soil types. Those changes in soil types comprise the most long-lasting

Summary

impact of the termites on the soil in the introduced pasture agro-ecosystem, as the upward transport of clay inverts soil genesis.

Zusammenfassung

Die Bodenfruchtbarkeit in den Tropen ist durch eine geringe Verfügbarkeit von Phosphor (P), die fehlende Anreicherung von organischer Substanz und die fortgeschrittene Pedogenese eingeschränkt. Termiten sind als Boden-Ingenieure bekannt, die Ton, organische Substanz und viele Nährstoffe in ihren Nestern anreichern. Die Unterschiede zwischen den Effekten von Termiten unterschiedlicher Nahrungsgilden auf Bodeneigenschaften sind jedoch ebenso wenig bekannt wie die Beeinflussung von Eigenschaften und Genese des nestumgebenden Bodens durch Termitenaktivitäten sowie die Persistenz der von Termiten verursachten Veränderungen im Boden. Das Ziel der vorliegenden Arbeit war es deshalb (i) die Effekte von Termiten unterschiedlicher Nahrungsgilden auf P-Fractionen in ihren Nestern in sieben tropischen Ökosystemen Brasiliens zu beschreiben, (ii) die räumlichen und zeitlichen Effekte von Termiten, welche in Weiden des Cerrado dominieren, auf die Verteilungsmuster von P und die Pedogenese zu verdeutlichen, (iii) Lignin, welches von Termiten nicht verdaut wird, als Marker für die Anreicherung von organischer Substanz durch Termiten zu nutzen und schließlich (iv) den Einfluss der Termiten des Cerrados auf Nährstoffe in der Bodenlösung zu untersuchen.

Um diese Ziele zu erreichen, habe ich Termitennester und Transekte der angrenzenden Böden mit sequenzieller P-Extraktion, ^{31}P -NMR-Spektroskopie, sowie den Gehalten von organischem Kohlenstoff (OC), Stickstoff und ligninbürtigen Phenolen charakterisiert. Infrarot-Spektroskopie in Kombination mit dem PLS-Verfahren half bei der Analyse dieser Bodeneigenschaften in dem großen Probensatz und wurde zum ersten Mal für tropische Böden angewendet.

Die P-Gehalte waren in Termitennestern teilweise bis zu 3650% höher als im nestumgebenden Boden. Insbesondere die holzfressenden Termiten erhöhten den Anteil leicht verfügbarer P-Formen, während geophage Termiten auch mineralgebundenen P in ihren Nestern anreicherten. Höhere Gehalte von leicht verfügbarem P wurden für *Cornitermes silvestrii* im Cerrado bis 30 cm unterhalb der unteren Nestgrenze und bis zu einer horizontalen Entfernung vom Nest von 60 cm nachgewiesen. Ähnliche Verteilungsmuster wurden für OC und Lignin dokumentiert, wobei die Gehalte und die räumliche Ausdehnung aller genannten Komponenten unter alten, sekundär bewohnten Termitennestern etwas geringer waren. Das bedeutet, dass Lignin zwar in jungen Nestern angereichert wird, aber dass es während der Nestalterung oxidiert und abgebaut wird. Das Volumen des Sickerwassers war sowohl unter jungen als auch unter alten Nestern im Vergleich zum Boden reduziert, aber nur unter den alten Nestern wurden fünfmal so niedrige Flüsse des gelösten organischen Kohlenstoffs und dreifach erhöhte Nitrat-Konzentration verzeichnet. Auch der Einfluss der Termiten auf die Bodenstruktur war nur unter alten Nestern signifikant. Dort war kein argic-Bodenhorizont vorhanden, was den Bodentyp von Alisols und Acrisols zu Umbrisols und Regosols veränderte.

Zusammenfassung

Insgesamt zeigen meine Daten, dass holzfressende Termiten aus allen Teilen Brasiliens die Verfügbarkeit von P erhöhen, und dass die Termiten des Cerrado Ton aufwärts transportieren, sowie verfügbaren P und Lignin in ihren Nestern und im angrenzenden Boden im Vergleich zum Referenzboden anreichern. Auf einem niedrigeren Level sind solche erhöhten Gehalte, genauso wie die geänderten Bodentypen, auch unter älteren Nestern feststellbar. Diese geänderten Bodentypen beinhalten den langfristigen Einfluss der Termitenaktivität auf den Boden im neuentstandenen Weideland, da die aufwärts gerichtete Tonverlagerung der Pedogenese entgegenläuft.

Sumário

A fertilidade dos solos tropicais é limitada pela baixa disponibilidade de fósforo, a falta de acumulação de matéria orgânica, e por estados avançados de pedogênese. Os térmitas ou cupins são bem-conhecidos 'engenheiros de ecossistemas', acumulando argila, matéria orgânica e muitos nutrientes nos seus ninhos, os cupinzeiros. Porém, as diferenças entre os efeitos de várias guildas alimentares de cupins sobre as propriedades de solo, a influência das atividades dos cupins na qualidade e gênese do solo adjacente, e o grau de persistência dos câmbios observados, são fatores não muito bem conhecidos. Por isso, o objetivo do presente trabalho foi de (i) estudar o efeito de diferentes guildas alimentares de cupins sobre as formas de fósforo nos cupinzeiros em sete ecossistemas tropicais do Brasil; (ii) elucidar os efeitos espaciais e temporais das espécies dominantes em pastagens do cerrado sobre padrões de distribuição de fósforo e sobre a gênese dos solos; (iii) usar a lignina, a qual não é digerida pelos cupins, como um indicador da influência dos cupins sobre a acumulação da matéria orgânica do solo, e (iv) decifrar o impacto das espécies de cerrado sobre os nutrientes na água drenada dos cupinzeiros.

Para alcançar estes objetivos, eu caracterizei ninhos de cupins e transectos de solos adjacentes através de análises sequenciais de fósforo, espectroscopia NMR usando o isótopo ^{31}P , e detecção dos conteúdos de carbono, nitrogênio e de fenóis derivados de lignina. Por causa do grande número de amostras, espectroscopia das bandas médias de infravermelho, seguida de regressão de least squares, ajudou em avaliar estas propriedades de solo pela primeira vez também na matriz dos solos tropicais.

Os conteúdos de fósforos nos ninhos foram elevados e excederam os dos solos adjacentes em até 3650%. Particularmente os cupins xilófagos mudaram a disponibilidade de fósforo para formas mais instáveis; enquanto que os cupins que se alimentam na interface do solo com a madeira enriqueceram nos seus ninhos também fósforo ligado a minerais. Para *Cornitermes silvestrii* do cerrado, conteúdos mais altos de fósforo lábil foram documentados até uma profundidade de 30 cm abaixo da margem inferior dos cupinzeiros, e numa distância horizontal de até 60 cm do ninho. Padrões similares foram encontrados para carbono orgânico e lignina, mas o enriquecimento e a extensão espacial destes constituintes foram menores abaixo de ninhos mais velhos, habitados secundariamente. Por isso, a lignina inicialmente se acumulou em ninhos mais jovens, e se encontrou oxidada e decomposta em ninhos envelhecidos. O volume de água drenada em baixo de ninhos novos e velhos foi menor que no solo, mas fluxos de carbono orgânico dissolvido cinco vezes menores e concentrações de nitrato tres vezes menores foram somente observados abaixo de ninhos velhos. Também, o efeito dos cupins sobre a composição química do solo foi mais significativo abaixo de ninhos velhos. Nestes, o horizonte argico desapareceu, assim mudando o tipo de solo de Alisols e Acrisols para Umbrisols e Regosols.

Sumário

Somando, meus dados mostram que os cupins xilófagos aumentam a disponibilidade de fósforo e que os cupins do cerrado transportam argila para cima e acumulam fósforo lábil e lignina dentro dos seus ninhos e no solo adjacente. Tanto estes conteúdos elevados quanto a modificação do tipo de solo foram também persistentes em cupinzeiros envelhecidos, porém num nível inferior. Estas mudanças no tipo de solo apresentam o impacto das térmitas mais duradouro nos solos da pastagem, que é um agro-ecossistema introduzido, porque o transporte da argila para cima inverte a gênese dos solos.

Chapter 1

General introduction

1.1 Termites as soil animals

1.1.1 Soil animals

Since the nineteenth century the relevance of soil animals for soil development has been increasingly recognized. Charles Darwin was one of the first to describe the effects of animals on soil. In his book “The formation of vegetable mould, through the action of worms, with observations on their habits” (Darwin, 1881) he calculated the masses transported by earthworm activities, and he stated that the “generation of the humus-acids is probably hastened during the digestion of the many half-decayed leaves” (Darwin, 1881, p. 309). In conclusion he points out that the ground was excellently prepared for plants by earthworms.

At the beginning of the 20th century, the relevance of soil animals was also recognized by Russian soil scientists like Vasily Vasili’evich Dokuchaev and his students Nikolai Mikhailovich Sibirtsev and Konstantin Dmitrievich Glinka. Their studies on Russian soils, especially on chernozems, resulted in the formula for soil formation (Glinka, 1914; 1927; Marbut, 1927; Afanasiev, 1927):

$$P = f(k, \phi, g, v)$$

where P equals to soil or soil property (Russian *pochva*), which is a function of k (climate, Russ. *klimat*), ϕ (organisms, Russ. *organism*), g (subsoil, Russ. *gornaya poroda*) and v (age, Russ. *vosrast*). More famous is the formula for soil formation of Hans Jenny (1941; 1994), who supplemented topography in his equation of soil formation:

$$s = f(cl, o, r, p, t, \dots)$$

where s is soil or soil property; and cl (climate), o (organisms), r (topography), p (parent material), and t (time) are the independent variables or soil-forming factors. With the inclusion of the dots to represent other potential variables Jenny’s model became the fundamental equation for describing soil-forming factors. Thus, soil animals as part of the

soil organisms were recognized as important components of the soil and as a soil forming factor since the beginning of soil science.

Five years after Charles Darwin's book, Henry Drummond wrote his essay about the "termite as the tropical analogue of the earth-worm" (Drummond, 1886). From then on, besides earthworms, termites were also characterized as important soil forming animals. Nevertheless, studies about the effects of termites were less common than studies about the effect of earthworms on soils in the following years. This is demonstrated by the fact that the next publications about the influence of termites on soils were in the nineteen-thirties (Burr, 1931; Cohen, 1933; Holdaway, 1933; Griffith, 1938; Murray, 1938).

1.1.2 Nesting strategies and feeding habits of termites

Before termite effects on soils (Section 1.1.3) are summarized, we have to understand nesting strategies and feeding habits of termites. Eggleton et al. (1996) as also Bignell & Eggleton (2000) introduced a classification of four nesting groups. i) "Wood nesting" termites that live in dead wood of standing trees or logs. ii) "Arboreal nests" are built on trees. Both nesting structures are commonly built of carton, which consists of chewed wood and saliva. iii) "Epigeal mounds" are well-defined above-ground nests; they are built with a high percentage of soil material and variable portions of carton. Those epigeal nests are often called mounds. The collected soil material is cemented with saliva and with feces rich in organic material. iv) Termites with "hypogeal nesting" have their colony center below the ground, in some cases a complete nest structure is clearly definable, and in other cases the nest structure is poorly delineated. Many termites of this nesting group are also inquilines, which live in epigeal mounds of other species together with the mound-building colony or after their dying.

As reflected by different nest types, termites have variable potential food sources. Wood (1978) listed living vegetation, fresh and dead vegetation, decomposing vegetation, humus, fungi, and other special food. That list induced efforts to classify termites into different feeding groups. A general applicable classification covers soil-feeders, soil/wood interface feeders, wood-feeders (xylophagous), litter foragers, grass-feeders and minor feeding groups like lichen-feeders (Bignell & Eggleton, 2000). Soil- and soil/wood interface feeder termites are sometimes combined; they can be called humivorous or geophagous termites (Martius, 1994a). Also litter-harvester and grass-feeders are sometimes aggregated; this group includes termites which grow fungi on collected organic material and feed on the fungus. The recent classification made by Donovan et al. (2001) grouped the termite species

according to the humification of their feeding substrate. Lower wood-feeding termites¹ are arranged in “Group I”; lichen-, grass-, litter-, and wood-feeder termites in “Group II”; soil/wood interface feeders in a crude generalization in “Group III”; and true soil-feeders in “Group IV”. This well-founded classification will be used in parts of my work, but in the text, the more popular terms like wood-feeder or grass-feeder will be used.

1.1.3 Effects of termites on soils

Termites perform several activities that qualify them as soil engineers. They collect organic material as food source and for nest construction, transport it to their nest, and alter it during digestion. For the transportation, they build galleries into the soil and also on the soils surface. Quite often the galleries are covered by termite-made sheetings. The termite species with epigeal and hypogeal nests have direct influence on soils through their nest building activities. Apart from their food, they transport inorganic material to their nest for construction purposes. Thus, organic and inorganic materials are concentrated in their nesting area and its compositions are altered by termite activities; though, effects of non-nest-building termites on soil properties are still largely unknown until today. **Due to the different feeding and nesting habits differences between the activities and effects of termite species exist, but differences between feeding guilds and their effects on soil properties are poorly studied.**

Known effects of termites on soil properties, driven by the above mentioned termite activities, will be introduced in the following section. The building of galleries and nests has different effects on physical soil properties. In general, galleries and foraging holes enhance the porosity of the soil (Elkins et al., 1986; Basappa & Rajagopal, 1990; Mando et al., 1996) and reduce the bulk density (Arshad, 1982; Elkins et al., 1986; Mando et al., 1996). The loosening of the soil and the building of foraging holes induces higher infiltration rates on sites with termites (Elkins et al., 1986; Mando et al., 1996; Léonard & Rajot, 2001). On the other hand, reduced infiltration rates were also observed for soils with termites (Spears et al., 1975). However, the outer wall of termite mounds is often very hard (Adepegba & Adegoke, 1974; Maduakor et al., 1995), and has a higher bulk density (Lal, 1988), which reduces infiltration rates into mounds (Arshad, 1982; Lal, 1988).

The hard crust of earth mounds is built by termites for protection purposes. Besides a compact stacking of soil particles and a cementing of the particles by organic substances, the higher clay content in termite mounds contributes to the outer wall compaction. The clay percentage in termite nests is raised, because termites prefer clay or the smallest silt

¹ The classification into lower and higher termites refers to the termites' level of evolution. The lower termites have bacteria and protozoa in their guts for digesting cellulose. The gut of the higher termites contains only bacteria, which also includes anaerobic bacteria. These termites can probably produce cellulase by themselves.

particles for nest construction (Lee & Wood, 1971b; Lal, 1987; Holt & Lepage, 2000). This preference is caused by a size limit of the termite workers transportation capacity and by the need to maintain high moisture contents in the nests (Lee & Wood, 1971a; Wood, 1988). The material for nest construction is frequently collected in the subsoil. Collection depths of 8.5, 23, and even 70 m are referred in the literature (Lee & Wood, 1971b; Lee, 1983; Coventry et al., 1988). The deep burrowing termite species are in most cases of the fungus-grower feeding class.

Particle selection involves also changes of the mineral composition in the termite nests. Generally, termites collect particles from the subsoil, and consequently, the mineral composition of the nest reflects this source. Lal (1987) and Sako et al. (2009) documented an upward transport of smectite, muscovite and illite. Additionally, Liu et al. (2007) referred to an upward transport of carbonate, and Abe & Wakatsuki (2010) documented a different sesquioxide composition in termite mounds than in the surrounding soil.

The intimate contact of clay particles and organic matter in the termite gut can favor the formation of stable aggregates (Miklós, 1992, cited by Schaefer, 2001), similar to earthworm casts. It is also expected that the higher clay content and the interconnected cation exchange capacity promote aggregate formation (Jouquet et al., 2004). Therefore, higher contents of microaggregates are found in termite mounds (Fall et al., 2001), termite affected sites (Spears et al., 1975), and in abandoned termite mounds (Jungerius et al., 1999). Those microaggregates are also discussed as source for “pseudo-sand”, a microgranular structure in tropical soils (Jungerius et al., 1999; Schaefer, 2001; Balbino et al., 2002; Reatto et al., 2009). The water-stability of the aggregates is enhanced (Sheikh & Kayani, 1982) or reduced (Jouquet et al., 2004) in termite mounds. Jouquet et al. (2004) attributed the reduced stability to the swelling of 2:1-type clays, which reduced the water penetration into the mounds in the field.

Termites do also change the chemical soil properties of their nest and the adjacent soil. The transport of inorganic and organic material into the nest causes an enrichment of nutrients, and these nutrients may then be depleted in the surrounding soil or in specific soil horizons. First of all, the content of organic material is regularly increased in termite nests, which directs to their higher carbon and nitrogen contents (Lee & Wood, 1971b; Lobry de Bruyn & Conacher, 1990; Holt & Lepage, 2000). Due to different origins of the organic material and the modification by termites, a diversity of organic substances is present in nests. Hence, the reported alteration of organic material in termite nests will be described in the next paragraphs. Other nutrients can be enriched by termites in addition to organic material, clay and other inorganic particles in their nests. Those particles can in addition elevate the cation exchange capacity, and consequently exchangeable cations like calcium, mag-

nesium and more seldom potassium (Lee & Wood, 1971b; Lobry de Bruyn & Conacher, 1990; Holt & Lepage, 2000). There is no obvious trend for a termite effect on the pH; the reported observations are contradictory (Lee & Wood, 1971b; Lobry de Bruyn & Conacher, 1990; Holt & Lepage, 2000). The same is true for phosphorus, which was enriched in nests in the studies of Okello-Oloya et al. (1985), López-Hernández et al. (1989), Garnier-Sillam (1990), and Mora et al. (2003), and depleted in the observations by Watson (1975), Singh et al. (1987), and Al-Houty (1998). The higher cation exchange capacity and the alteration of organic matter by termite digestion change, of course, also the availability of nutrients (including nitrate and ammonium) for plants. This was for example shown for available phosphorus by Kang (1978), Arshad (1981), Wood et al. (1983), Ndiaye et al. (2003), and López-Hernández et al. (2006). **However, a systematic approach to understanding the contradictory results of different feeding guilds on total and plant available phosphorus is missing.**

Trace elements are as well influenced by termite activity. Fageria & Baligar (2004), Mills et al. (2009) and Sako et al. (2009) reported an enrichment of the micro-nutrients iron, manganese, zinc, and copper in termite nests, while Ackerman et al. (2007) and Mills et al. (2009, other termite species than above) found no differences or even higher values in the control soil. Nevertheless, in many studies, termite mounds are used as a tool for geochemical exploration, because termite nests show higher values of rare metal elements, which originate from deeper horizons (Prasad & Saradhi, 1984; Prasad et al., 1987; Le Roux & Hambleton-Jones, 1991; Kebede, 2004).

As stated above, the organic matter content is regularly raised in termite nests. This is due to the incorporation of food or digested food in the form of saliva or feces into the nest. The composition of the organic matter is above all driven by the feeding habit of the termites. For example, soil-feeding termites feed on humified material, and wood-feeding termites on relatively unchanged wood. The feeding habits have also an influence on the termites' ability to degrade organic matter. Termites feeding on wood use the easily degradable cellulose components rather than lignin as a source for carbon and energy (Breznak & Brune, 1994). Several studies show that those wood-feeding termites and their symbiotic gut microorganisms can only degrade mono- or diaromatic lignin compounds, and the core of larger lignin molecules resists degradation (Butler & Buckerfield, 1979; Cookson, 1987; Brune et al., 1995; Kuhnigk & König, 1997). On the other hand, fungus-growing termites are able to use the lignocellulose nearly completely, because the symbiotic *Termitomyces* fungi can degrade lignin like other white-rot fungi (Hyodo et al., 2000; Ohkuma, 2003). Thus, an enrichment of lignin is found in wood-feeding (and soil/wood interface feeders) termite nests (Hopkins et al., 1998; Amelung et al., 2002). Cellulose and peptidic com-

pounds are more degraded than aromatic compounds during experiments with soil-feeding termites, which led to smaller molecular weights (Ji et al., 2000; Ji & Brune, 2001). Studies of the poly- and monosaccharide contents in nests of soil-feeding and fungus-growing termites reveal higher contents for the soil-feeding termites in comparison to the control soil (Contour-Ansel et al., 2000; Sall et al., 2002). While this is mainly attributed to the much higher carbon content in those nests, the percental contribution of carbohydrate-C to total nest organic carbon is reduced. The sugars are residues of collected food, which is supported by a high content of plant-born polysaccharides in the termite nests (Contour-Ansel et al., 2000). Hopkins et al. (1998) reported a preferential loss of polysaccharides during digestion by wood-feeding termites. Humic acids have a different constitution in nests of fungus-growing termites than in the reference soil: they contain more oxygen, have a higher aromaticity, and lower molecular weight (Arshad et al., 1988). Experiments with soil-feeding termites showed that they convert humic and fulvic acids to humins (Ji et al., 2000). Field studies indicated a greater portion of humic acids in nests of fungus-growing and wood-feeding termites (Garnier-Sillam & Harry, 1995; Garnier-Sillam, 1987, cited by Brauman, 2000; Richard et al., 2006). **Consequently, it can be said that the more stable lignin is enriched in termite nests relative to easily available organic compounds. However, the persistence of such lignin enrichments and the consequences for organic matter in the soil below termite nests are unknown.**

Despite a decomposition of easily available organic compounds, like sugars, by termites, the absolute content of such compounds is elevated in termite nests compared to adjacent soil due to a strong enrichment together with other organic materials. Hence, those easily available compounds can serve as energy source for microorganisms. Also the optimal humidity in termite nests can support the growth of microorganisms (Holt, 1998). Consequently, a higher activity, a higher biomass, or a higher number of microorganisms in termite nests relative to the surrounding soil were reported in many studies (Gupta et al., 1981; Abbadie & Lepage, 1989; Holt, 1998; Fall et al., 2004; Ndiaye et al., 2004a). The termites' activities influence also the composition of microorganism communities in general (Harry et al., 2001), the composition of bacterial communities (Fall et al., 2004; Jouquet et al., 2005), and the composition of fungal communities (apart from fungus in fungus-growing termite nests; Roose-Amsaleg et al., 2004; Jouquet et al., 2005; Diouf et al., 2005; 2006). Roose-Amsaleg et al. (2004) reported that only 6.3% of rDNA sequences of ascomycete communities were the same for nests and soils. The spores of ectomycorrhiza were more diverse in several Australian termite nests (Spain et al., 2004), and the number of arbuscular mycorrhizal spores were elevated around nests of soil-feeding termites (Ndiaye et al., 2003). The latter stated that mycorrhizal establishment was depressed in the nests itself. A

fumigation effect against fungi was also postulated by Wiltz et al. (1998) for naphthalene found in termite nests, although more recent studies suggest that naphthalene was produced by microorganisms occurring in termite nests (Bandowe et al., 2009). Solavan et al. (2007) stated that termite mound extracts had an effect against the growth of bacteria.

Termite mounds or their immediate surroundings have been known as a place of a better growth of plants for a long time (e.g. chitemene agriculture: Mielke & Mielke, 1982). This was shown in studies of termite mounds in the natural environment (Spain & McIvor, 1988; Miura et al., 1990; Miedema et al., 1994; Brody et al., 2010) and in manipulation experiments (Rajagopal, 1983; Gutierrez & Whitford, 1989; Batalha et al., 1995; Mando et al., 1999). Higher yields of plants were reported in the studies of Watson (1977), Okello-Oloya & Spain (1986), Batalha et al. (1995), Duponnois et al. (2005), and Andrianjaka et al. (2007). Andrianjaka et al. (2007) observed additionally a biological control effect of mound powder on a root parasite. For this reason, termite mound materials were used as soil amendments. However, little or no effect of mound material on plant growth has also been reported (Potineni & Veeresh, 1989; Vivekanandan & Kandasamy, 1983), while others reported even a suppression of plant growth directly on the mound (Spain & McIvor, 1988; Rogers et al., 1999).

All in all it can be summarized that termites alter the physical, chemical, and biological properties of their nest material in comparison to the original material. This can also have consequences for the whole soil. The nature of the soil horizons and the soil classification can be changed. Due to bioturbation the differentiation of the soil horizons can be leveled, but also the formation of stone lines (Nye, 1955; Jungerius et al., 1999; IUSS Working Group WRB, 2006), the microgranular structure of Ferralsols (Sys, 1956; Jungerius et al., 1999; Schaefer, 2001; Balbino et al., 2002; Reatto et al., 2009; Sarcinelli et al., 2009), and plinthite (Yakushev, 1968; Tardy & Roquin, 1992) has been attributed to termite action. However, all these changes are restricted to the spatial extent which can be directly reached by termites. Therefore, the mosaic of nutrient patches in tropical soils, which can be found especially in tropical savannas (Pärtel et al., 2008), can be raised by termite activities (Salick et al., 1983; Garner & Steinberger, 1989; Tongway et al., 1989; Holdo & McDowell, 2004; Grant & Scholes, 2006; Obi & Ogunkunle, 2009). This patchiness can also be intensified by the termite mounds, which alter the microtopography (Sattaur, 1991; Miller et al., 1994; McCarthy et al., 1998). Though, the direct effect of termites on the underlying and adjacent soil was only studied at single mounds (Watson, 1962; Laker et al., 1982a; b; Coventry et al., 1988; McCarthy et al., 1998). **Thus, the degree of spatial extent that is influenced by termites is poorly quantified to date.**

Furthermore, the termite induced changes in soils and nest materials can be altered after the death of a termite colony, but also when the nest is still inhabited. Termites might directly relocate nest materials into the soil or partial erosion and leaching from inhabited termite nests may add nutrients to the soil. For example, leaching of nitrate and ammonium from termite nests into the surrounding soil was observed by Congdon et al. (1993, cited by Holt & Lepage, 2000) and Schwiede et al. (2005). Studies on development of physical or chemical properties of nests after nest abandonment are rare (Nye, 1955; Stoops, 1964; Vallachmedov, 1981; Steinke & Nel, 1989; Roose-Amsaleg et al., 2005). Most studies concerning nest longevity only estimated the age of the nests (Lee & Butler, 1977; Nutting et al., 1987) or calculated only the mass loss of nest material (see e.g. Lobry de Bruyn & Conacher, 1990). **Hence, it is unknown how the modified materials continue to change over time after the colony dies, and if still inhabited nests have an influence on the surrounding soil.**

In summary, there is a lot of data about the alteration of soil properties in termite nests relative to a control soil, but several open questions remain.

- Are there any systematic differences in the way various termite feeding guilds affect the chemical characteristics of their nest materials?
- How do termites influence the content and availability of phosphorus, which is important for plant nutrition, in their nests?
- Are relatively stable lignin compounds enriched in termite nests, and if so, how long will it be enriched?
- How far do termites influence the soils surrounding their epigeal nests?
- Is there any transport of nutrients from living nests to the surrounding soil?
- What happens to the nests and enriched nutrients when the colony dies?

1.2 Focus on Brazil

1.2.1 Documented impacts of termites on soils in Brazil

From the literature review in Section 1.1.3 it is clear that most studies on the relation of termites and soil properties were conducted in Africa. Figure 1.1, which illustrates this point, is based on 168 international original research papers and conference proceedings papers (1955-2010; data from ISI Web of Knowledge and Scifinder), which examine the

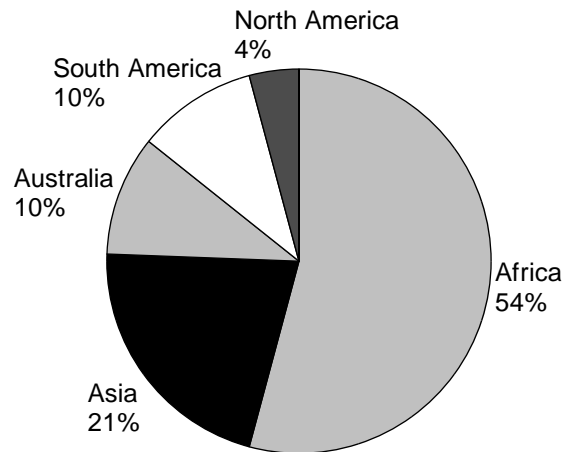


Figure 1.1 Percentages of studies on the relation of termites and a control soil done in the different continents. The diagram is based on 168 international publications (1955-2010; data from ISI Web of Knowledge and Scifinder).

relation of termites and soil properties in the field, and which have informative data. Seven of the 17 studies done in South America were carried out in Brazil.

Sarcinelli et al. (2009) studied the difference between termite mounds and control soils in the Mata Atlântica (see Section 1.2.2 for an explanation of the ecosystems), and the study of Fageria & Baligar (2004) was carried out in the Cerrado. The five other studies were conducted in the Amazon region (Martius, 1990; Amelung et al., 1998; 2002; Richard et al., 2006; Ackerman et al., 2007). All above listed authors reported an enrichment of organic matter (carbon, nitrogen, sulfur) in termite nests in comparison to reference soils (Martius, 1990; Amelung et al., 1998; 2002; Ackerman et al., 2007) or to litter (Richard et al., 2006). The lignin percentage is higher in nests of wood- and soil/wood interface-feeding termites, and lower in nests of lichen-feeder termites in comparison to the reference soil (Amelung et al., 1998; 2002). Richard et al. (2006) reported a higher content of humic acids and a higher fraction of low-molecular-weight molecules in nests than in litter. Nutrients like phosphorus, potassium, calcium, and magnesium are also enriched in termite mounds (Fageria & Baligar, 2004; Ackerman et al., 2007; Sarcinelli et al., 2009). The results for pH and aluminum are contradictory; Fageria & Baligar (2004) and Sarcinelli et al. (2009) showed higher pH values and less aluminum in termite nests; while Ackerman et al. (2007) found the opposite in the Amazon region. The nests of the latter study are also exceptional for available micronutrients; Ackerman et al. (2007) recorded no difference for iron, zinc, and copper. On the other hand, Fageria & Baligar (2004) measured higher contents of iron, zinc, copper, and manganese in termite mounds. Changes of physical properties were as well examined by the same authors. The clay content is higher, and the sand content is lower in termite mounds than in the control soil (Fageria & Baligar, 2004). Furthermore,

the proportion of large aggregates is higher, and the proportion of the small aggregates is reduced in termite nests in comparison to soils (Sarcinelli et al., 2009). Ackerman et al. (2007) stated that termite mounds have a higher penetration resistance and a higher infiltration rate. However, as the studies are restricted to a comparison of termite nests and a reference soil, it remains unclear how the termites influence the adjacent and underlying soil. Also, the persistence of these changes was not examined. A systematic assessment is lacking, because most studies were done in the Amazon region, where the feeding guilds or the termite genera were unknown (Fageria & Baligar, 2004). Ackerman et al. (2007) and Sarcinelli et al. (2009) even averaged values for different termite species and feeding guilds. **In view of that, the present work tries to systematize and extend the knowledge about the influence of termites on soils, nest and soil properties in Brazil.**

1.2.2 Climate and ecosystems in Brazil

Brazil is the fifth largest country in the world and the largest one in South America. With an extension from 5°North to 34°South and from the Atlantic Ocean to the Andes it shows a variety of climates, and consequently a variety of ecosystems.

The mean annual temperatures are the highest in the north close to the equator, and lower in the south of Brazil (Figure 1.2). The highest mean annual precipitations are recorded at the equator, and the lowest in the northeast. These differences cause the forming of different ecosystems (Figure 1.3). The equator region is dominated by the Amazon and the tropical rain forest. Differences of the flooding regime induce different ecosystems within the Amazon region. The Terra firme is never flooded; the Várzea is flooded by whitewater rivers, and the Igapó by blackwater rivers. The ecosystem lying in the east and south of the Amazon region is the Cerrado (the Brazilian savanna), which is drier than the Amazon region and has a pronounced dry season. It includes a variety of vegetation types, which range from an open savanna to a closed canopy forest. A small part of the Cerrado, but more dominated by floodings, is the specific floodplain ecosystem of the Pantanal. The northeast region of Brazil has a more pronounced dry season, which causes xerophytic vegetation. This region is called Caatinga. The Mata Atlântica extends along the coast of the Atlantic and comprises the more mountainous parts of Brazil. Caused by the mountains it is humid the whole year, but distinctive rainy seasons are induced by the specific location. The humid Pampa in the south of Brazil is a grass steppe with a mild climate. **Yet it is still unclear whether termites in the different ecosystems have different effects on soil and nest properties or whether it is the termite genus rather than climate that induce such differences.**

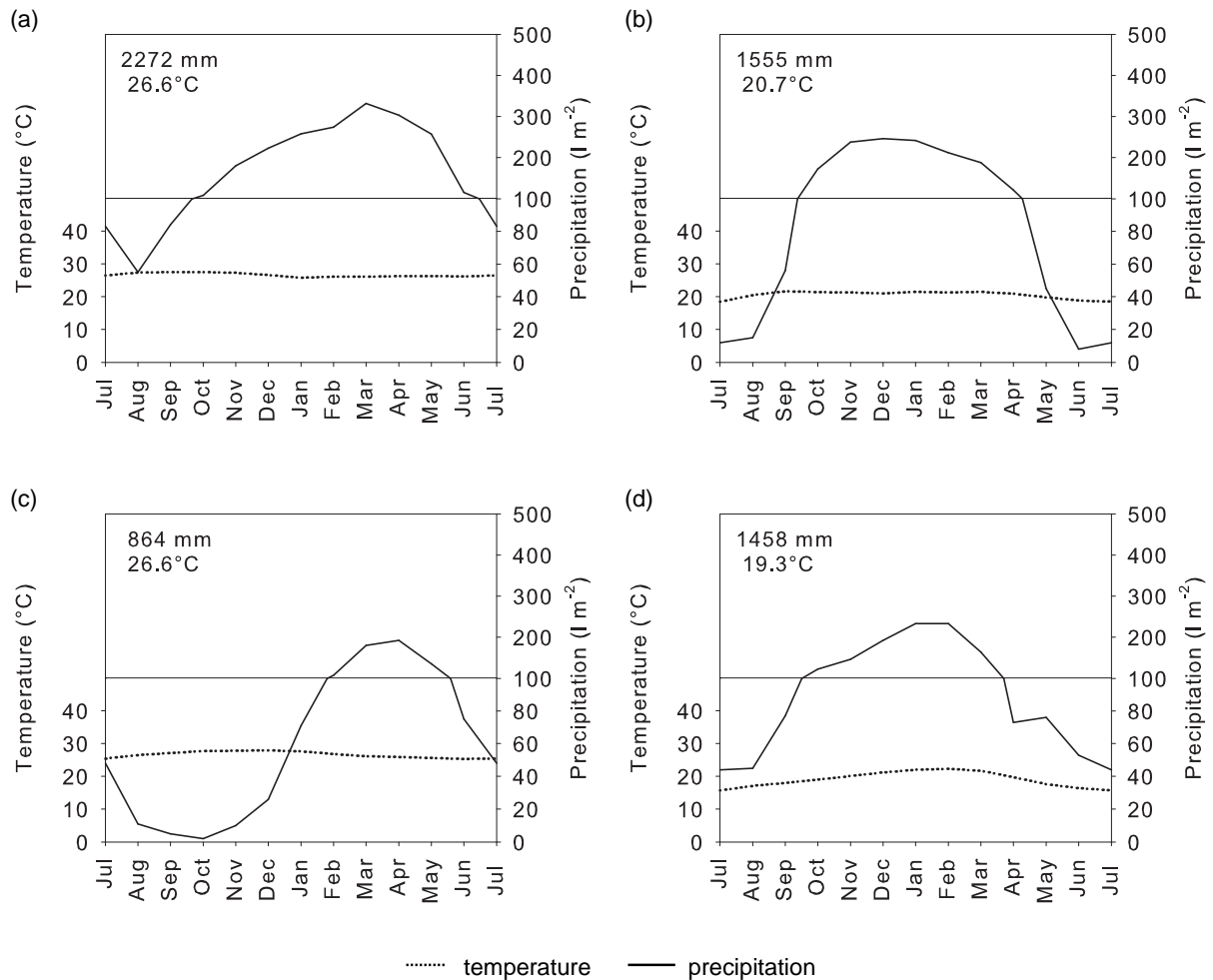


Figure 1.2 Climate charts of four Brazilian cities: (a) Amazon region (Manaus, 3° 08' S, 60° 01' W, 72 m); (b) Cerrado (Brasília, 15° 47' S, 47° 56' W, 1158 m); (c) Caatinga (Quixeramobim, 5° 12' S, 39° 18' W, 198 m); (d) Mata Atlântica (São Paulo, 23° 30' S, 46° 37' W, 795 m) of different ecosystems (data from Mühr, 2009). The mean annual precipitation and temperature were given for each chart.

1.2.3 The soils of Brazil

The present Brazilian soils are influenced by the old land surfaces and the tropical climate. Therefore, highly weathered Ferralsols (according to WRB: ISSS-ISRIC-FAO, 1998) are the dominating soil group in Brazil; they cover one third of the territory (Ker, 1997). Though, the abundance of Ferralsols in the six ecosystems is different. Ferralsols are dominating in the Amazon region alongside with Plinthosols, Acrisols and Fluvisols (Figure 1.4; Ker, 1997). Ferralsols and Acrisols are also, together with Arenosols, the most common soils in the Cerrado (Figure 1.4; Batlle-Bayer et al., 2010). In the Pantanal one can find Solonetz, Alisols and Fluvisols (Figure 1.4; Zeilhofer & Schessl, 2000); and in the Caatinga, Planosols, Luvisols, and Cambisols besides Ferralsols, Acrisols, and Alisols are most frequent (Figure 1.4). The soils of the Mata Atlântica are more influenced by the re-

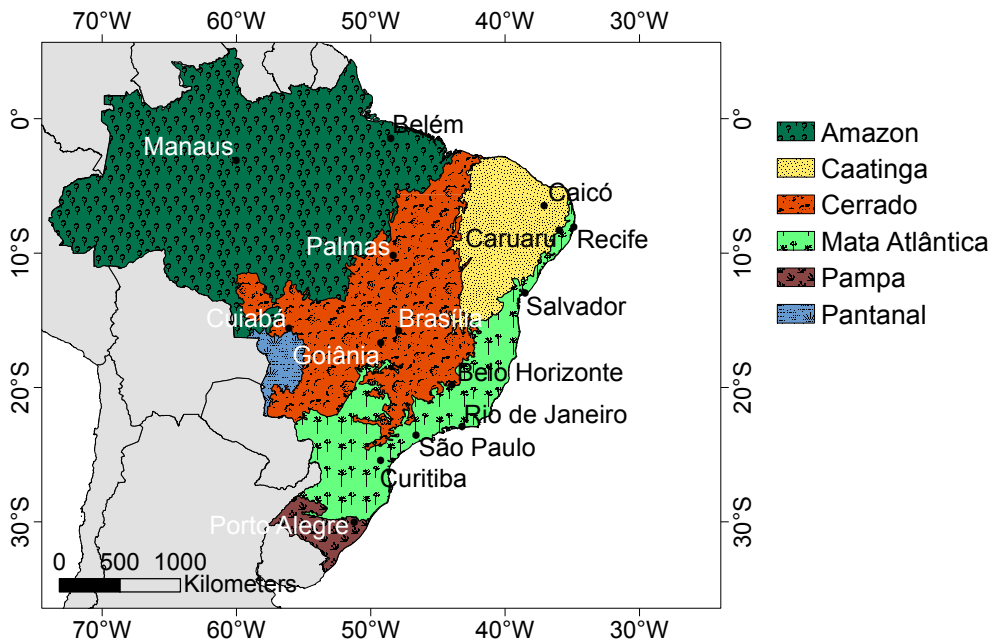


Figure 1.3 The six dominant ecosystems of Brazil (data from IBGE, 2004).

lief position. In general, Cambisols, Leptosols, and Nitisols occur together with Ferralsols and Acrisols (Figure 1.4). The south of Brazil is dominated by Phaeozems (Figure 1.4).

In general, the soils may have good physical soil properties, but the chemical properties are unfavorable for land use. Most of the tropical soils (Ferralsols, Acrisols) have low nutrient availability. This is due to the intensive weathering, the formation of low activity

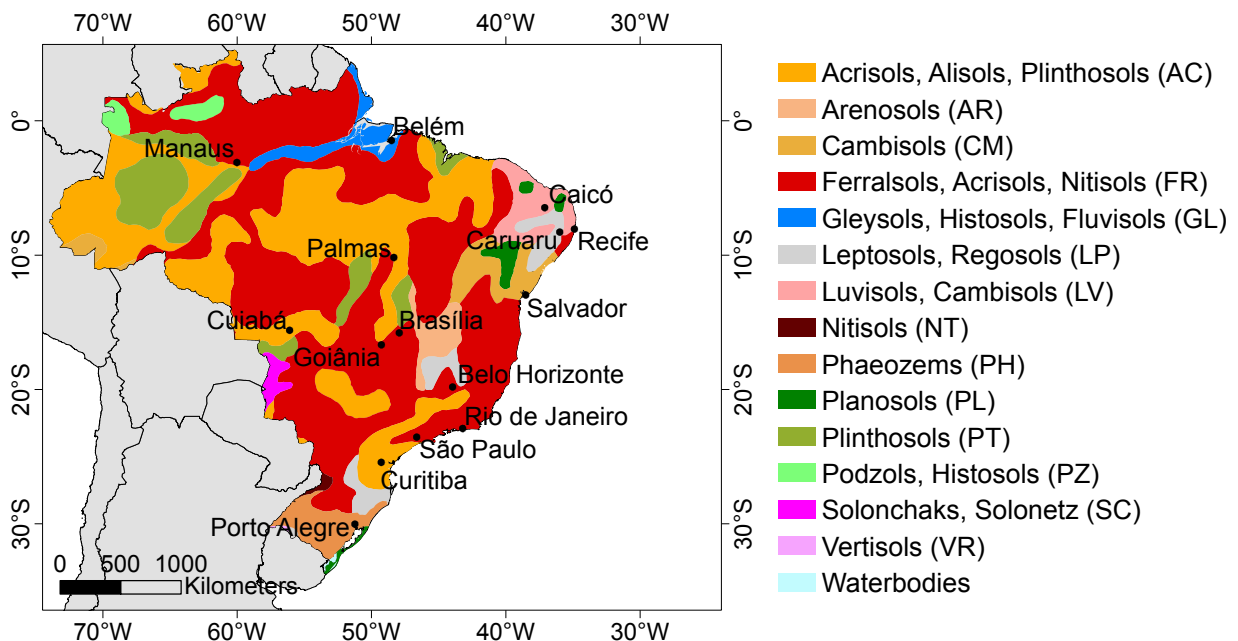


Figure 1.4 The soil groups of Brazil according to WRB (ISSS-ISRIC-FAO, 1998; data from FAO, 2003).

clays like kaolinite, and the low pH value. Correlated with the low pH is a high content of exchangeable aluminum, which is a plant toxin. The low total phosphorus contents and the high phosphorus fixation cause low phosphorus availability (Sanchez & Logan, 1992; Demattê & Demattê, 1997; Lehmann et al., 2001). Demattê & Demattê (1997) reported that 96% of the soils in the Amazon basin had limited phosphorus availability. Access to soil organic matter can promote the nutrient availability for plants and microorganisms; therefore, an adapted humus management may be required for sustainable land use. Termites can have a positive effect on the soils and the suitability for land use, when they raise the organic matter content, and the content and availability of nutrients. **Thus, the aim of the present work is to examine the effect of termites particularly on phosphorus and organic matter in termite nests and the adjacent soil, and also their effect on soil genesis.**

1.2.4 Termites in Brazil

About 2800 termite species are described worldwide. The Neotropical region has the second highest number with about 500 species. 280 species are described in Brazil (Araujo, 1970; da Cunha et al., 2006). Coles de Negret & Redford (1982) stated that termites “are probably the dominant form of animal life in many areas of central Brazil, both in number of species and biomass”.

While termites are distributed over the whole of Brazil, the colder south is relatively free of termites (Constantino, 2002). The Terra firme is the greatest part of the Amazon region and has the highest species abundance. Constantino (1992) found 25 to 64 species in study sites on the Terra firme (Figure 1.5). The density of termite species is constantly lower in the flooding areas of *Várzea* and *Igapó* (Figure 1.5; Constantino, 1992; Martius, 1994b; 1997). The second highest species abundances on sampling plots are found in the Cerrado with 16 to 46 species (Figure 1.5; Gontijo & Domingos, 1991; Sena et al., 2003; da Cunha et al., 2006). The Caatinga has between 8 and 17 termite species per study site (Figure 1.5; Martius et al., 1999; Mélo & Bandeira, 2004), and the Mata Atlântica has between 2 and 27 termite species (Figure 1.5; Bandeira & Vasconcellos, 2002; Florencio & Diehl, 2006; Reis & Canello, 2007; Vasconcellos et al., 2008).

In Figure 1.5, it becomes obvious that the termite species of the Amazon region, the Caatinga, and the Mata Atlântica are dominated by wood-feeding species, but also humus-feeder species are frequently present. On the contrary, grass- and litter-feeder species have a great proportion in the Cerrado, while such termites are negligible in other ecosystems of Brazil.

Reports on termite nest densities in Brazil are seldom and contradictory. For instance, Gontijo & Domingos (1991) documented 528 nests ha⁻¹ and Coles de Negret & Redford (1982) 180–324 nests ha⁻¹ in the Cerrado region. Furthermore, Vasconcellos et al. (2008) reported 93–110 nests ha⁻¹ in the Mata Atlântica. Besides natural causes, also the diversity of sampling methods or the counting of dead or inquilines nests can induce such discrepancies.

In addition to the nest density, the area covered by epigeal termite mounds is interesting for an evaluation of termite effects on soils. Such epigeal mounds are numerous in the Cerrado, where they are mainly built by *Cornitermes* species. *C. cumulans* occurs in the southern to the middle grasslands and *C. silvestrii* in the middle to the northern parts of Brazil (Constantino, 2002). For both species, similar mound diameters and nest densities are reported. With a mound density of approximately 40 nests ha⁻¹ (Coles de Negret & Redford, 1982; Redford, 1984; Gontijo & Domingos, 1991; Buschini, 2006) and a diameter of 80 cm (personal observations; Coles de Negret & Redford, 1982; Redford, 1984) 0.25%

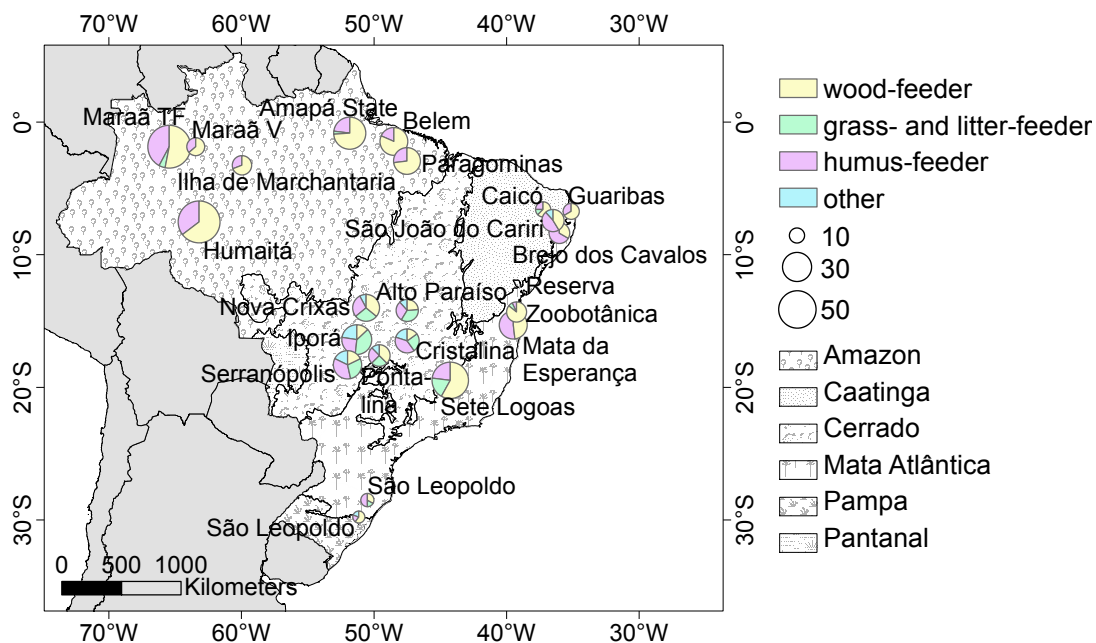


Figure 1.5 Termite species abundance (circle size) and the partition into feeding habits in Brazilian ecosystems. Composed of data for the Terra firme from Constantino (1992; Amapá State, Belem, Humaitá, Maraã TF, Paragominas); for the Várzea from Constantino (1992; Maraã V) and Martius (1994b; Ilha de Marchantaria); for the Cerrado from Gontijo & Domingos (1991; Sete Logoas), and da Cunha et al. (2006; Alto Paraíso, Cristalina, Iporá, Nova Crixás, Pontalina, Serranópolis); for the Caatinga from Martius et al. (1999; Caicó), and Mélo & Bandeira (2004; São João do Cariri); and for the (fragments of) Mata Atlântica from Bandeira & Vasconcellos (2002; Brejo dos Cavalos), Florencio & Diehl (2006; São Leopoldo), Vasconcellos et al. (2008; Guaribas), and Reis & Canello (2007; Mata da Esperança, Reserva Zoobotânica).

of the area is on average covered by *Cornitermes* mounds. However, if the termites affects the surrounding soil and the induced changes are stable when the termite colony dies, the total area influenced by termites can be larger. **Hence, studying soil properties within and around *Cornitermes* mounds may provide a first representative insight into the role of these termites for soil genesis, and both organic matter and nutrient accumulation patterns.**

1.3 Objectives

The aim of the present work is to investigate the effects of termites on selected soil properties, the impact on the soil surrounding termite nests, and the persistence of the observed changes. The focus is set on Brazil, where termites are a dominating part of the soil fauna, but studies on their influence on soil properties are scarce (see Section 1.2.1). The investigated effects of termites on soils include the chemical alteration of organic matter, comprising changes of organic carbon, lignin and phosphorus; as well as the genesis of the soil types under termite mounds. Considering the concluding questions in Sections 1.1.3 & 1.2.1, the specific objectives for my study are described by the following questions:

1. Which effects do different termite feeding guilds have on phosphorus forms?

In Chapter 2, the relevance of different termite feeding guilds for changes of phosphorus forms and contents in termite nests is evaluated. As stated above in Section 1.2.4, different feeding guilds occur in Brazil, which have a varying distribution in the Brazilian ecosystems. It is assumed that they have distinct impacts on soil properties in general and on phosphorus in particular. Their effect on phosphorus is studied, because its availability is limited in most tropical soils, and it is hypothesized that termites have a positive influence on the availability through the incorporation of clay and organic matter into their nests and the chemical alteration of the organic matter.

2. What are the spatial and temporal effects of termites on their mound and the underlying soil?

The second part (Chapter 3) is restricted to one termite species, but the termite effects are studied in more detail and extended to their influence on nest surroundings. First I address the question whether the activities of *C. silvestrii* alter the soil type under their earth mounds in the Brazilian Cerrado. Second, I was interested to know the spatial extent to which *C. silvestrii* may modify the phosphorus forms in the soil near to their mounds. To elucidate the temporal development of phosphorus forms and soil genesis, I also investigated soil below presumably older mounds. Those

older mounds are originally built by *C. silvestrii*, but are now occupied by secondary termite colonies. There are in fact no abandoned termite mounds, but uninhabited nests are rare in the Brazilian Cerrado; therefore, older mounds are the best available approximation for studying the temporal development after colony death.

3. How is the temporal development of organic matter in termite mounds, which resists degradation by termites?

Chapter 4 extends the knowledge on the above-mentioned mounds of *C. silvestrii* through measurements of organic carbon and lignin, which is a prominent part of the organic matter not decomposed by termites. This chapter allows insights into the chronological development of relatively stable lignin in termite nests and the adjacent soil from sites not affected by termites, to sites with young termite mounds, and to sites with old mounds.

4. Is there any effect of termite mounds on nutrients in draining water?

In the last part (Chapter 5), a potential pathway for the movement of enriched nutrients from termite nests to the surrounding soil is examined by measuring carbon, phosphorus and nitrogen forms in drainage water. This addresses the question of whether nutrients can be leached out of young, inhabited nests, and whether the leaching is higher in older, more weathered mounds.

Chapter 2

Phosphorus forms in Brazilian termite nests and soils: Relevance of feeding guild and ecosystems¹

2.1 Introduction

Termites have enormous influence on soil properties and are often considered to be soil engineers. It is well documented that they enrich carbon, nitrogen, clay and exchangeable cations inside their mounds compared to the adjacent soil (e. g. Lobry de Bruyn & Conacher, 1990; Holt & Lepage, 2000). Our understanding of their effect on soil phosphorus (P) is less well advanced, and existing information is contradictory.

Most authors reported an enrichment of total P in termite mounds and sheetings compared to reference soils, as for example shown by Okello-Oloya et al. (1985) and López-Hernández et al. (1989) for litter-feeding and by Mora et al. (2003) and Garnier-Sillam (1990) for fungus-growing and soil/wood-feeding termites. Nevertheless, in some cases depletion of total P was observed in termite constructions (litter-feeders: Al-Houty, 1998; fungus-growers: Watson, 1975 and Singh et al., 1987).

Ecologically more important than the total P status in soils and nests are P fractions available for plant nutrition. Available P is frequently deficient in tropical soils. Termites can alter P availability through alteration of plant detritus (wood, leaf litter) and soil organic matter, and incorporation into their mounds. Studies on available P fractions in termite nests used a variety of extraction methods. The commonly used Bray and Olsen extractions showed an accumulation of available P in mounds compared to adjacent soils for soil-feeding termites (Wood et al., 1983; Ndiaye et al., 2003) and depletion for fungus-growing termites (Kang, 1978; Arshad, 1981). Aside from López-Hernández et al. (2006), who studied the effect of several feeding groups on water-soluble P, reports on other feeding guilds are scarce, and only one international published report listed the impact of termites on P in Brazil (Fageria & Baligar, 2004).

However, sequential fractionation of P and ³¹P-NMR spectroscopy are useful tools for characterization of the soil P status (Tiessen & Moir, 1993; Cross & Schlesinger, 1995; Sumann et al., 1998). These tools provide a much deeper insight into the composition and

¹ This chapter was already published in a journal: Rückamp, D. et al. (2010). Phosphorus forms in Brazilian termite nests and soils: Relevance of feeding guild and ecosystems. *Geoderma* 155(3-4), 269–279.

availability of different P pools than may be derived from common Bray and Olsen procedures. For example, Guggenberger et al. (1996) were able to demonstrate an enrichment of available P, especially of organic P, in earthworm casts. Likewise, Kristiansen et al. (2001) showed an enrichment of P pools in anthills and preferentially NaHCO_3 -extractable P and diester-P were enriched in younger nests.

To my knowledge, these sophisticated techniques have not been used to distinguish different P pools in tropical termite nests. I expect that termites of different feeding guilds have a similar effect on P forms in the nests and will all enrich available P in their constructions. However, as a result of different feeding habits, termites collect different amounts of soil and various organic compounds, leading to the hypothesis that the degree of P alterations in the nests should at least result in clear distinctions between humivorous and wood-feeding termites. The aim of my study was to use sequential P fractionation, partly in combination with ^{31}P -NMR spectroscopy, to investigate the effects of termites of different feeding groups on available and bounded P forms in seven Brazilian ecosystems.

2.2 Materials and methods

2.2.1 Samples

Most samples were collected in 1998, and originated from the Amazon region (Terra firme, Várzea and Igapó, near Manaus), the swamps of the Pantanal (near Cuiabá), the Atlantic rain forest (Mata Atlântica, near Caruaru) and the dry savanna (Caatinga, near Caicó).

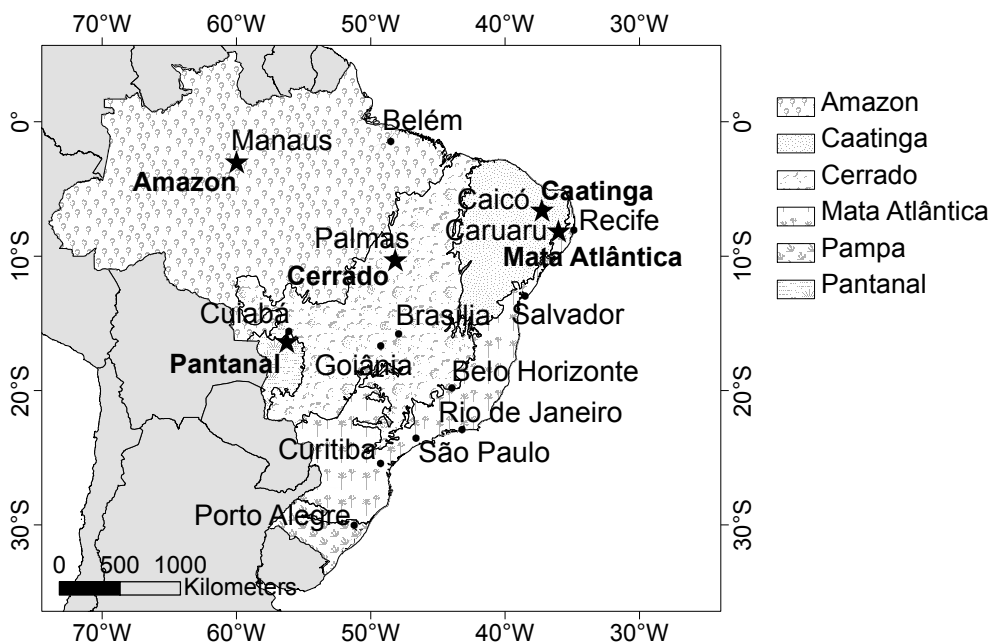


Figure 2.1 Locality of the study sites (★) in different ecological zones of Brazil.

Those samples were also used for screening of polycyclic aromatic hydrocarbons (Wilcke et al., 2003), and partially for lignin studies (Amelung et al., 2002). Additionally, the Cerrado was sampled near Palmas in 2006 (Table 2.1, Figure 2.1).

I searched for any nest I could find (especially in the rain forest), however, I only sampled two or three intact and inhabited nests of the dominant species. Samples of different nest parts (outer wall, inner wall, central part) belonging to different termite genera and species were collected (Table 2.2). It was not possible to separate the nests into discriminable parts for every termite species. According to Donovan et al. (2001), wood-feeding, lichen-feeding and grass-feeding termites were assigned to group II. For simplification, they were called xylophagous or wood-feeders in the following. The soil/wood interface-feeder or humivorous termites were classified into group III.

Samples of mineral soil (0–10 cm) were taken with a core sampler corresponding to each nest at five subsites. The soil subsamples were combined to one sample per nest. The subsites were allocated around the nests, approximately 5 m away, and had no obvious termite influence. Wood of potential food trees with termite foraging galleries were sampled close to the nests of wood-feeding termites. All samples were immediately air dried and sieved to < 2 mm.

2.2.2 Chemical analyses

Organic carbon (C) was determined in dried samples of termite nests, soil, and wood using a Fisons NA 2000 elemental analyzer (Fisons Instruments, Rodano, Milan, Italy).

Total P of wood samples was measured with an inductively coupled plasma spectrometer (ICP-AES, JY70PLUS, Jobin Yvon, Edison, USA) after combustion with ammonium nitrate. The sequential extraction of phosphorus fractions in nest and soil samples followed Tiessen & Moir (1993) with a modification of the determination of residual P, which was

Table 2.1 Location, climatic properties, and soils (after IUSS Working Group WRB, 2006) of the sampling sites in different ecological zones of Brazil.

Region	Coordinates		Mean annual precipitation	Mean annual temperature	Duration of the dry season	Soil
	Latitude	Longitude				
Caatinga	06° 34' S	37° 15' W	500mm	29 °C	9 months	Haplic Alisol
Mata Atlântica	08° 07' S	36° 01' W	1400mm	26 °C	5 months	Cambisol
Pantanal	16° 21' S	56° 15' W	1400mm	24 °C	5 months	Fluvisol
Cerrado	10° 16' S	48° 10' W	1800mm	24 °C	5 months	Umbric Acrisol
Amazon basin	02° 59' S	59° 59' W	2100mm	25 °C	2 months	
Terra firme						Xanthic Ferralsol
Igapó						Fluvisol
Várzea						Fluvisol

Table 2.2 Feeding and nesting habit of the sampled termite species; and the number of termite nest, soil, and wood samples. (A = outer nest wall, B = inner nest wall, C = central nest part, + combined sample).

Region	Termite species	Nesting group	Feeding habit	Feeding group ^a	Number of sampled nests	Sampled nest compartments	Number of soil samples	Number of wood samples
Caatinga	<i>Constrictotermes cyphergaster</i>	arboreal/epigeic	wood-feeder ^b	II	3	A, B, C	8	7
	<i>Microcerotermes sp.</i>	arboreal	wood-feeder ^c	II	3	A, B, C		
	<i>Nasutitermes sp.</i>	arboreal	wood-feeder ^c	II	3	A, B, C		
Mata Atlântica	<i>Embiratermes parvirostris</i>	epigeic	soil/wood interface-feeder ^f	III	2	A, B, C	4	4
	<i>Nasutitermes corniger</i>	arboreal	wood-feeder ^d	II	2	A, B, C		
Pantanal	<i>Anoplotermes sp.</i>	arboreal	soil/wood interface-feeder ^c	III	2	A, B, C	8	6
	<i>Cornitermes sp.</i>	epigeic	wood-feeder ^c	II	3	A, B, C		
	<i>Embiratermes sp.</i>	epigeic	soil/wood interface-feeder ^c	III	2	A, B, C		
	<i>Nasutitermes sp.</i>	arboreal	wood-feeder ^c	II	2	A, B, C		
Cerrado	<i>Cornitermes silvestrii</i>	epigeic	grass-feeder; litter-forager ^{d, e}	II	3	A, B+C	3	–
Amazon basin								
Terra firme	<i>Anoplotermes banksi</i>	arboreal	soil/wood interface-feeder ^f	III	2	Whole nest	8	6
	<i>Constrictotermes cavifrons</i>	arboreal	lichen-feeder ^g	II	2	Whole nest		
	<i>Cornitermes aff. weberi</i>	subterranean	wood-feeder ^f	II	2	A+B, C		
	<i>Embiratermes aff. neotenicus</i>	epigeic	soil/wood interface-feeder ^f	III	2	A+B, C		
	<i>Nasutitermes ephratae</i>	arboreal	wood-feeder ^d	II	2	A, B, C		
	<i>Termes fatalis</i>	epigeic	soil/wood interface-feeder ^{d, f}	III	2	A, B, C		
Igapó	<i>Nasutitermes corniger</i>	arboreal	wood-feeder ^d	II	2	A, B, C	2	5
	<i>Termes sp.</i>	epigeic	soil/wood interface-feeder ^c	III	2	Whole nest		
Várzea	<i>Nasutitermes ephratae</i>	arboreal	wood-feeder ^d	II	2	A, B, C	2	3

^a new feeding group classification of Donovan et al. (2001): group II wood-,grass-, and lichen-feeder; group III soil/wood interface-feeder; ^b Moura et al. (2006);

^c Martius, personal observation; ^d Constantino (2002); ^e Gontijo & Domingos (1991); ^f Davies et al. (2003); ^g Martius et al. (2000)

done with aqua regia. Inorganic P (P_i) was determined in every extract by the Molybdenum-Blue-method (Murphy & Riley, 1962) with a spectrophotometer (SPECORD 205, Analytik Jena, Jena, Germany), and total P in the extracts (P_t) was measured with an ICP-AES. Organic P (P_o) was calculated by difference of P_t and P_i .

Terminology and characterization of the different P pools followed Hedley et al. (1982), Tiessen & Moir (1993) and Cross & Schlesinger (1995):

- Resin- P_i is the biologically most available P form, and is adsorbed on surfaces of crystalline compounds.
- NaHCO_3 - P_i and NaHCO_3 - P_o are also both highly labile P-Pools, with the first being readily plant available and the latter easily mineralizable.
- NaOH - P_i has been considered as moderately labile and NaOH - P_o as stable and involved in long term transformations of P in soils. Both, NaHCO_3 -P and NaOH -P are described as associated with Fe and Al oxides, i. e., they do not really form separated pools.
- HCl_{dil} - P_i refers to stable Ca-bound P (Apatite).
- HCl_{conc} - P_i is very stable and covers recalcitrant P_i , occluded in sesquioxides. The HCl_{conc} - P_o fraction eventually also derives from particulate organic matter that is not alkali extractable, but may potentially be bioavailable.
- Residual-P comprises highly resistant and occluded P forms.

Sum- P_i and sum- P_o were calculated from the sum amount of the fractions and total P is the sum of sum- P_i , sum- P_o and residual-P.

For selected liquid-state ^{31}P -NMR analysis, alkali soluble P was extracted using 0.1 M NaOH and 0.4 M NaF as described by Sumann et al. (1998). The spectra were taken on a Bruker Avance DRX 500 NMR spectrometer (11.7 T; 202.5 MHz for ^{31}P) without proton decoupling at a temperature of 190 K. An acquisition time of 0.1 s, a 90° pulse, and 0.2 s relaxation delay were used. Chemical shifts were measured relative to 85% orthophosphoric acid in a 5-mm tube that had been inserted into the 10-mm sample tube before the measurement of each sample. Spectra were recorded with a line broadening of 20 Hz.

The assignment of individual P forms to NMR signals followed Newman & Tate (1980), Hawkes et al. (1984), Mahieu et al. (2000), Makarov et al. (2002), Turner et al. (2003), and Makarov et al. (2005). The labile phosphonates ($\delta = 17.5 - 20$ ppm) thought to be of microbial origin and have been found under wet and moist conditions or in acid soils. Orthophosphate ($\delta = 6 - 6.6$ ppm) and pyrophosphate ($\delta = -5.5 - -4$ ppm) are the dominating inorganic P forms. Orthophosphate monoester-P ($\delta = 3 - 6$ ppm) comprise inositol phosphates,

sugar phosphates and mononucleotides. In general, it is assumed that monoester-P are more stable than diester-P forms. Orthophosphate diester1-P ($\delta = 0.5 - 2.5$ ppm) include teichoic acids, phospholipids and unknown non-lipidic and non-teichoic acids of microbial origin. Diester2-P ($\delta = -1.0 - 0.5$ ppm) contain DNA and unknown non-lipidic P of microbial origin. The form of the diester-P at $\delta = -1.5$ ppm is unknown, it might be of microbial origin. Polyphosphates ($\delta = -20 - -18$ ppm) may be a result of microbial activity.

2.2.3 Statistical analyses

Differences between groups were examined with an analysis of variance (ANOVA). The Scheffé test was used as post-hoc test for comparisons of more than two groups, which is a robust test suitable for different sample sizes (Table 2.2). The significance level was set at $P < 0.05$. Statistical analyses were conducted with SPSS 14.0 (SPSS Inc., 2005, Chicago, USA).

2.3 Results

2.3.1 Sequential P extraction

Soils. The amount of total P in the soils ranged from 141 (Terra firme) to 1997 mg kg⁻¹ (Cerrado), with a median P content of 370 mg kg⁻¹ (Figure 2.2c). Inorganic P (including residual-P) usually accounted for >57% of all P forms (Table 2.3). The partition into P_i fractions was different for the soils. The very stable HCl_{conc}-P_i represented always an important proportion of the total P, it reached 62% of total P for the Cerrado Acrisols. Residual-P was most prominent, explaining 37 and 29% of total P forms in the Pantanal and the Mata Atlântica, respectively. HCl_{dil}-P_i was most important in the Várzea, these Fluvisols also had a prominent proportion of NaOH-P_i, as had those in the Pantanal. Hence, the availability of P_i greatly varied across the different ecological zones of Brazil. This was also reflected in a considerable variability of the different P_o forms. The rainforest soils of the Terra firme were dominated by highly labile NaHCO₃-P_o, while the Pantanal and Mata Atlântica soil had high proportions of the stable NaOH-P_o, and the driest soils in the Caatinga and Cerrado were dominated by the most stable HCl_{conc}-P_o.

Wood. The total P content of wood samples ranged from 28 (Terra firme) to 768 mg kg⁻¹ (Várzea). The Igapó samples had low P contents similar to those of the Terra firme, the other samples besides the mentioned ones exhibited a similar range of P contents between 200 and 344 mg kg⁻¹ (Figure 2.2d). Hence, the wood samples also had highly variable P contents, reflecting the P contents of the soils.

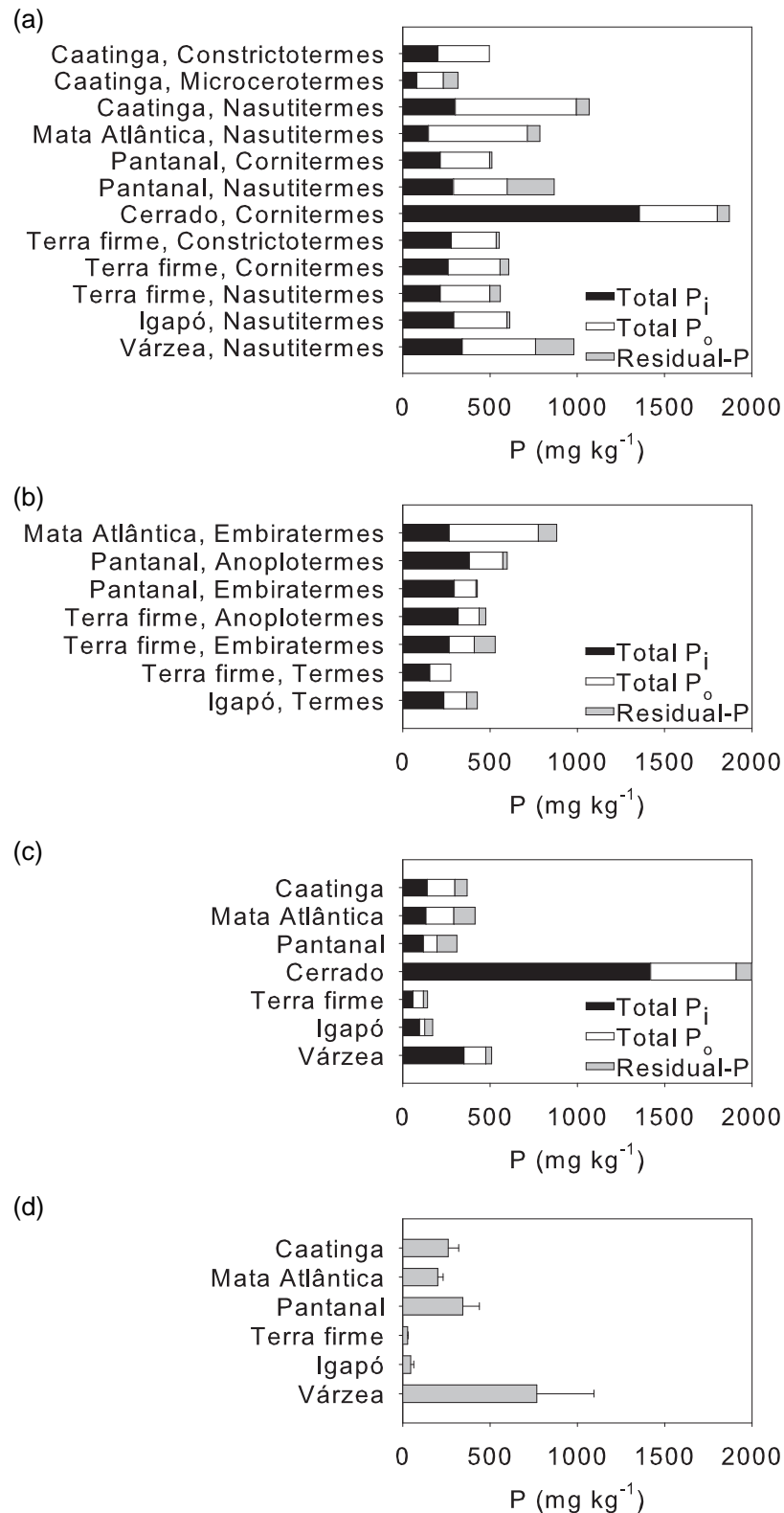


Figure 2.2 Results of the sequential P-extraction in termite nests (a: xylophagous termites; b: humivorous termites) and soils (c), and total P of wood samples (d). For termite nests were averages of all nest compartments shown. The error bars mark the standard error based on the number of samples presented in Table 2.2.

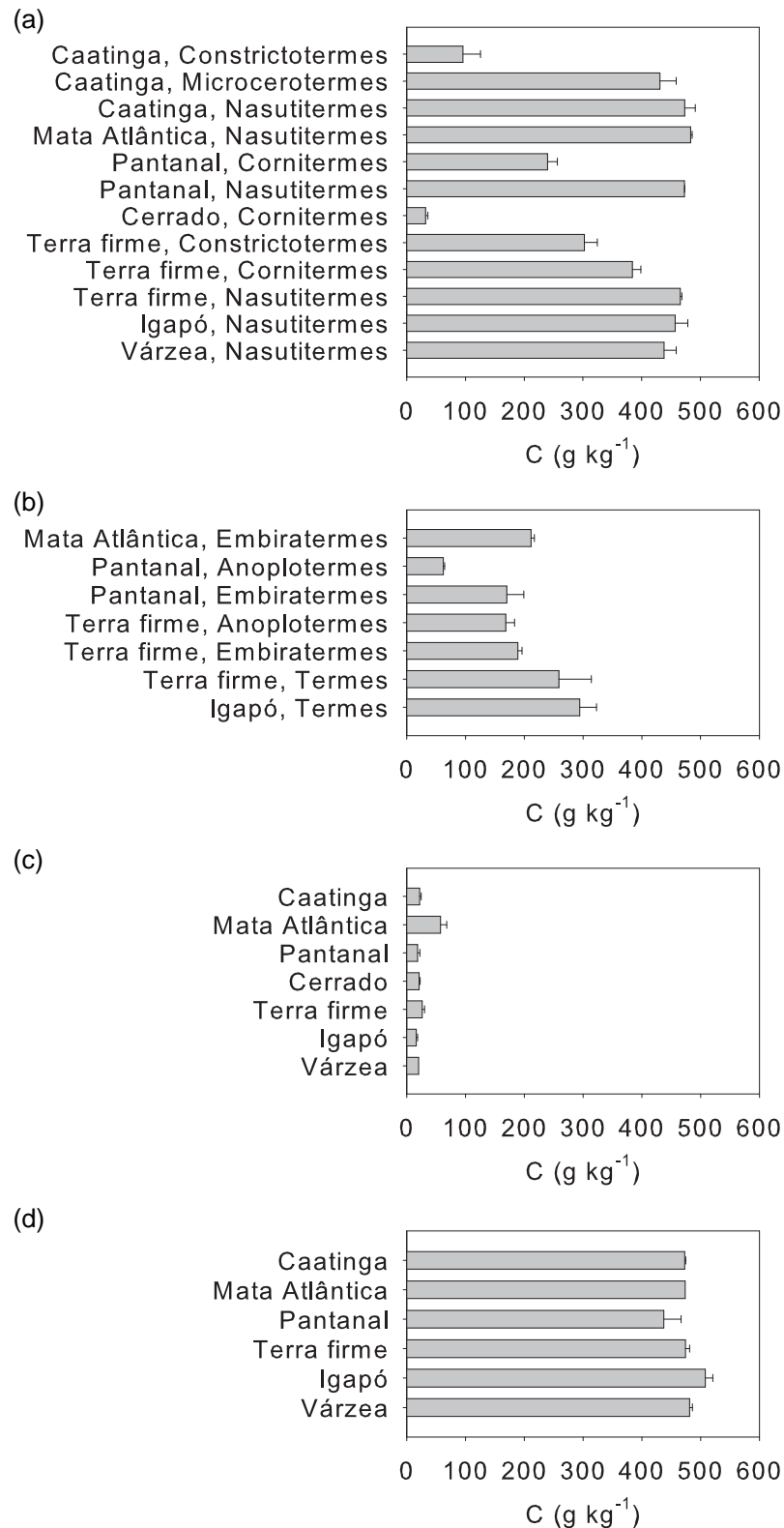


Figure 2.3 Organic carbon content of all samples (a: xylophagous termites; b: humivorous termites; c: soils; d: wood). For termite nests were averages of all nest compartments shown. The error bars mark the standard error based on the number of samples presented in Table 2.2.

Table 2.3 Proportion of each P fraction and of sum-P_i and sum-P_o (standard error) of humivorous termite nests, xylophagous termite nests and soils as result of the sequential P-extraction. Within a row different letters designate significant ($P < 0.05$) differences.

	resin-P _i	NaHCO ₃ -P _i	NaOH-P _i	HCl _{dil} -P _i	HCl _{conc} -P _i	residual-P	NaHCO ₃ -P _o	NaOH-P _o	HCl _{conc} -P _o	sum-P _i	sum-P _o
	% of total P										
Xylophagous termite nests											
Caatinga, <i>Constrictot.</i> ^a	– ^b	11 (2) ab	4 (1) a	2 (1) a	24 (5) c	nd ^c	19 (3) bc	24 (5) c	17 (5) bc	41 (9)	59 (12)
Caatinga, <i>Microcerot.</i>	15 (6) abc	4 (3) b	5 (2) bc	2 (1) b	nd	27 (17) ac	5 (4) abc	15 (6) abc	28 (7) c	52 (45)	48 (17)
Caatinga, <i>Nasutit.</i>	–	18 (11) abc	2 (1) a	2 (1) a	6 (3) ab	7 (2) ab	28 (9) c	23 (6) bc	13 (5) abc	35 (25)	65 (20)
Mata Atlântica, <i>Nasutit.</i>	–	5 (0) ab	2 (0) a	3 (0) ab	9 (1) bc	9 (2) bc	19 (1) d	37 (4) e	15 (2) cd	28 (9)	72 (7)
Pantanal, <i>Cornit.</i>	26 (4) a	8 (2) bc	5 (1) bc	2 (0) b	1 (1) b	3 (1) bc	25 (6) a	19 (4) ad	12 (2) cd	45 (22)	55 (12)
Pantanal, <i>Nasutit.</i>	23 (12) ab	1 (1) a	3 (1) a	1 (0) a	5 (3) a	31 (12) b	5 (2) a	14 (4) ab	17 (8) ab	65 (46)	35 (14)
Cerrado, <i>Cornit.</i>	1 (0) a	1 (0) a	7 (1) b	0 (0) a	63 (6) c	4 (1) ab	2 (0) a	3 (1) ab	19 (2) d	76 (29)	24 (3)
Terra firme, <i>Constrictot.</i>	26 (6) a	7 (2) bc	8 (4) bc	1 (1) b	8 (4) bc	3 (3) b	8 (2) bc	20 (5) ac	19 (8) ac	53 (55)	47 (15)
Terra firme, <i>Cornit.</i>	30 (7) a	6 (2) bcd	4 (2) bc	1 (0) b	3 (3) bc	8 (7) bcd	14 (3) bcd	18 (5) d	17 (4) cd	51 (52)	49 (13)
Terra firme, <i>Nasutit.</i>	18 (6) a	3 (2) a	4 (3) a	0 (0) a	12 (14) a	11 (11) a	10 (6) a	19 (7) a	22 (8) a	49 (68)	51 (21)
Igapó, <i>Nasutit.</i>	30 (6) a	11 (4) bcd	4 (2) bc	1 (0) b	2 (2) b	3 (1) bc	14 (5) bcd	19 (7) ad	16 (6) acd	51 (29)	49 (18)
Várzea, <i>Nasutit.</i>	22 (11) a	3 (2) a	4 (1) a	1 (1) a	5 (5) a	22 (9) a	17 (9) a	13 (6) a	13 (6) a	57 (42)	43 (20)
Humivorous termite nests											
Mata Atlântica, <i>Embirat.</i>	–	5 (1) a	10 (2) ab	nd	16 (3) b	12 (2) ab	18 (3) bc	26 (3) c	14 (2) b	42 (14)	58 (7)
Pantanal, <i>Anoplot.</i>	8 (3) a	13 (7) a	27 (11) a	5 (1) a	10 (7) a	4 (2) a	13 (5) a	17 (7) a	2 (2) a	68 (49)	32 (14)
Pantanal, <i>Embirat.</i>	8 (4) ab	14 (4) ab	33 (9) c	2 (0) a	12 (4) ab	1 (2) a	19 (5) bc	9 (5) ab	2 (2) a	71 (82)	29 (12)
Terra firme, <i>Anoplot.</i>	17 (9) a	5 (3) a	8 (6) a	0 (0) a	37 (29) a	8 (8) a	8 (4) a	14 (5) a	3 (3) a	75 (105)	25 (12)
Terra firme, <i>Embirat.</i>	7 (2) a	3 (1) a	9 (2) a	0 (0) a	31 (10) b	23 (5) bc	10 (2) c	8 (2) a	9 (2) a	73 (29)	27 (6)
Terra firme, <i>Termes</i>	17 (5) a	14 (7) a	10 (6) a	1 (1) a	14 (14) a	0 (0) a	15 (4) a	26 (14) a	3 (3) a	57 (33)	43 (21)
Igapó, <i>Termes</i>	21 (10) a	8 (6) a	11 (5) a	1 (1) a	13 (14) a	14 (15) a	8 (9) a	17 (11) a	5 (6) a	69 (93)	31 (26)
Soil											
Caatinga	1 (1) a	5 (3) a	1 (1) a	4 (1) a	27 (15) a	19 (8) a	1 (1) a	20 (7) a	21 (8) a	57 (43)	43 (17)
Mata Atlântica	–	nd	7 (1) a	nd	25 (3) b	29 (4) b	nd	25 (3) b	13 (1) a	61 (12)	39 (4)
Pantanal	5 (4) a	9 (7) a	11 (10) a	2 (2) a	12 (8) a	37 (36) a	5 (4) a	19 (14) a	1 (1) a	75 (102)	25 (18)
Cerrado	0 (0) a	0 (0) a	8 (2) a	1 (0) a	62 (8) b	4 (2) a	1 (0) a	2 (0) a	21 (4) c	75 (33)	25 (5)
Terra firme	4 (2) a	6 (5) a	4 (3) a	5 (7) a	21 (16) a	16 (16) a	23 (14) a	15 (9) a	5 (3) a	58 (80)	42 (26)
Igapó	3 (2) a	4 (4) a	2 (2) a	2 (2) a	46 (46) a	26 (29) a	11 (9) a	4 (3) a	2 (2) a	83 (133)	17 (14)
Várzea	4 (1) a	3 (4) a	12 (6) a	26 (2) a	23 (2) a	7 (1) a	12 (1) a	7 (1) a	5 (0) a	76 (17)	24 (2)

^a t. = termes; ^b was not performed; ^c not detected

Termite nests. Different nest parts usually have different ecological functions, with an outer wall protecting the nest from rain and predators, an inner wall for defense usually inhabited by the majority of soldiers, and an central nursery. Many humivorous termites with a nest made mainly of soil have a nest center which consists of organic material. Xylophagous *Nasutitermes* have nests which are nearly completely build of organic material (carton), but the three nest compartments are distinguishable in the field.

Analysis of inner and outer nest compartments revealed different distribution patterns of the P fractions (Figure 2.4). Several termite species had the highest total P contents in the central nest compartment, which was mainly related to higher C contents. An effect of higher C contents on higher P_o contents was not always present. Many *Nasutitermes*

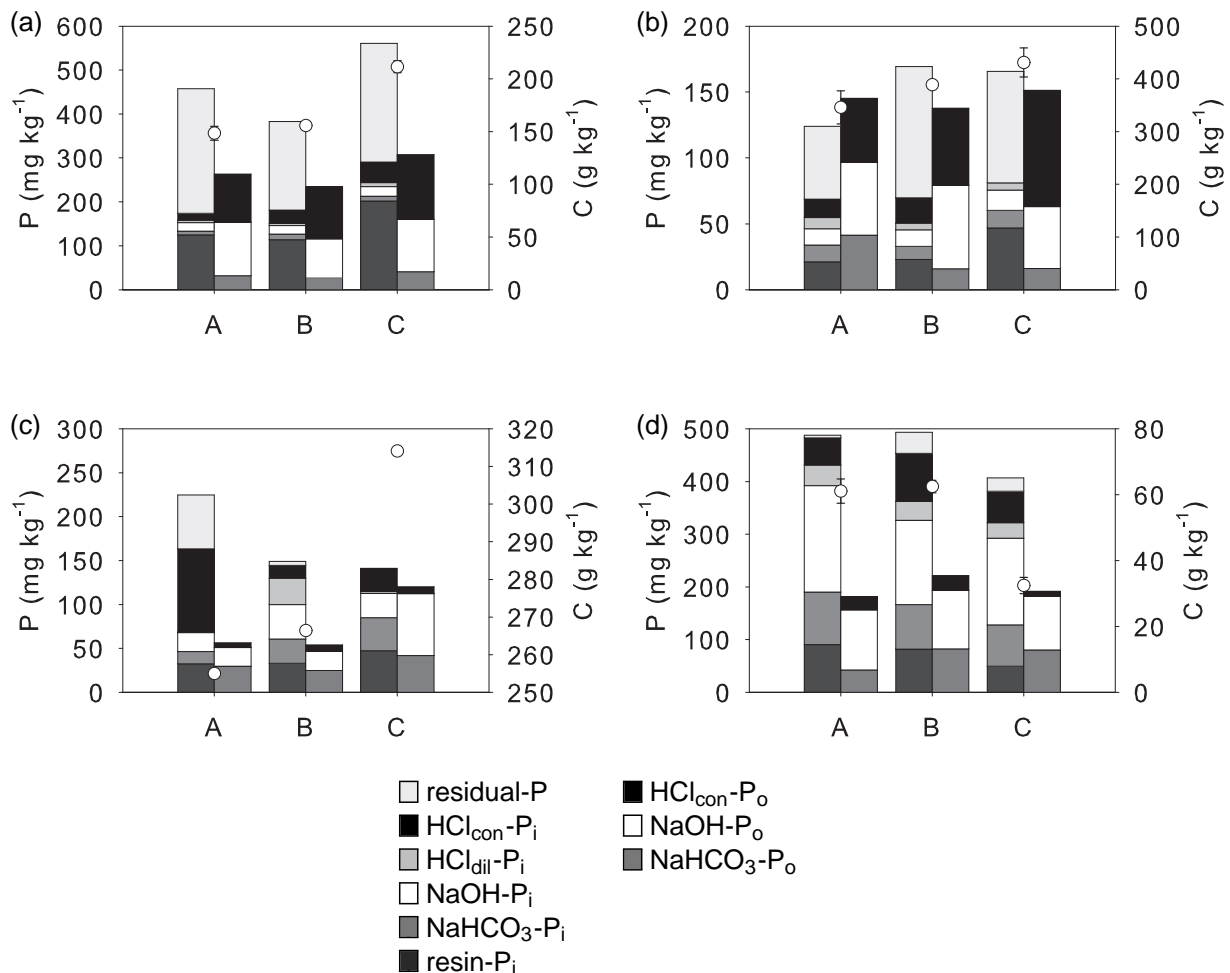


Figure 2.4 Results of the sequential P-extraction and the C analyses of different nest compartments (A = outer nest wall, B = inner nest wall, C = central nest). (a) Xylophagous *Nasutitermes* of the Pantanal, (b) Xylophagous *Microcerotermes* of the Caatinga, (c) Humivorous *Termes* of the Terra firme, (d) Humivorous *Anoplotermes* of the Pantanal. The left bar comprises P_i plus residual-P and the right one P_o. The \circ marks the C content and the error bars indicate the standard error based on the number of samples presented in Table 2.2.

nesses (Figure 2.4a) had the lowest P_o and P_i contents in the intermediate nest compartment. Some humivorous termites such as *Anoplotermes* (Figure 2.4d) had the lowest C contents in the nest center, which correlated with lower P_i contents, while P_o had the same contents in all nest compartments. Nevertheless, there was no clear difference in the distribution pattern between humivorous and xylophagous termites. I conclude that the distribution of P forms in the nests is highly species-dependent, but not systematically different for different feeding guilds or ecosystems. For a better gross understanding of the degree of P allocation in termite nests I used whole nests when no parts could be separated (Table 2.2); the intermediate part of *Anoplotermes* of the Pantanal and *Embiratermes* of the Terra firme, where the content of P and C was highest in this part; and the central part of the nests in all other cases for further evaluations.

Xylophagous termite nests contained between 317 and 1871 mg kg⁻¹ P (Figure 2.2a) with portions of sum- P_o between 24 and 72% (Table 2.3). HCl_{conc}- P_o was not the dominant P_o fraction, but it had with a proportion of 12–28% of total P a higher relevance than in nests of humivorous termites. The *Cornitermes* nest of the Cerrado was an exception with the highest P content and the lowest P_o percentage. The nest was dominated by HCl_{conc}- P_i with 63% and HCl_{conc}- P_o with 19% of total P (Table 2.3). The biologically most available resin- P_i was the major P_i fraction in all nests except the mentioned *Cornitermes* nest (not measured in nests of *Nasutitermes* in the Mata Atlântica and the Caatinga; Table 2.3). Intriguingly, the nests of *Microcerotermes* and *Nasutitermes* had also a considerable proportion of residual-P, especially in the Pantanal, Várzea and Terra firme. Other P_i fractions were less meaningful, their single portions not exceeding 12% of total P.

The amount of total P in nests of humivorous termites was lower than in nests of wood-feeding termites, it ranged from 275 to 882 mg kg⁻¹ (Figure 2.2b). In contrast to wood-feeding termites, Sum- P_i dominated in the nests of humivorous termites with approximately 70% of total P (Table 2.3). Only the nest of *Embiratermes* of the Mata Atlântica had a higher proportion of sum- P_o , explaining 58% of total P. *Anoplotermes* and *Termes* nests of the Terra firme and the *Termes* nest of the Igapó were characterized by almost 20% resin- P_i . High portions of NaOH- P_i were detected in nests of *Anoplotermes* and *Embiratermes* of the Pantanal, 27 and 33% of total P, respectively. Hence, humivorous and xylophagous termites could roughly be separated, but within the feeding guilds prominent distinctions between species and ecosystems existed.

The relation of P fractions in termite nests to the corresponding fraction of the reference soil indicated mostly an enrichment in nests. Resin- P_i was enriched in all nests, but it was not always significantly different from one at $P < 0.05$. The enrichment factor was between 1.6 and 36.5 for xylophagous termites (Figure 2.5a) and between 2.3 and 16.9 for humiv-

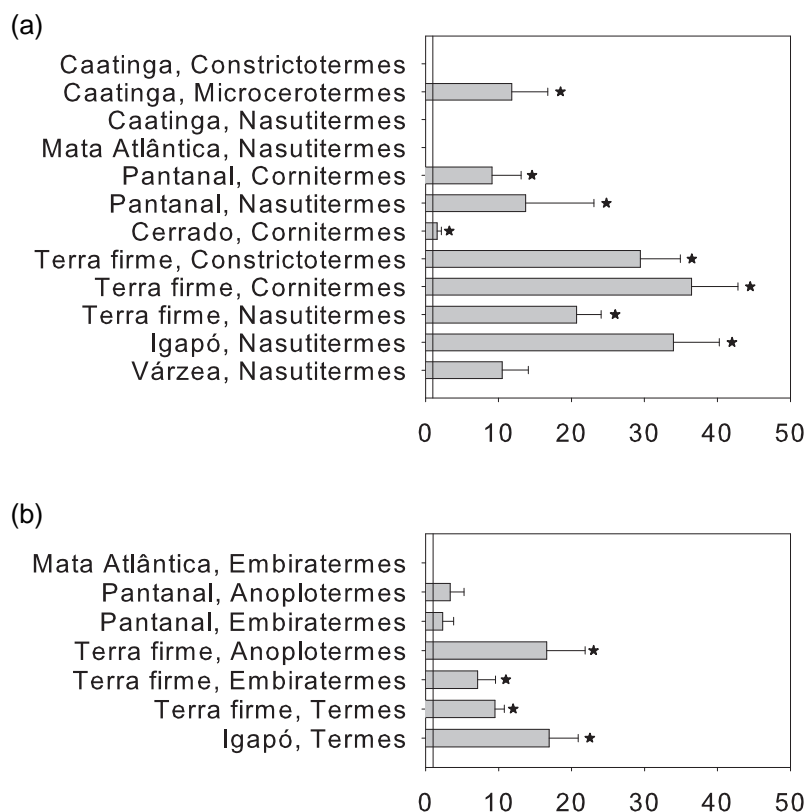


Figure 2.5 Enrichment for resin- P_i in xylophagous (a) and humivorous (b) termite nests in relation to the corresponding soil. A reference line at 1:1 and the standard error of each bar are marked. The ★ denotes significant ($P < 0.05$) differences between nest and soil P. Note the different scaling of the x-axis.

orous termites (Figure 2.5b). Except for two wood-feeding termites, this was also true for $\text{NaHCO}_3\text{-}P_i$, though the enrichment was smaller with a factor up to 11.4 (data not shown). The third labile fraction, $\text{NaOH-}P_i$, was also higher concentrated in nests in most cases, but was depleted in nests of some *Nasutitermes* and *Cornitermes* (Figure 2.6a & 2.6b). The stable P_i fractions showed more variations between termite species. The contents of $\text{HCl}_{\text{conc}}\text{-}P_i$ were six times larger in *Anoplotermes* nests of the Terra firme, and seven times smaller in *Nasutitermes* nests of the Igapó compared with the surrounding soil, but it was mostly at a comparable level in nests and soils (Figure 2.7a & 2.7b). All enrichment factors of $\text{HCl}_{\text{conc}}\text{-}P_i$ were not significantly different from one at $P < 0.05$. All P_o fractions were constantly accumulated in nests or at the same level as the corresponding soil. Figure 2.8a & 2.8b illustrates the results of $\text{NaOH-}P_o$ analyses, showing high enrichment factors for *Termes* (11.9) and *Nasutitermes* (19.2), both in the Igapó. The two other fractions showed a similar picture with some outstanding enrichments in termite nests. $\text{NaHCO}_3\text{-}P_o$ was accumulated to a factor of 21.1 in nests of the xylophagous termite *Constrictotermes* and to a factor of 69.4 in *Nasutitermes*, both in the Caatinga (data not shown). $\text{HCl}_{\text{conc}}\text{-}P_o$

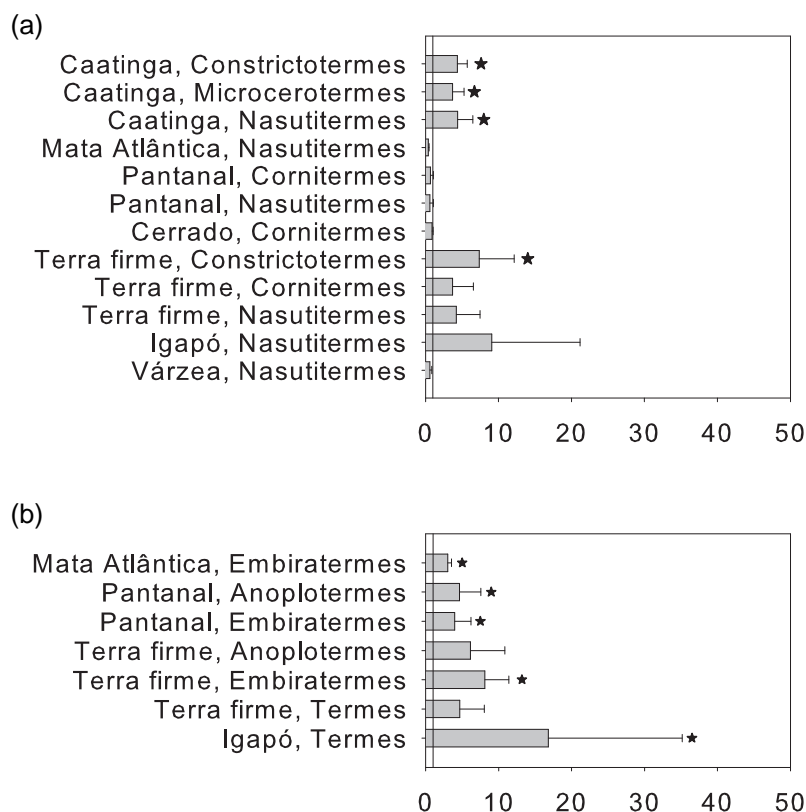


Figure 2.6 Enrichment for NaOH-P_i in xylophagous (a) and humivorous (b) termite nests in relation to the corresponding soil. A reference line at 1:1 and the standard error of each bar are marked. The ★ denotes significant ($P < 0.05$) differences between nest and soil P. Note the different scaling of the x-axis.

was enriched in nests of the Pantanal, with a factor of 38 for *Cornitermes* and up to 94 for wood-feeding *Nasutitermes* (data not shown).

2.3.2 Carbon content and C/P ratio

The organic C content of the wood samples was between 437 and 508 g kg⁻¹ (Figure 2.3d) and of the soil samples between 16 and 58 g kg⁻¹ (Figure 2.3c). Many nests of wood-feeding termites had C contents in the same dimension as that of the wood samples (Figure 2.3a), but some had low C amounts. This was related to the nesting habit, epigeic nests had the lowest C content, especially those of the *Cornitermes* in the Cerrado. The amount of C in humivorous termite nests was constantly higher than that in the surrounding soil (Figure 2.3b), though the enrichment in the nests varied.

The C/P ratio was generally higher in nests than in soils, but lower than in wood. It ranged from 11 to 186 (C to total P, both in mg kg⁻¹) in soils, from 627 to 17076 in wood, from 104 to 943 in humivorous termite nests and from 17 to 1360 in xylophagous termite

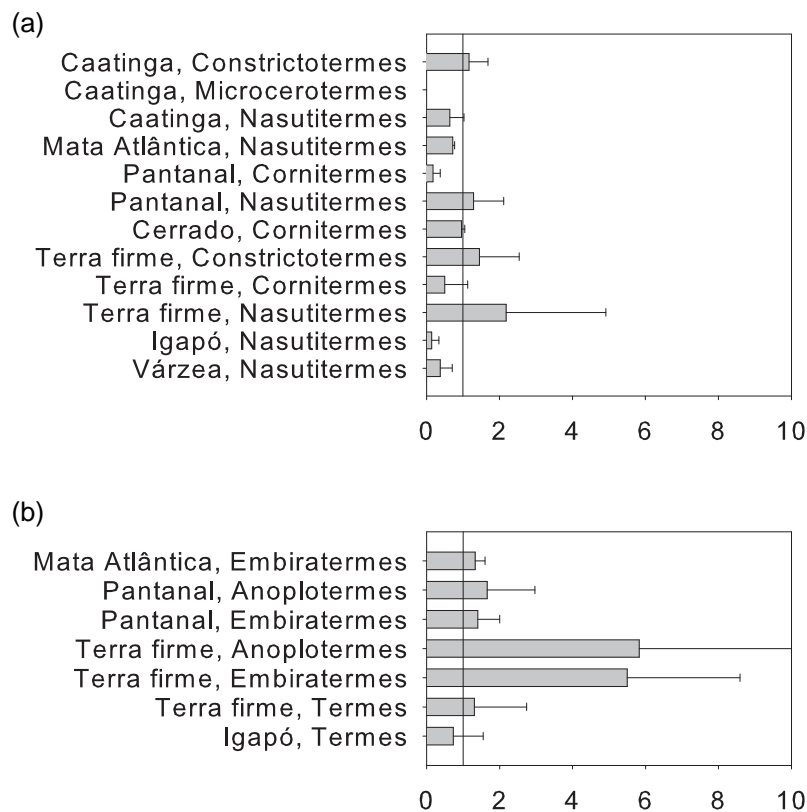


Figure 2.7 Enrichment for $\text{HCl}_{\text{conc}}\text{-P}_i$ in xylophagous (a) and humivorous (b) termite nests in relation to the corresponding soil. A reference line at 1:1 and the standard error of each bar are marked. The ★ denotes significant ($P < 0.05$) differences between nest and soil P. Note the different scaling of the x-axis.

nests. Consequently, organic C was more efficiently concentrated in the nests than P, despite C may escape in gaseous form.

2.3.3 ^{31}P -NMR spectra

Alkaline P extraction for ^{31}P -NMR analysis yielded 18.2 to 88.3% of the total P. Only a small amount of the detected peaks were inorganic forms. In the Terra firme, diester- P_o forms dominated over the more stable monoester- P_o forms (Table 2.4). *Cornitermes* and *Nasutitermes* of the Terra firme had a higher proportion of monoester- P_o than the soil or the other termite nests. The Terra firme wood had the smallest monoester- P_o portion. The nests of *Constrictotermes* of the Caatinga and *Embiratermes* of the Mata Atlântica tended to a higher proportion of diester- P_o than the soils (Figure 2.9). But the monoester- P_o portions were in both ecosystems higher than in the Terra firme.

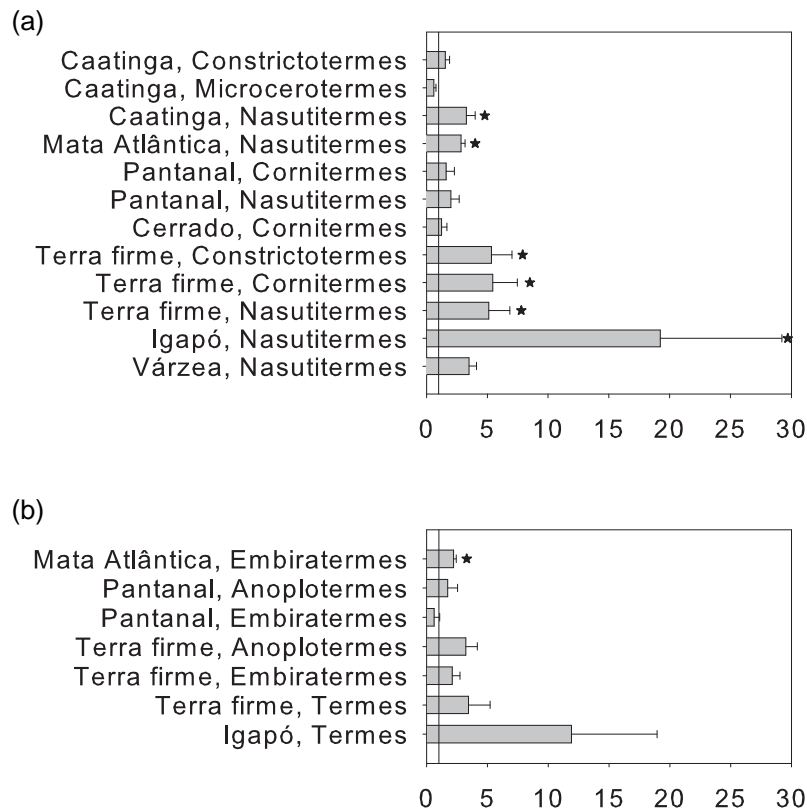


Figure 2.8 Enrichment for NaOH-P_0 in xylophagous (a) and humivorous (b) termite nests in relation to the corresponding soil. A reference line at 1:1 and the standard error of each bar are marked. The ★ denotes significant ($P < 0.05$) differences between nest and soil P.

2.4 Discussion

The contents of P fractions found in soils were similar in magnitude to those found by other authors. The measurements from the Caatinga soil (Haplic Alisol) match well the values determined in Luvisols and Argissols (see Palmieri et al., 2003, Brazilian soil classification) found by Araujo et al. (2003) and Silveira et al. (2006). Only the contents of resin- P_i were slightly lower in my results. Araujo et al. (2004) reported C/ P_0 values between 171 and 263, which is also in the same dimension like my result of 137. I found an astonishing high P content in the Cerrado (Umbric Acrisol). Lilienfein et al. (2000) and Neufeldt et al. (2000) reported much lower values for Oxisols (Soil Survey Staff, 1999) of the Cerrado. Yet, such high P contents were reported for young soils. Busato et al. (2005) found similar portions of total P in a Fluventic Eutrochrepts (Soil Survey Staff, 1999), though the proportions of P fractions were different. In a Neossolo Flúvico (Palmieri et al., 2003) described by Silveira et al. (2006) total P content and the proportion of the stable fractions were also in the same dimension as in my soils. I only found slightly lower total P contents with a higher proportion of P_0 in soils of the Mata Atlântica (Cambisol) than Cunha et al. (2007) and Cardoso et al. (2003), however the latter examined an Oxisol (Soil

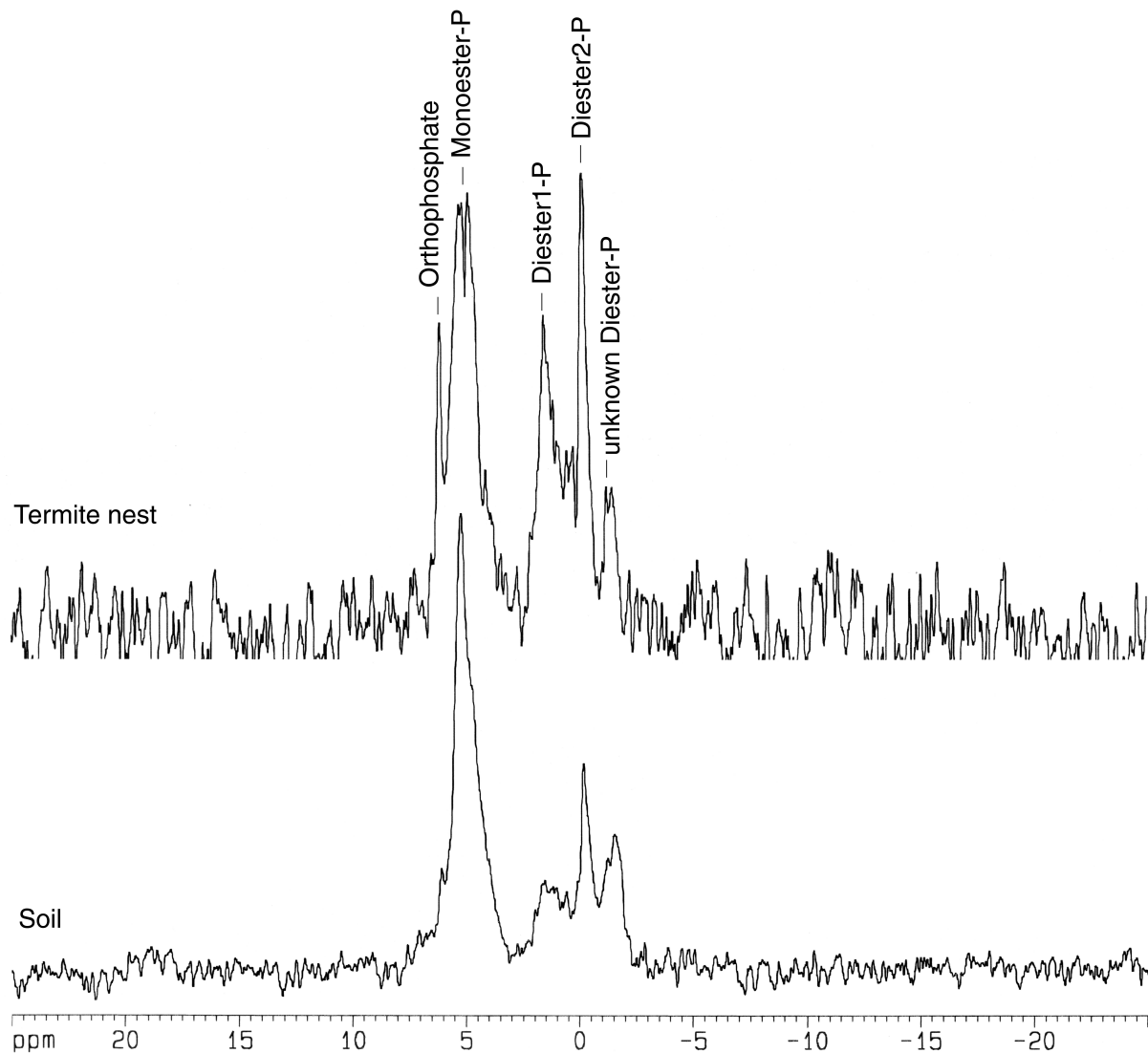


Figure 2.9 ^{31}P -NMR spectra of the Caatinga. The upper spectrum of an inner nest wall of a *Constrictotermes* nest, and the lower one of the soil.

Survey Staff, 1999). And my results of the Terra firme soils (Xanthic Ferralsol, Fluvisols) agreed well with the measurements of Frizano et al. (2003). In conclusion, I deem my P analyses to be representative for the range of studied soil types in Brazil.

The C content in nests of wood-feeding termites is mainly driven by the C content of the used wood, it is lower when also soil material is incorporated into the nest. The nests of soil/wood interface-feeder termites consists of a mixture of soil and wood materials, which results in a C content between the values of wood and soils, and thus in higher C/P ratios compared with the surrounding soils. As reported by Amelung et al. (2002), the C content in nests of humivorous termites of the Terra firme depends on the degree of wood-feeding. The degree of wood-feeding increased in the order *Anoplotermes* < *Embiratermes* < *Termes*, which was followed by the C content, and also the P composition changed along

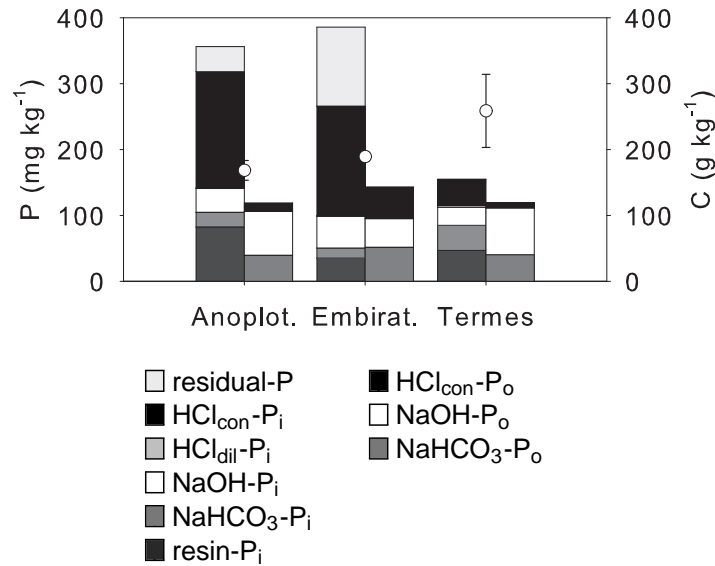


Figure 2.10 Sequential P-extraction and C analyses of humivorous termite nests of the Terra firme. In the order *Anoplotermes* < *Embiratermes* < *Termes* increased the degree of wood-feeding within the soil/wood interface-feeding guild (Amelung et al., 2002). The left bar comprises P_i plus residual-P and the right one P_o. The \circ marks the C content and the error bars indicate the standard error based on the number of samples presented in Table 2.2.

this gradient (Figure 2.10). As a result of different food sources, termites incorporate various amounts of organic matter, which appears in variable C contents in the nests of termite species.

With accumulation of organic matter, P content is generally raised. And indeed, the amounts of total P and P_o were, with two exceptions (*Microcerotermes* of the Caatinga and *Cornitermes* of the Cerrado), higher in nests than in soil or wood. But the enhancement in humivorous termite nests achieved not the same degree as the C content, reflected by a higher C/P ratio in the nests. Furthermore, xylophagous nests were more enriched in P than in C compared to wood, while the opposite was true compared with soil, where the C/P ratios were smaller than in nests. Likely, the termites do not only collect organic matter but preferentially enrich C or P. Brauman et al. (2000) suggested that humivorous termites prefer silt and clay fractions, which would result in higher C contents from associations with these texture fractions.

Not only the content of sum-P_o, also the portion of sum-P_o was elevated in preference to other P forms in all nests (excluding the above mentioned *Microcerotermes* of the Mata Atlântica and *Cornitermes* of the Cerrado). This is in contradiction to López-Hernández et al. (1989) who reported indeed higher contents of all P forms in mounds of *Nasutitermes*, but only 44% P_o in contrast to 70% in the soil. In my study it was not only an enrichment

Table 2.4 Phosphorus composition in alkali extracts as peak areas in percentage of total peak area in ^{31}P -NMR spectra.

Sample	Feeding group	Ortho-phosphate	Monoester-P	Diester1-P	Diester2-P	unknown Diester-P	Pyro-phosphate	Monoester to diester1 and diester2 ratio	Extraction yield	
		6–6.6 ppm	3–6 ppm	0.5–2.5 ppm	–1.0–0.5 ppm	–1.5 ppm	–5.5– –4 ppm		% of total P	
		% of total extracted P								
Caatinga										
Constrictotermes, B	xylophagous	6.3	43.8	24.6	18.9	6.3		1.01	19.2	
Soil		3.2	54.9	15.3	13.4	13.1		1.91	18.2	
Mata Atlântica										
Embiratermes, B	humivorous		45.0	40.0	15.0			0.82	28.6	
Soil			52.0	40.0	8.0			1.08	88.3	
Terra firme										
Constrictotermes, A-C	xylophagous	5.2	21.2	22.5	42.9	2.5	5.7	0.32	29.2	
Cornitermes, A+B	xylophagous		45.6	7.4	47.1			0.84	45.7	
Nasutitermes, B	xylophagous		42.8	31.2	26.0			0.75	28.7	
Anoplotermes, A-C	humivorous	9.3	31.8	13.7	45.2			0.54	57.0	
Embiratermes, A+B	humivorous	11.7	25.2	22.1	25.7		15.4	0.53	52.8	
Termes, B	humivorous	4.6	23.2	10.9	34.0		27.2	0.52	82.0	
Soil			29.2	21.5	32.5		16.8	0.54	35.6	
Wood			24.1	35.9	40.0			0.32	57.0	

of sum- P_o , but also a variable accumulation of different P_o fractions. Figure 2.9 showed an enrichment of labile diester forms in nests of *Constrictotermes* of the Caatinga, which is in line with an enrichment factor of 21 for the $\text{NaHCO}_3\text{-}P_o$ fraction. Yet inside the nests, the other P_o fractions were enriched as well. Especially the $\text{HCl}_{\text{conc}}\text{-}P_o$ fraction had high enrichment factors comparing to soils, which I attribute to the preservation of stable particulate organic material derived from wood.

When comparing the different P_i fractions, it may be resumed that in general labile P_i forms were more enriched in the nests than the stable ones (Figure 2.5–2.7). The enrichment of $\text{NaHCO}_3\text{-}P_i$ and $\text{NaOH}\text{-}P_i$ in nests of humivorous termites may be related to an enrichment of fine soil particles (sesquioxides, clay) by termites. Intriguingly, such an enrichment of P_i fractions normally bonded to sesquioxides was also observed in the carton nests of xylophagous termites, where an enrichment of sesquioxides is unlikely, suggesting that at least parts of these enrichments resulted from direct P transformations in the nests. The stable P_i forms, especially $\text{HCl}_{\text{conc}}\text{-}P_i$ and residual-P, were also accumulated in nests, but had a smaller proportion of total P than in soils (Table 2.3). This is in line with López-Hernández et al. (1989) who found labile water-soluble P was enriched in *Nasutitermes* mounds by a factor of 21 while stable P forms were enriched by a factor of 1.9 only. The wide range of termite genera studied here allows me to generalize this finding: The accumulation of P in termite mounds creates hot spots, also of higher P availability, within this P deficient environment. These P enriched mound materials could be used as soil amendment as shown by Watson (1977), Batalha et al. (1995) and Duponnois et al. (2005).

The weakly bonded resin- P_i was particularly enriched in nests of wood-feeding termites, while the other P_i forms, which are primarily bonded to minerals, rather accumulated in the nests of humivorous termites. Hence, the degree to which P availability is raised depends on the major feeding guild. Yet, a higher degree of wood-feeding within the soil/wood interface-feeding guild correlated with smaller amounts of P_i (Figure 2.10). I suggest, therefore, that alteration during food digestion and intimate contact with soil minerals altered the P distribution slightly. In contrast to, e. g., lignin analyses (Amelung et al., 2002), the feeding guild may not be directly derivable from the P composition of the mound.

The degree of P enrichment in the nests depended partly on the P content in the soils of the various ecosystems. For instance, the termites of the Terra firme and Igapó had large enrichment factors of P_i (Figure 2.5–2.7), whereas the contents of the respective P fraction in the soils were low (Figure 2.11a & 2.11b). Similarly, high enrichment factors of P_o fractions were observed particular in those ecosystems where the respective fraction is lowly concentrated in the reference soil (Figure 2.11c & 2.11d).

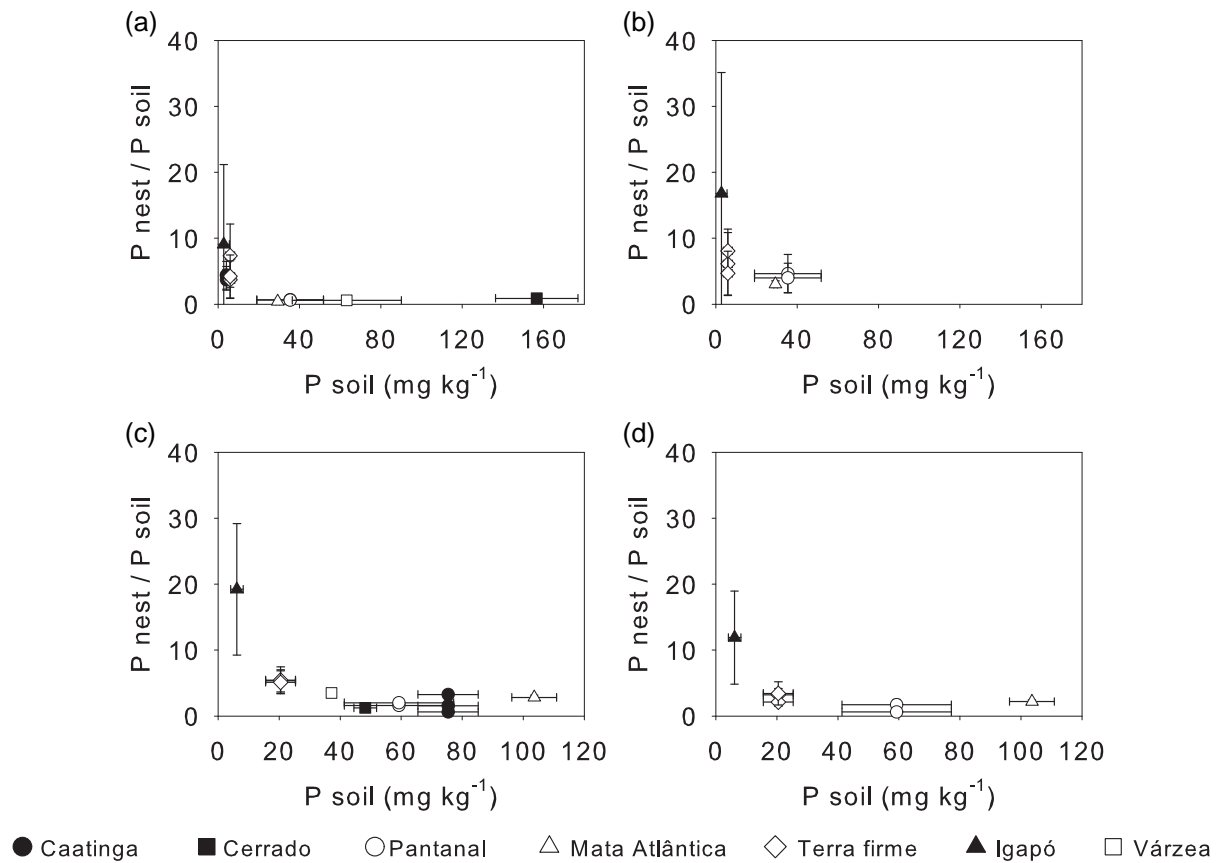


Figure 2.11 P enrichment in termite nests of the various ecosystems against the amount of the P fraction in the corresponding soil. (a) NaOH-P_i of xylophagous termite nests, (b) NaOH-P_i of humivorous termite nests, (c) NaOH-P_o of xylophagous termite nests, (d) NaOH-P_o of humivorous termite nests.

In summary, the effect of the different species can be classified as follows.

- Termites exhibit variable P contents in their different nest parts. The steepest gradients in P composition across different nest parts were in the nests of *Cornitermes* in the Pantanal, who used the outer nest wall not for living but only for protective purposes.
- About 50% of total P in the nests of the wood-feeding genera was P_o, likely co-accumulated with the wood and preserved during wood digestion. Also the resin-P_i content in the nests was elevated, possibly indicating an alteration of P forms within the nests.
- Humivorous termites did also enrich P inside their mounds. More than 60% of this P were inorganic P forms, but no specific P_i fraction was representative for this feeding guild. Portions of P_i tended to be lower in the nests at a higher degree of wood-feeding inside the soil/wood interface-feeding guild.

- The P composition in the nests of the grass-feeder termite *Cornitermes* of the Cerrado was significantly different from that of the wood-feeding termites.
- Different P stocks in the soils of the various ecosystems influenced the composition and degree of P enrichment in the nests.

2.5 Conclusion

All studied termite species alter the composition of materials used in nest construction. Total P is widely enriched in termite nests in comparison to soils. The enrichment of labile P_i forms and the reduction of the proportion of stable P_i forms documented the selective collection or a modification of the used materials by termites. In general, resin- P_i is enriched in nests of wood-feeding termites, while soil/wood interface-feeder termites have in addition prominent proportions of other labile P_i forms. In any case, all these transformations are beneficial for increasing P availability in these usually P deficient environments, thus supporting the ecological role of termites in tropical ecosystems. Yet I have little information on the development of those nests over time. Completely abandoned termite nests may be reintroduced into the soil, but also nutrients of the nests can be released into the soil. Both sustains and contributes to patchiness and spatio-temporal diversity of nutrient stocks in the tropics.

Chapter 3

Soil genesis and heterogeneity of phosphorus forms and carbon below mounds inhabited by primary and secondary termites¹

3.1 Introduction

Tropical ecosystems, especially savannas, show a mosaic of vegetation and nutrient patches in soils (Pärtel et al., 2008). Both, the occurrence of single trees, but also termite activities may account for those patterns (Salick et al., 1983; Tongway et al., 1989; Holdo & McDowell, 2004; Grant & Scholes, 2006; Obi & Ogunkunle, 2009). Many studies also demonstrated that termites influence soil properties by enriching carbon, nitrogen, clay and exchangeable cations inside their mounds relative to a reference soil (e.g. Lee & Wood, 1971b; Lobry de Bruyn & Conacher, 1990; Holt & Lepage, 2000).

Only a few studies addressed the soil heterogeneity below termite mounds and its immediate vicinity. Watson (1962), Coventry et al. (1988), and McCarthy et al. (1998) documented lateral and vertical changes of soil properties from termite nests to the surrounding soils in grid schemes. Watson (1962) showed an enrichment of carbonates in the central part below a termite mound. Coventry et al. (1988) found that besides carbon, also exchangeable calcium and magnesium were enriched in the central nest, and in nest surroundings. McCarthy et al. (1998) reported higher contents of calcium, potassium, and phosphorus in, and directly beneath islands in the floodplain of the Okavango alluvial fan, which were initiated by termite activity. However, all three studies addressed only single mounds and the temporal development was not regarded.

Besides an effect on single chemical properties, termites might alter soil characteristics so drastically that soil genesis is affected. Such termite-related impacts on soils were discussed for the microgranular structure of Ferralsols (Sys, 1956; Schaefer, 2001; Balbino et al., 2002; Reatto et al., 2009; Sarcinelli et al., 2009), the development of stone lines (Nye, 1955; Jungerius et al., 1999; IUSS Working Group WRB, 2006), and the formation of plinthite (Yakushev, 1968; Tardy & Roquin, 1992). Yet, we are not aware of studies addressing also the potential role of termites for reverting soil genesis, e.g., by eliminating

¹ This chapter was already published in a journal: Rückamp, D. et al. (2012). Soil genesis and heterogeneity of phosphorus forms and carbon below mounds inhabited by primary and secondary termites. *Geoderma* 170(1), 239–250.

certain diagnostic horizons that may have formed across several hundreds of years (discussed, e.g., for ants; Kristiansen & Amelung, 2001).

The significance of such termite-induced changes could be higher below older mounds, because of the longer time periods involved in soil alteration. Alternatively, weathering and organic matter decomposition in older mounds may cause a decrease of their nutrient contents (Roose-Amsaleg et al., 2005). Chapter 5 shows higher nitrate concentrations and lower carbon fluxes in soil water leached out of older mounds inhabited by secondary termites (inquiline species that colonize mounds built by other species) than in water from mounds inhabited by primary termites (the original nest builders) or reference soils. Because most of the older mounds in savannas are secondarily inhabited by inquilines (Redford, 1984; Lacher et al., 1986; Domingos & Gontijo, 1996), it is in general impossible to find older nests without termites in the Brazilian savanna (Cerrado).

Mid-infrared spectroscopy (MIRS), in combination with partial least squares regression (PLSR), enables accurate determinations of various organic and inorganic soil properties with a high sample throughput at low cost. In soil science, MIRS has been increasingly used during the last years. Janik et al. (1998) were able to predict organic and inorganic soil properties; Viscarra Rossel et al. (2006) quartz, clay minerals and various organic constituents; Zimmermann et al. (2007) organic carbon fractions with varying recalcitrance; Bornemann et al. (2008) black carbon; and Bornemann et al. (2010) particulate organic matter and lignin. Accordingly, MIRS also represents the method of choice to study soil heterogeneity below termite nests at high spatial resolution.

Consequently, this study was designed to

- (i) understand the impact of an important termite feeding guild (grass- and litter-feeder) of the Brazilian Cerrado on soil genesis;
- (ii) test the suitability of MIRS for quantifying organic carbon, as well as organic and inorganic phosphorus in available and stable P fractions;
- (iii) see to which degree the spatial heterogeneity of carbon and the phosphorus forms differed in the soil under, and adjacent to termite mounds from that in control soils; and
- (iv) evaluate the abundance of organic carbon and phosphorus forms as an indicator of chronological development from younger mounds to older ones, which were built by the same termite species, but already inhabited by secondary termites.

3.2 Materials and methods

3.2.1 Study site

The study was conducted on the farm of the Instituto Ecológica (10°16'S, 48°10'W, 630 m above sea level) in Taquaruçu, 20 km southeast of Palmas, Tocantins, Brazil (see Figure 2.1), in the dry season 2006. The mean annual temperature in this region is 24 °C, and the mean annual rainfall is 1800 mm with a 5-month dry season from May to September. The natural vegetation is savanna (Cerrado sensu lato), but the site is disturbed. The area burned in 2002, and it is now used as an extensive pasture. The dominant grass is *Brachiaria sp.*, and the most abundant tree species is *Caryocar brasiliense* Camb, but also trees of *Sclerolobium paniculatum* Vogel, *Rauvolfia sellowii* Müll. Arg., *Eremanthus sp.*, and *Byrsonima verbascifolia* Rich. ex Juss. occur. The density of all trees (trunk diameter > 10 cm) was 40 ha⁻¹.

3.2.2 Sampling

The whole study area had a density of epigeic mounds of various termite species of 72 ha⁻¹. Flat dome-shaped mounds of *Cornitermes silvestrii*, which feeds on grass and litter (Gontijo & Domingos, 1991; Marques, 2008), were most abundant and selected for the study (see Figure 5.1). I examined three sites with nests which looked fresh and were primarily inhabited by *C. silvestrii*; three sites with old nests, which were apparently constructed by *C. silvestrii*, but were now abandoned, weathered, overgrown by mosses, and partly inhabited by other termite species as secondary inquilines, mostly *Nasutitermes kemneri*; and three reference soil sites (Table 3.1). The control sites were situated 5 m away from termite nests at minimum and showed no evident termite influence, but some termite specimens were found during sampling (Table 3.1).

Four soil transects from the site center to the cardinal points were dug at every sampling site. Samples were taken at every transect width of 0, 40, 80, and 120 cm at the depths of 10, 30, 60, and 100 cm. Horizon boundaries were avoided and samples were taken 5 or 10 cm above or below. Mounds were sampled 5, 20 and 35 cm above the soil surface if existing. Sampling was done with five 100 cm³ cores at each sampling point. All samples were air dried immediately and balanced for calculation of the bulk density. Then the samples were sieved to < 2 mm, and subsequently ground with a ball mill.

3.2.3 Chemical analyses

The following analyses used for soil classification were only performed for the samples of the center of each sampling site. Particle-size distribution was analyzed with the sieve-pipette method according to Köhn (1928) and the DIN standard (DIN ISO 11277, 2002). Organic carbon (OC) and total nitrogen were determined using a Fisons NA 2000 elemental analyzer (Fisons Instruments, Rodano, Milan, Italy). The pH was measured in supernatant in water (1:2.5 w/v) with a glass electrode (Wissenschaftlich-Technische Werkstätten, Weilheim, Germany). The determination of the potential cation exchange capacity (CEC_{pot}) and exchangeable bases (Ca^{2+} , Mg^{2+} , K^+ , Na^+) was done with ammonium acetate following Summer & Miller (1996). The bases were measured with flame atomic absorption spectroscopy (AAS, AAnalyst 300, Perkin Elmer, Shelton, USA), and the analysis of ammonium for the CEC_{pot} determination was done with a spectrophotometer (SPECORD 205, Analytik Jena, Jena, Germany) following Keeney & Nelson (1982). Free pedogenic

Table 3.1 Metrics (Height, diameter in south-north (S–N) and east-west (E–W) direction) of sampled mounds, and the termite species detected at each site.

No.	Diameter		Height	Termite species	Termite feeding habit
	S–N	E–W			
cm					
Reference soils					
1				<i>Dihoplotermes inusitatus</i> <i>Procornitermes araujo</i>	soil/wood interface-feeder ^a grass- and litter-feeder ^{a, b}
2				<i>Embiratermes silvestrii</i> <i>Labiotermes emersoni</i>	unknown soil/wood interface-feeder ^c
3				<i>Dihoplotermes inusitatus</i> <i>Cornitermes silvestrii</i>	soil/wood interface-feeder ^a grass- and litter-feeder ^{a, c}
Mounds inhabited by primary termites					
1	114	136	33	<i>Cornitermes silvestrii</i> <i>Nasutitermes kemneri</i> <i>Serritermes serrifer</i>	grass- and litter-feeder ^{a, c} wood- and cattle dung-feeder ^d wood-feeder ^e
2	132	144	42	<i>Cornitermes silvestrii</i>	grass- and litter-feeder ^{a, c}
3	88	91	18	<i>Cornitermes silvestrii</i>	grass- and litter-feeder ^{a, c}
Mounds inhabited by secondary termites					
1	118	96	35	<i>Nasutitermes kemneri</i>	wood- and cattle dung-feeder ^d
2	115	89	34	<i>Nasutitermes kemneri</i> <i>Armitermes euamignathus</i> <i>Embiratermes festivellus</i> <i>Labiotermes orthocephalus</i>	wood- and cattle dung-feeder ^d wood- and grass-feeder ^{a, b} soil/wood interface-feeder ^a soil/wood interface-feeder ^f
3	112	127	42	<i>Nasutitermes kemneri</i> <i>Procornitermes araujo</i>	wood- and cattle dung-feeder ^d grass- and litter-feeder ^b

^a Gontijo & Domingos (1991); ^b Coles de Negret & Redford (1982); ^c Marques (2008); ^d Freymann et al. (2008); ^e Donovan et al. (2001); ^f Constantino et al. (2006)

Fe- and Al-oxides (Fe_d and Al_d) were extracted with dithionite-citrate buffer (Mehra & Jackson, 1958); and amorphous, active oxides (Fe_o and Al_o) with acid oxalate solution (Schwertmann, 1964). Fe and Al were measured with an inductively coupled plasma spectrometer (ICP-OES, JY70PLUS, Jobin Yvon, Edison, USA).

Phosphorus measurements were the basis for the following MIRS-PLSR predictions. The measurements were performed for one replicate of each, reference soils and sites with mounds inhabited by primary and secondary termites. $\text{NaHCO}_3\text{-P}$ and $\text{HCl}_{\text{conc}}\text{-P}$ were identified as the relevant labile and stable phosphorus forms in the studied termite nests (Chapter 2). The extractions were done accordingly to Olsen et al. (1954) and Colwell (1963) for $\text{NaHCO}_3\text{-P}$, and to Metha et al. (1954) for $\text{HCl}_{\text{conc}}\text{-P}$. $\text{NaHCO}_3\text{-P}$ refers to labile, easily available P, and $\text{HCl}_{\text{conc}}\text{-P}$ to potentially bioavailable organic P (P_o), and to very stable inorganic P (P_i) (Tiessen & Moir, 1993). P_i was determined in both extracts by the Molybdenum-Blue-method (Murphy & Riley, 1962) with a spectrophotometer. Total P in the extracts (P_t) was measured with an ICP-OES. P_o was then calculated by difference of P_t and P_i .

3.2.4 MIRS-PLSR

Mid-infrared spectra (MIRS) measurements for all samples were taken using a Bruker Tensor 27 (Bruker AXS, Madison, USA) equipped with an automated high-throughput device. About 20 mg ground soil material were transferred to microplates and compacted with a plunger to provide a plain and dense surface for spectroscopic measurement of the diffuse reflectance. Five replicates of measurements, each comprising 120 scans, were conducted for each sample in order to minimize errors in spectroscopic measurement. A partial least squares regression (PLSR) quantification of OC and P fractions with the OPUS QUANT software (2006, Bruker AXS, Madison, USA) followed. Utilizing the PLS 1 algorithm (Martens & Næs, 1989), the software decomposes the data plotted in the spectral matrix and the laboratory data matrix into latent variables (loadings). For each sample set, I conducted calibration procedures employing leave-one-out, full-cross validations (Efron, 2004). Measured spectra that obviously did not fit the prediction model or exceeded the properly described range were treated as outliers and removed from the sample sets. After removal, the full-cross validation was repeated.

Apart from the coefficient of determination (R^2) between measured and predicted values, the predictive power of the spectroscopic measurement was also estimated by calculating the root mean square error of cross validation (RMSECV), which should be minimized in the validation procedure. Further on, I calculated the relative percent deviation (RPD) as dimensionless quality parameter. The RPD represents the quotient of standard deviation

of the reference data and standard error of the calibration procedures. The higher the RPD value, the better the predictive power of the calibration model. Chang et al. (2001) even reported that RPD values > 2 might be sufficient for the prediction of various soil properties. Finally, the prediction models with the best statistical parameters were used. Table 3.2 summarized the settings of the prediction models used for the estimation of OC and P fractions.

3.2.5 Data analyses

The spatial patterns of soil properties were illustrated using kriging with standard settings of the software program Surfer 8 (Golden Software, 2002, Golden, USA). The generated maps were compared using the fuzzy numerical algorithm within the Map Comparison Kit 3.2.0 (Research Institute for Knowledge Systems, Maastricht, The Netherlands; Visser & de Nijs, 2006). Before doing this, maps with normalized (mean = 0; standard deviation = 1) values were constructed, which enabled me to compare maps with unequal units. The fuzzy algorithm takes neighboring values into account (neighborhood radius 15 cm, exponential decay); in this respect the map comparison has advantages over cell by cell regression analyses, also because a similarity map, in addition to the average similarity index for the whole comparison, is produced. The similarity index can get values between 0 (no similarity) and 1 (absolute similarity). Differences between groups were examined with an analysis of variance (ANOVA), and the Scheffé test as post-hoc test for comparisons of more than two groups. The significance level was set at $P < 0.05$. The ANOVA was conducted with SPSS 14.0 (SPSS Inc., 2005, Chicago, USA). The photographs of the soil transects were rectified by using ShiftN 3.5 (Marcus Hebel, 2009, Ettlingen, Germany).

3.3 Results

3.3.1 Soil under termite mounds – morphological changes and classification

Table 3.3 summarizes the chemical soil properties and the particle size distributions measured at the center of each sampling site. In general, the soils were relatively rich in organic material (topsoils: 13.4 – 41.5 g C kg⁻¹), had a high Fe content (Fe_d: 100.6 – 131.6 g kg⁻¹ in the topsoil), and had a very low base saturation. The reference sites and the ones with primarily inhabited mounds had an argic horizon (IUSS Working Group WRB, 2006; argillic horizon according to Soil Survey Staff, 2010), reflected by the higher clay contents than the overlying horizons. Consequently, the soils at the reference site centers were classified as Alisols, if the CEC_{pot} to a depth of 50 cm was greater than 24 cmol_c kg⁻¹ clay, or as Acrisols, if the CEC_{pot} was lower than 24 cmol_c kg⁻¹ clay (Table 3.3 & 3.4; Figure 3.1;

Table 3.2 Settings and statistical parameters of the calibration models for predicting soil variables by mid-infrared spectroscopy and partial least squares regression (MIRS-PLSR).

Soil variable	Samples	Data Pretreatment	Spectral Ranges cm ⁻¹	Latent variables	Outliers ^a	R ² ^b	RPD ^c	RMSECV ^d
Organic carbon	53	first derivative + MSC ^e	5382 – 883	8	0	0.99	6.76	0.16
NaHCO ₃ -P _i	165	none	3230 – 725	9	15	0.62	1.63	3.74
NaHCO ₃ -P _o	127	first derivative	3760 – 3311, 3076 – 2756, 2420 – 2266, 1585 – 1240	5	8	0.71	1.86	5.92
HCl _{conc} -P _i	165	first derivative + MSC	2601 – 748	11	13	0.80	2.26	41.7
HCl _{conc} -P _o	prediction was not possible							

^a number of measured spectra removed from the calibration set, which consists of five times the number of samples; ^b coefficient of determination; ^c relative percent deviation; ^d root mean square error of cross validation; ^e MSC = multiplicative scatter correction

Table 3.3 Particle-size distribution and chemical soil properties of the soils at each sampling site center.

Horizon cm	Sand % of fine earth	Silt	Clay	OC ^a g kg ⁻¹	N	pH	CEC _{pot} ^b cmol _c kg ⁻¹	Ca ²⁺	Mg ²⁺	K ⁺	Na ⁺	Fe _d ^c g kg ⁻¹	Fe _o ^d	Al _d ^e	Al _o ^f
Reference soil no. 1															
0– 26	75.1	6.9	18.0	32.7	1.40	4.6	14.02	0.07	0.04	0.06	0.01	131.6	3.7	19.2	1.8
26– 75	51.4	19.9	28.7	12.8	0.66	5.4	7.04	0.02	0.01	0.02	0.01	154.8	2.6	23.4	1.3
75– 100+	51.8	27.4	20.8	4.7	0.20	5.4	3.72	nd ^g	nd	nd	nd	152.0	1.3	15.6	0.7
Reference soil no. 2															
0– 26	66.4	11.6	22.0	13.4	0.68	4.9	9.00	0.24	0.01	0.05	0.01	114.4	3.6	15.8	1.3
26– 46	49.5	17.2	33.3	14.5	0.76	5.0	7.51	0.01	0.04	0.23	0.01	141.1	2.8	21.1	1.4
46– 100+	50.2	24.8	25.1	10.1	0.47	5.2	6.42	0.01	0.03	0.04	0.04	141.1	2.2	21.1	1.2
Reference soil no. 3															
0– 25	60.5	10.6	29.0	17.6	0.97	5.0	7.98	0.50	0.03	0.05	0.02	129.3	3.3	20.5	1.3
25– 100+	46.5	17.5	36.0	9.4	0.43	5.3	5.79	0.15	0.03	0.03	0.02	151.7	2.3	21.1	1.2
Mound inhabited by primary termites no. 1															
0– 28	55.2	19.1	25.7	41.5	1.91	4.5	14.65	1.42	1.82	0.21	0.02	119.3	2.5	19.8	1.3
28– 85	52.3	13.9	33.9	13.9	0.62	5.5	6.36	0.06	0.04	0.02	0.02	121.4	2.3	18.8	1.1
Mound inhabited by primary termites no. 2															
0– 20	52.9	23.0	24.1	39.1	1.91	4.7	13.57	1.31	2.02	0.20	0.02	130.5	2.8	18.9	1.3
20– 60	46.3	20.2	33.5	18.2	0.91	5.3	8.16	0.35	0.53	0.06	0.01	175.2	2.4	24.2	1.2
60– 100+	52.9	18.3	28.8	7.4	0.36	5.3	3.89	0.01	0.02	0.00	0.00	152.6	1.9	15.6	1.0
Mound inhabited by primary termites no. 3															
0– 45	59.5	17.0	23.5	25.4	1.29	5.2	8.69	0.79	0.99	0.15	0.02	130.4	2.6	18.8	1.3
45– 67	53.8	18.1	28.0	14.7	0.73	5.0	7.02	0.10	0.18	0.09	0.05	144.6	3.0	21.4	1.3
67– 100+	48.6	25.8	25.5	6.1	0.30	5.4	3.31	0.04	0.01	0.00	nd	150.7	1.9	19.1	1.0
Mound inhabited by secondary termites no. 1															
0– 29	57.9	13.9	28.2	27.6	1.25	4.1	10.96	0.09	0.07	0.06	0.02	100.6	3.4	15.9	1.5
29– 54	59.8	12.2	28.0	18.4	0.92	4.4	9.67	0.08	0.07	0.05	0.04	108.2	3.1	15.0	1.4
54– 100+	57.4	13.4	29.2	11.4	0.54	5.9	7.26	0.08	0.06	0.01	0.02	125.6	2.6	18.2	1.5
Mound inhabited by secondary termites no. 2															
0– 60	49.4	20.3	30.4	32.5	1.88	5.2	12.37	0.45	0.61	0.17	0.02	117.6	3.2	20.5	1.6
60– 100+	50.9	27.5	21.6	7.3	0.28	5.6	4.14	0.60	0.03	0.01	0.02	136.6	1.9	18.6	1.0
Mound inhabited by secondary termites no. 3															
0– 18	53.5	19.8	26.6	33.5	1.73	3.9	13.58	0.81	0.62	0.11	0.02	124.3	3.6	18.9	1.7
18– 60	52.8	18.8	28.4	12.5	0.60	5.2	6.10	0.32	0.09	0.00	0.02	128.0	2.7	19.3	1.3
60– 100+	48.6	24.5	26.9	7.2	0.31	5.4	4.16	0.11	0.05	0.00	0.02	139.0	1.3	13.0	0.7

^a organic carbon; ^b potential cation exchange capacity; ^c free pedogenic Fe-oxides; ^d amorphous Fe-oxides; ^e free pedogenic Al-oxides; ^f amorphous Al-oxides; ^g nd = below limit of detection

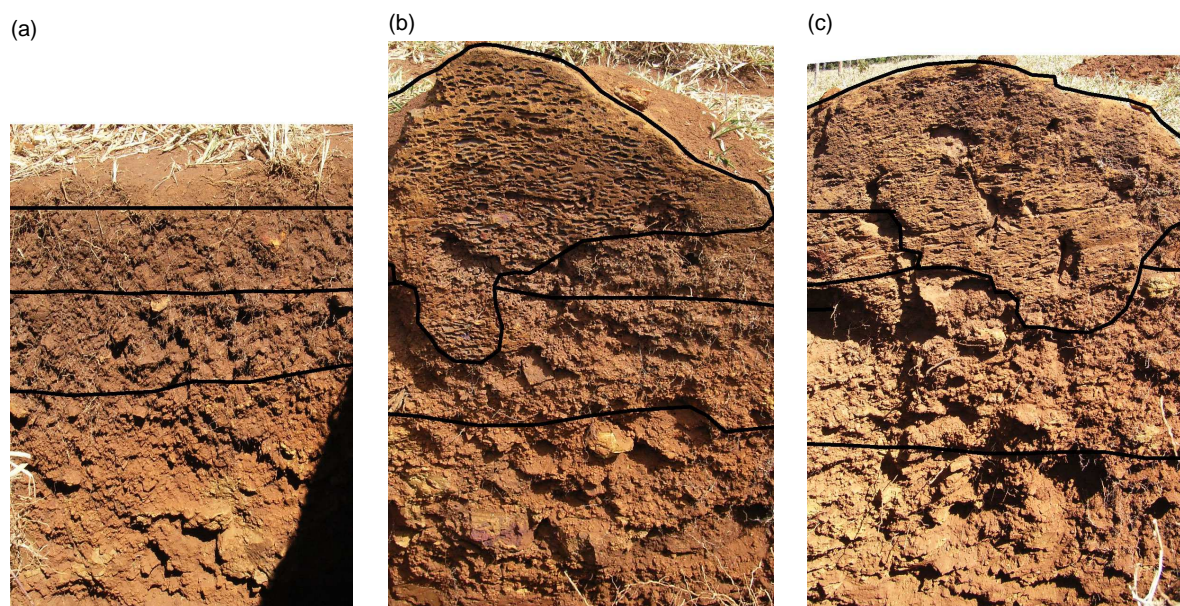


Figure 3.1 Photographs of soil transect parts at (a) the reference site no. 2, (b) the site no. 2 with a mound inhabited by primary termites, and (c) the site no. 3 with a mound inhabited by secondary termites. The horizon and nest boundaries were drawn with respect to the rectified photographs; therefore, they may slightly differ from the data in Table 3.3, Figure 3.4, 3.5 & 3.8–3.11. Note that the mound in (b) was opened at the left side before the photograph was taken.

IUSS Working Group WRB, 2006). According to Soil Survey Staff (2010) the soils were classified as Ultisols (Table 3.4). There were no changes in overall soil classification below mounds inhabited by primary termites in comparison to the reference sites. However, the soils below mounds inhabited by secondary termites had to be classified as Umbrisols, because at these sites no argic horizon was present, whereas the diagnostic criteria for an umbric surface horizon were fulfilled (Table 3.3 & 3.4; Figure 3.1). These umbric horizons are generally rich in organic matter and require a surface thickness of 20 cm or larger, which has either been reached directly (for two of the three sites), or may be reached after mixing the first 20 cm of soil (for the third site). Also the Soil Taxonomy classification (Soil Survey Staff, 2010) was changed under mounds inhabited by secondary termites. The soils had to be classified as Inceptisols (Table 3.4).

3.3.2 Soil properties under termite mounds

Significant differences for some mean soil properties relevant also for soil classification (for OC see Section 3.3.3) were observed when comparing the topsoil (10 cm sampling depth) of the reference site with samples from 10 cm depth below ground level under mounds inhabited by primary and secondary termites. The average contents of exchangeable Ca^{2+} , Mg^{2+} , and K^{+} were significantly higher, and those of Fe_0 were significantly lower below

Table 3.4 Soil types at the nine site centers classified accordingly to WRB (IUSS Working Group WRB, 2006) and to Soil Taxonomy (Soil Survey Staff, 2010).

No.	WRB classification	Soil Taxonomy classification
Reference soils		
1	Umbric Alisols (Humic, Hyperdystric, Skeletic, Chromic)	Ustic Haplohumults
2	Umbric Acrisols (Humic, Hyperdystric, Skeletic)	Ustic Haplohumults
3	Umbric Acrisols (Humic, Hyperdystric, Skeletic, Chromic)	Ustic Haplohumults
Mounds inhabited by primary termites		
1	Umbric Acrisols (Humic, Hyperdystric, Skeletic, Chromic)	Ustic Haplohumults
2	Haplic Alisols (Humic, Hyperdystric, Skeletic)	Ustic Haplohumults
3	Umbric Alisols (Humic, Hyperdystric, Skeletic)	Typic Humustepts
Mounds inhabited by secondary termites		
1	Haplic Umbrisols (Humic, Hyperdystric, Pachic)	Typic Humustepts
2	Haplic Umbrisols (Humic, Hyperdystric, Pachic, Skeletic)	Typic Humustepts
3	Haplic Umbrisols ^a (Humic, Hyperdystric, Skeletic)	Typic Humustepts

^a umbric horizon identified after mixing of the upper 20 cm of the mineral soil (IUSS Working Group WRB, 2006)

primarily inhabited mounds (Figure 3.2). The values below secondarily inhabited mounds were in-between those of the primarily inhabited sites and the reference soil, but were not significantly different from the latter. The pH(H₂O) was lowest at 10 cm depth below secondarily inhabited mounds (Figure 3.2); and the contents of silt, but not those of clay, were significantly elevated below both types of termite mounds (Figure 3.2; averaged data not shown for clay contents). While the contents showed different values for mound and reference sites, the overall stocks of elements and particles did not exhibit differences for the whole 100 cm soil profile. This suggests that differences in soil heterogeneity were mostly due to redistribution of these particles in the soil profile and not by a site-inherent heterogeneity, though the mounds itself were not analyzed for all soil properties. Only the exchangeable Mg²⁺ stock in the 100 cm soil profile was significantly higher below primarily inhabited mounds than below the secondarily inhabited mounds or the reference soil (data not shown).

3.3.3 Carbon patterns in soils surrounding termite nests

To be able to use the material from all nine sites at reasonable workload, the assessment of nutrient patterns was based on MIRS-PLSR analyses. The prediction of OC contents using MIRS-PLSR was excellent as shown in Figure 3.3a, which was also confirmed by the statistical parameters in Table 3.2.

Averaged OC contents (n = 3) based on the MIRS-PLSR predictions decreased in the reference soil from the topsoil to the subsoil from 18.5 g C kg⁻¹ in 10 cm depth to 6.5 g C kg⁻¹ in 100 cm depth (Figure 3.4). The highest OC contents were found in primarily inhabited

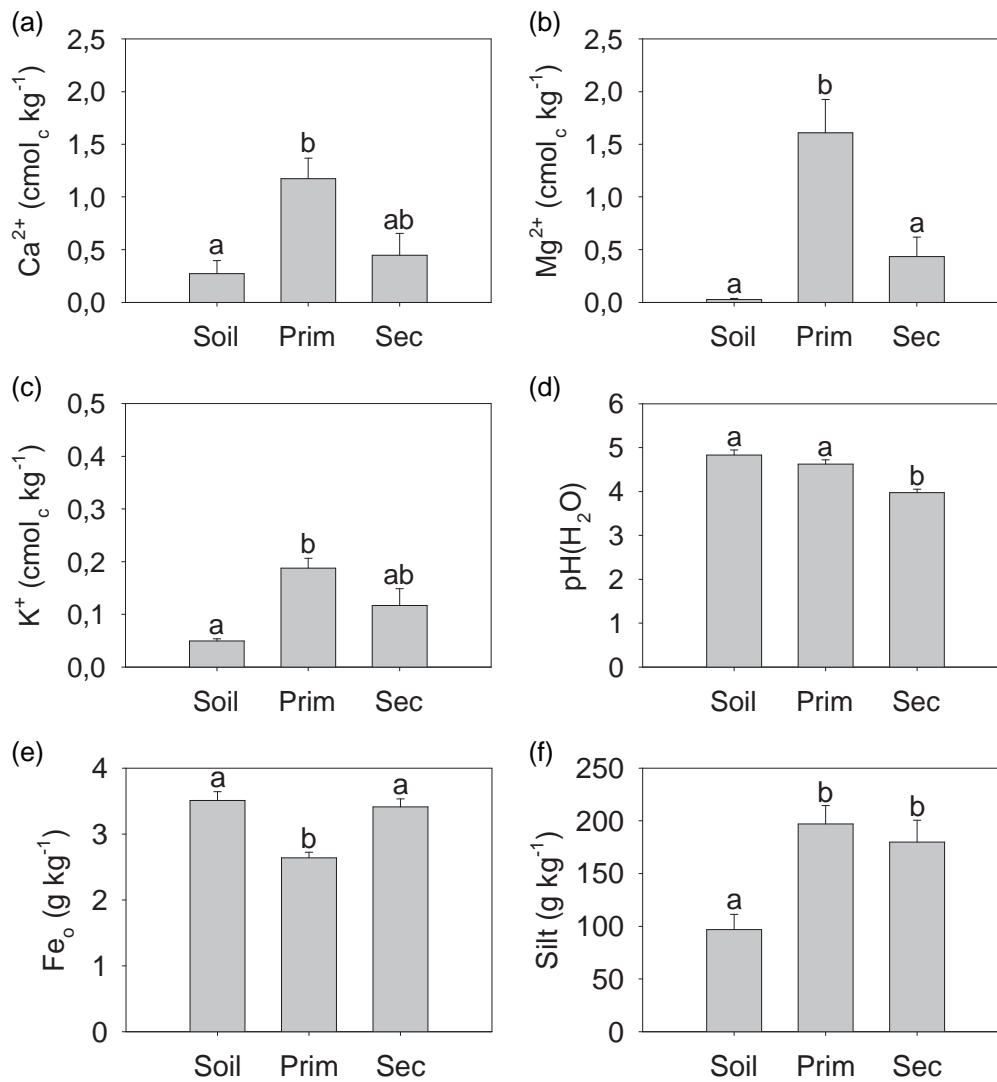


Figure 3.2 Averaged contents ($n=3$) of exchangeable cations (a: Ca^{2+} ; b: Mg^{2+} ; c: K^+), (d) $\text{pH}(\text{H}_2\text{O})$, (e) Fe_0 , and (f) silt at 10 cm soil depth in reference soils, soils under primarily (Prim) and under secondarily (Sec) inhabited termite mounds. Significant differences ($P < 0.05$) were marked with different letters.

nesses with an average of 35.3 g C kg^{-1} in the above ground nest parts, and 37.7 g C kg^{-1} in 10 cm soil depth at the site centers, which was also part of the nest, thus exceeding the respective OC contents of the reference topsoil by a factor of 1.9 and 2.0, respectively (Figure 3.4). The OC enrichment in the mounds inhabited by secondary termites was also evident, though less pronounced (factors of 1.5 and 1.9, respectively; Figure 3.4). Similarity indices of OC patterns in soils under mounds and at the control sites showed that higher carbon contents were found to a lateral width of 120 cm and to vertical depth of 50–70 cm (Figure 3.6a), below both, primarily and secondarily inhabited mounds. Dissimilarities at depths of 100 cm were caused by a high coefficient of variation at this depth in the reference soils. It was four times higher than at the upper sampling depths, probably reflecting variable stone contents at that depth.

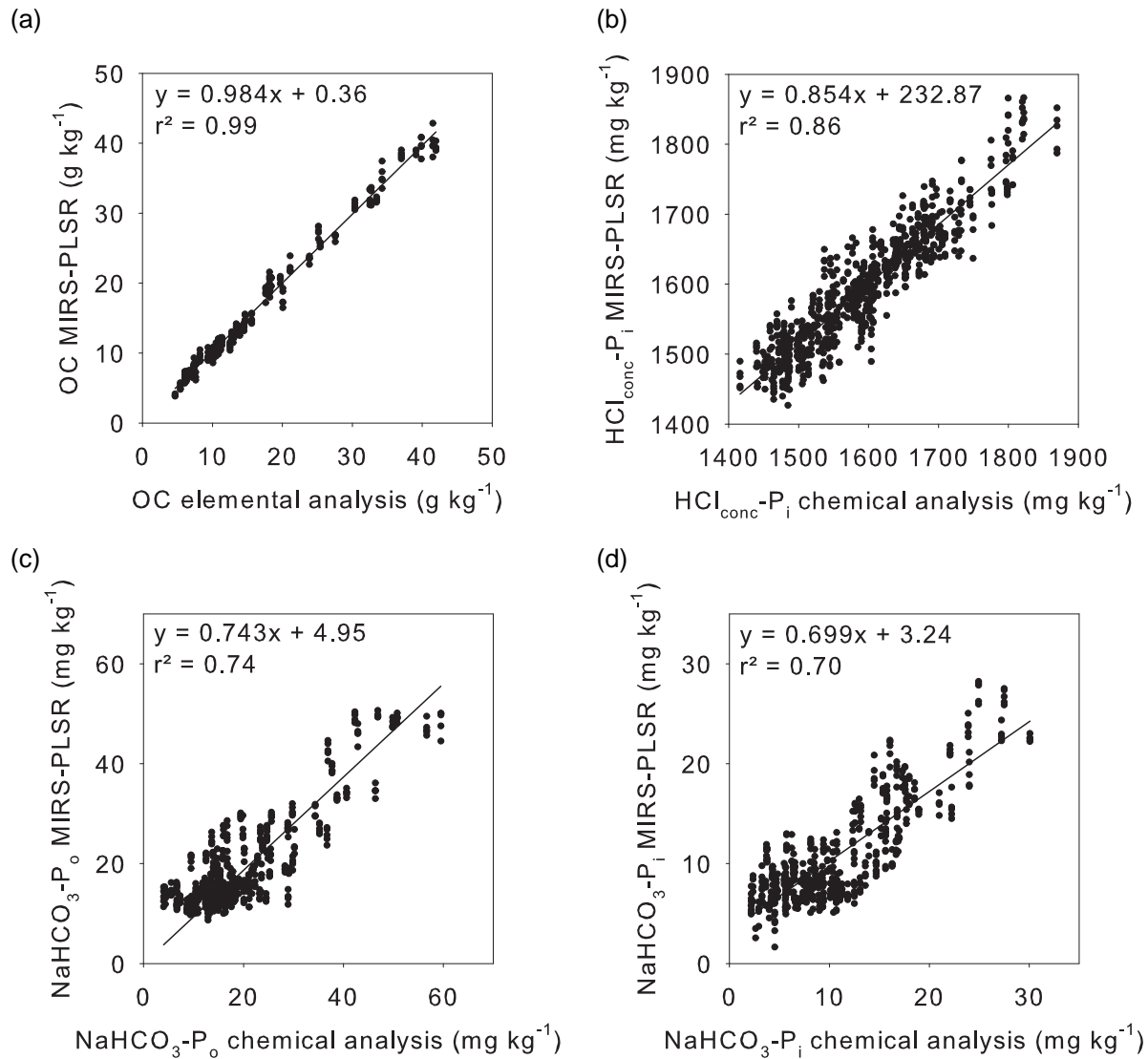


Figure 3.3 Predictions of (a) organic carbon, (b) HCl_{conc}-P_i, (c) NaHCO₃-P_o, and (d) NaHCO₃-P_i by mid-infrared spectroscopy and partial least squares regression (MIRS-PLSR) in comparison to conventional analyses. Predictions from five individual spectroscopic measurements are plotted per sample. The organic carbon prediction was done with a set of 53 samples, and the predictions of phosphorus pools with 165 or 127 samples.

Apart from OC contents, also OC stocks were raised in the soils below mounds (Figure 3.7a). The stock was slightly but consistently higher below the secondarily than below the primarily inhabited mounds, which could be attributed to the lower bulk density in the topsoil below primarily inhabited mounds (Figure 3.5). If OC contents of the mounds were included in the stock calculation, the total OC stocks were even higher for both mound types.

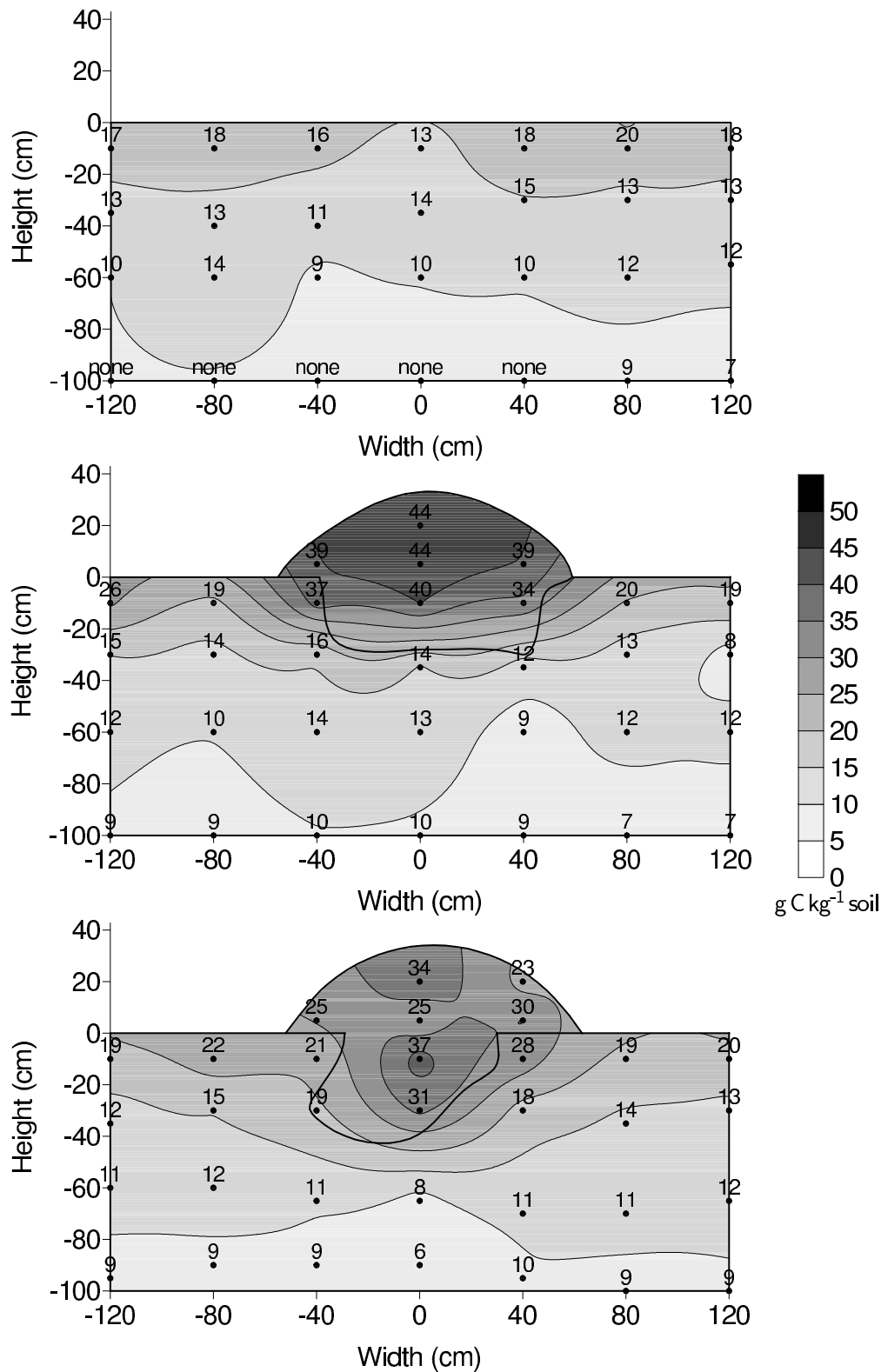


Figure 3.4 Interpolated patterns of organic carbon (predicted by MIRS-PLSR) in representative transects ($n=1$) of the reference soils (top), the mound sites inhabited by primary (center) and the ones inhabited by secondary termites (bottom). The sampling points are marked and denoted with the predicted/measured value. Lines mark the termite nest boundaries.

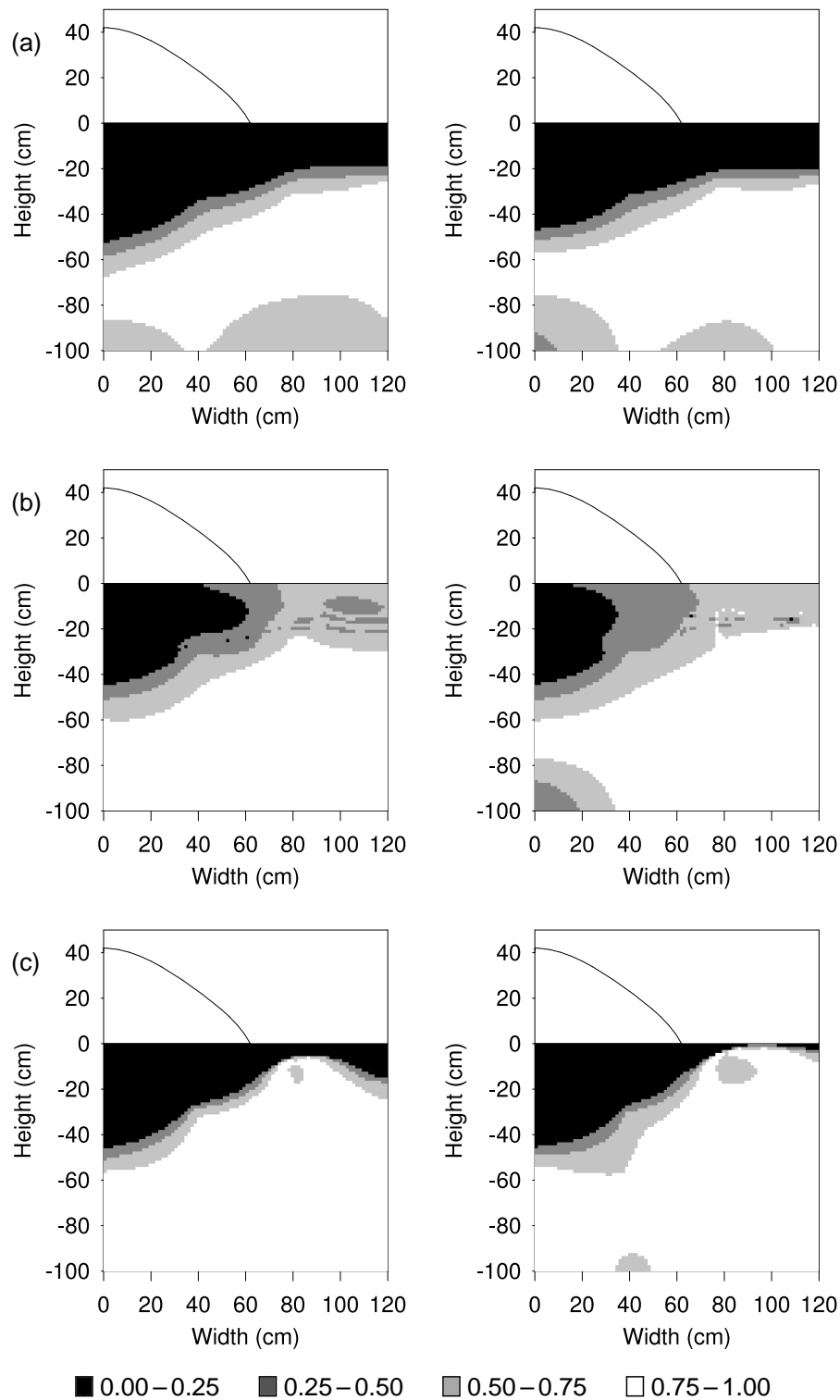


Figure 3.6 Maps of similarity indices of averaged (site center to a width of 120 cm; $n = 12$, and $n = 3$ for the site center) (a) organic carbon contents between the soil below primarily inhabited mounds and the reference soil (left), and between the soil below secondarily inhabited mounds and the reference soil (right). (b) shows the similarity index of the averaged $\text{NaHCO}_3\text{-P}_i$ contents, and (c) shows the similarity indices of the averaged $\text{NaHCO}_3\text{-P}_o$ contents, in each case the similarity between the reference soil and the primarily inhabited mound is shown at the left and the similarity between the reference soil and the secondarily inhabited mounds at the right. The termite mound position is drawn above as reference.

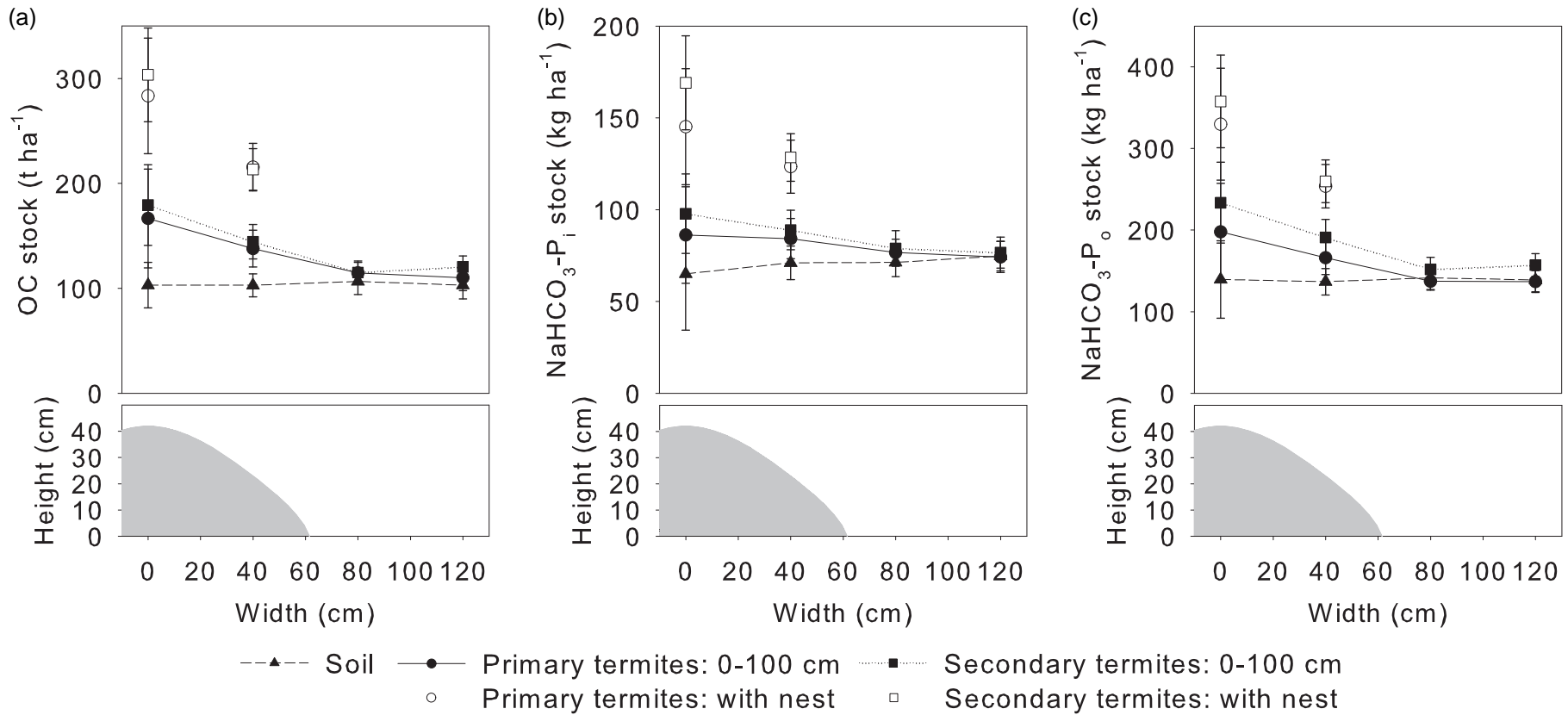


Figure 3.7 (a) Organic carbon, (b) NaHCO₃-P_i, and (c) NaHCO₃-P_o stocks (0–100 cm soil depth, without and with nest parts above ground) from the site center to a width of 120 cm for the reference soil, the mound sites inhabited by primary and by secondary termites. Means of replicates and directions were shown ($n = 12$, and $n = 3$ for the site center). The connecting lines were only drawn for visualization. A mound silhouette is shown beneath as reference.

3.3.4 Phosphorus patterns in soils surrounding termite nests

The success in the prediction of P fractions by MIRS-PLSR was variable. It was not possible to determine $\text{HCl}_{\text{conc}}\text{-P}_0$ by MIRS-PLSR, whereas $\text{HCl}_{\text{conc}}\text{-P}_i$ could be estimated well (Table 3.2; Figure 3.3b). The determination of $\text{NaHCO}_3\text{-P}_0$ and $\text{NaHCO}_3\text{-P}_i$ by MIRS-PLSR could be done, but it was more imprecise than for OC or $\text{HCl}_{\text{conc}}\text{-P}_i$ (Table 3.2; Figure 3.3c & d). Hence, the patterns of P fractions are less accurate than those of OC; nevertheless some consistent changes in the P distribution below the mounds could be revealed.

The MIRS-PLSR predictions showed similar trends across soil depths for $\text{NaHCO}_3\text{-P}_i$ and $\text{NaHCO}_3\text{-P}_0$ contents at the reference sites (Figure 3.6, 3.8 & 3.9). Those sites exhibited averaged phosphorus contents of $11.3 \text{ mg P kg}^{-1}$ soil for the $\text{NaHCO}_3\text{-P}_i$ fraction, and $20.5 \text{ mg P kg}^{-1}$ soil for the $\text{NaHCO}_3\text{-P}_0$ fraction at 10 cm soil depth. On the contrary, the other three sampling depths had only average contents of 7.4 mg P kg^{-1} soil for the $\text{NaHCO}_3\text{-P}_i$ fraction, and $15.0 \text{ mg P kg}^{-1}$ soil for the $\text{NaHCO}_3\text{-P}_0$ fraction. Termite mounds and the nest parts below the ground level (to approximately 30 cm soil depth) were enriched in these P forms relative to the reference soil at 10 cm depth (enrichment factors for $\text{NaHCO}_3\text{-P}_i$ 1.1 – 1.6, and for $\text{NaHCO}_3\text{-P}_0$ 1.3 – 2.1). The enrichment was slightly higher in mounds inhabited by primary termites relative to those inhabited by secondary ones. Elevated $\text{NaHCO}_3\text{-P}_i$ contents extended to widths of approximately 120 cm, and to soil depths of 50 – 60 cm below the ground level (Figure 3.6b). $\text{NaHCO}_3\text{-P}_0$ was as well enriched to depths of 50 – 60 cm directly below the mounds, but a trend for a lateral influence could not clearly be observed (Figure 3.6c). Some values were indeed higher at the mound sites, but also the opposite or no differences were found. In summary, termites exhibited similar effects on the distribution patterns of $\text{NaHCO}_3\text{-P}_i$ and OC, though the enrichment level was different.

As observed for the OC stocks (Figure 3.7), also the $\text{NaHCO}_3\text{-P}$ stocks were increased in the soil under termite mounds in comparison to the reference soil. Again, the accumulation was a bit less pronounced below primarily inhabited mounds than below secondarily inhabited mounds. The inclusion of mounds into stock calculation raised the stocks further, but the observed trends remained identical. As the $\text{NaHCO}_3\text{-P}_0$ contents were twice as high as the $\text{NaHCO}_3\text{-P}_i$ contents, also the $\text{NaHCO}_3\text{-P}_0$ stocks exceeded those of $\text{NaHCO}_3\text{-P}_i$ stocks at all sites.

The predictions of $\text{HCl}_{\text{conc}}\text{-P}_i$ by MIRS-PLSR showed a similar content in all samples (Figure 3.10). Thus there was little if any effect of termites on $\text{HCl}_{\text{conc}}\text{-P}_i$. As the contents of $\text{HCl}_{\text{conc}}\text{-P}_0$ could not be predicted by MIRS-PLSR, the results (Figure 3.11), which are based on chemical analyzed data for one replicate only, indicate a trend to higher contents

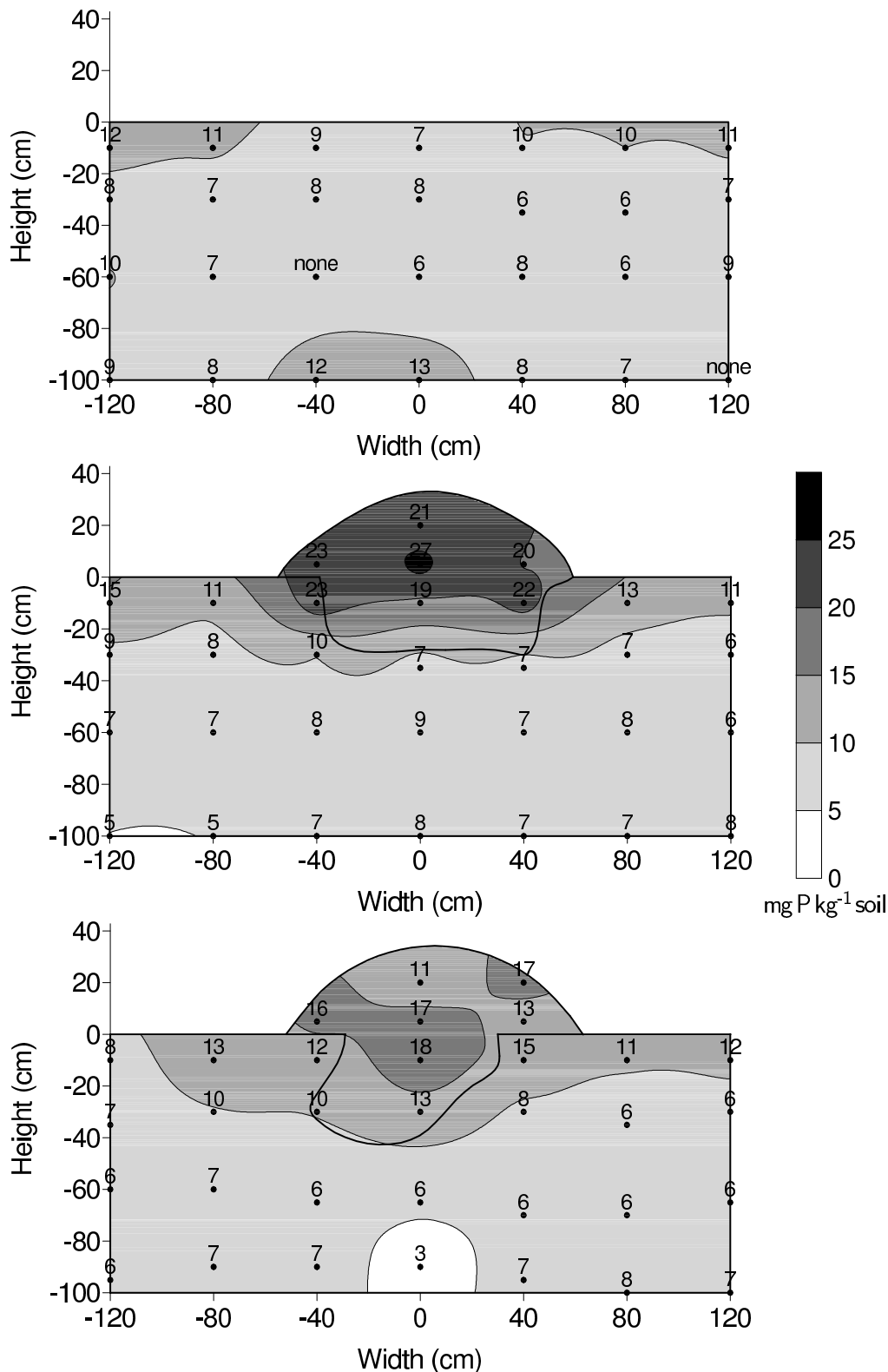


Figure 3.8 Interpolated patterns of $\text{NaHCO}_3\text{-P}_i$ (predicted by MIRS-PLSR) in representative transects ($n = 1$) of the reference soils (top), the mound sites inhabited by primary (center) and the ones inhabited by secondary termites (bottom). The sampling points are marked and denoted with the predicted value. Lines mark the termite nest boundaries.

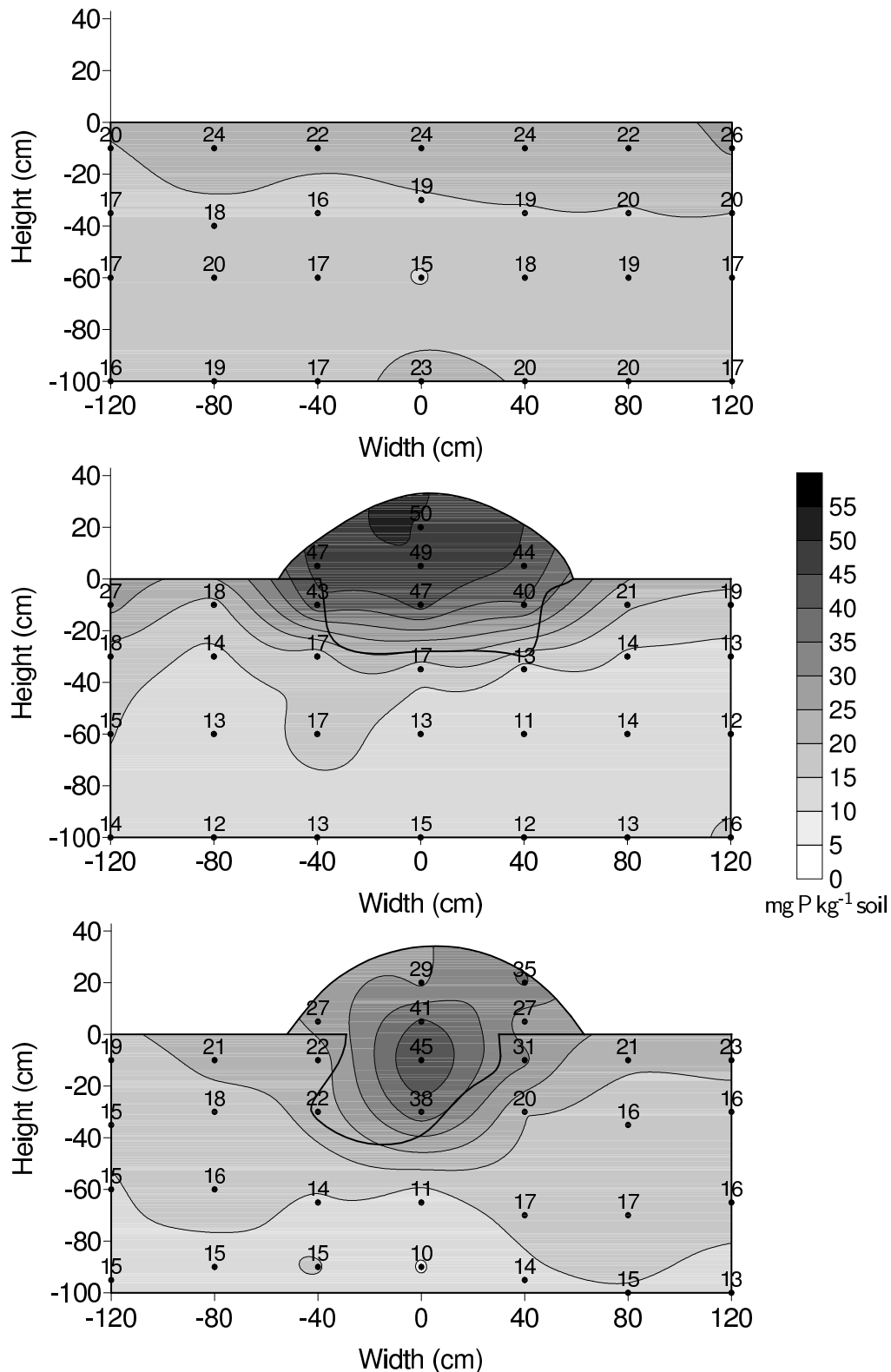


Figure 3.9 Interpolated patterns of $\text{NaHCO}_3\text{-P}_0$ (predicted by MIRS-PLSR) in representative transects ($n=1$) of the reference soils (top), the mound sites inhabited by primary (center) and the ones inhabited by secondary termites (bottom). The sampling points are marked and denoted with the predicted value. Lines mark the termite nest boundaries.

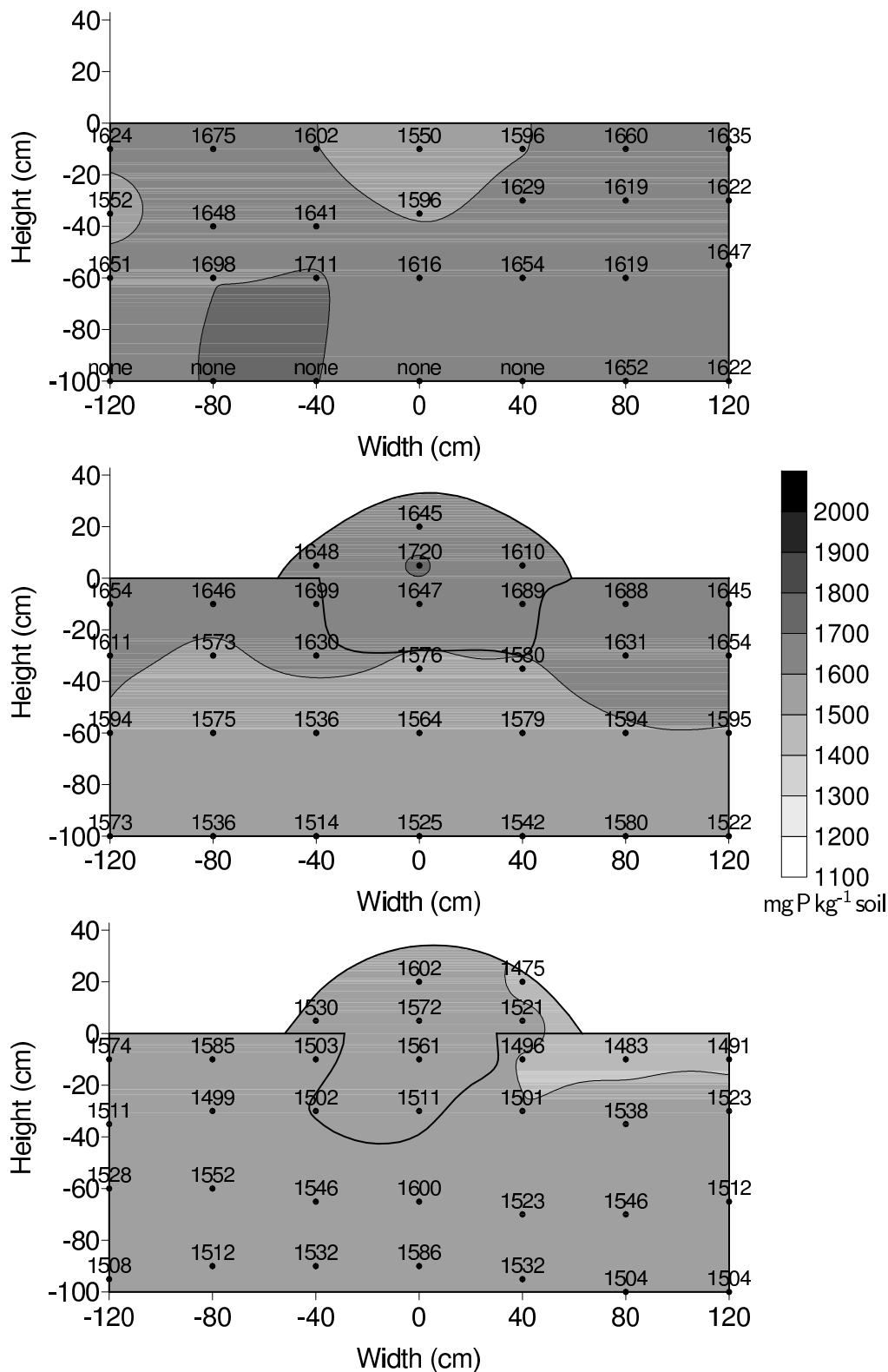


Figure 3.10 Interpolated patterns of $\text{HCl}_{\text{conc}}\text{-P}_i$ (predicted by MIRS-PLSR) in representative transects ($n = 1$) of the reference soils (top), the mound sites inhabited by primary (center) and the ones inhabited by secondary termites (bottom). The sampling points are marked and denoted with the predicted value. Lines mark the termite nest boundaries.

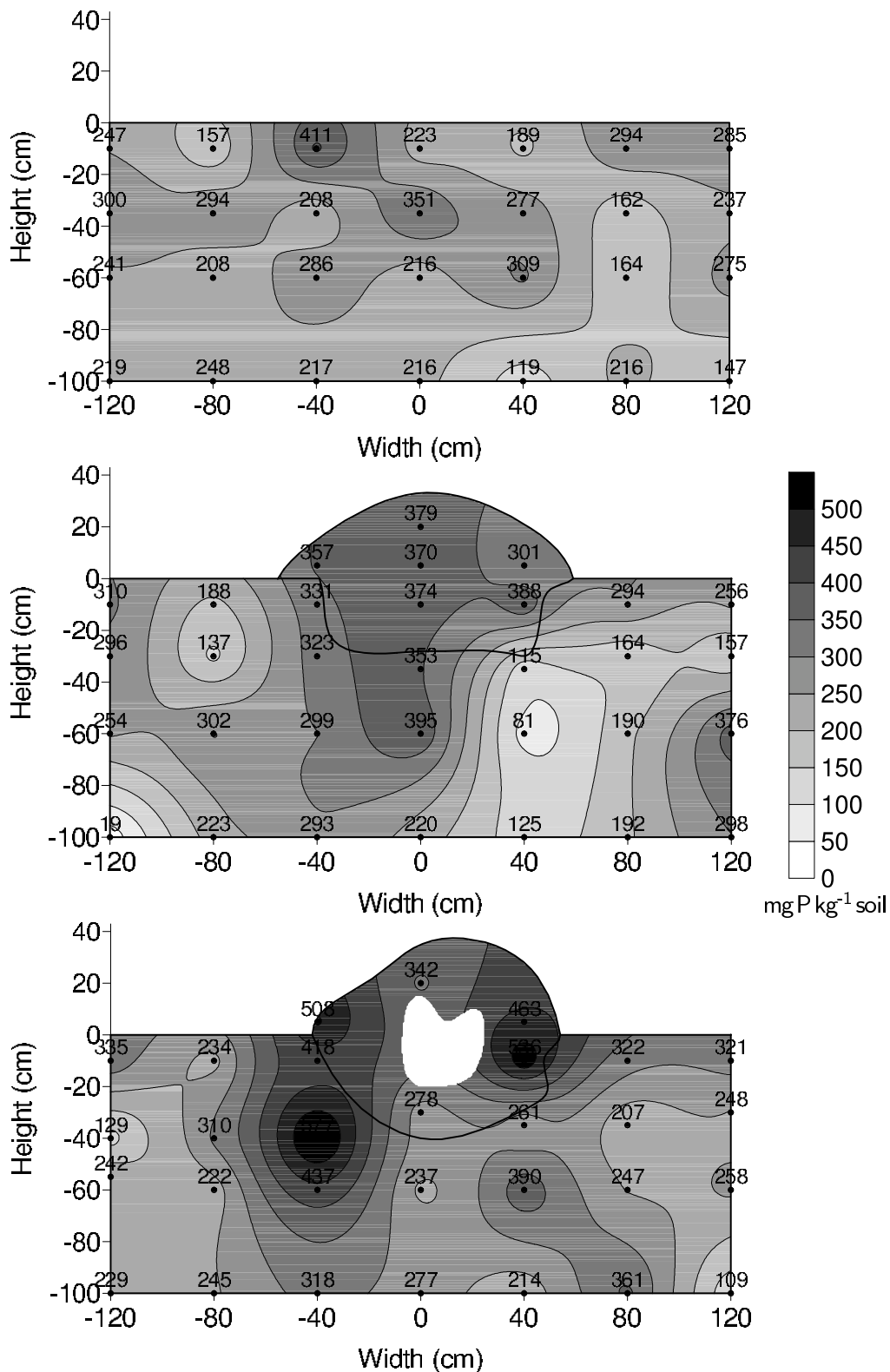


Figure 3.11 Interpolated patterns of $\text{HCl}_{\text{conc}}\text{-P}_o$ (predicted by MIRS-PLSR) in representative transects ($n=1$) of the reference soils (top), the mound sites inhabited by primary (center) and the ones inhabited by secondary termites (bottom). The sampling points are marked and denoted with the predicted value. Lines mark the termite nest boundaries.

and stocks in the secondarily inhabited nest, but this nest had a cavity inside, and therefore, the prominent nest center was missing.

3.4 Discussion

3.4.1 Soil genesis and changes in the soil horizons under termite mounds

The properties of the reference soils were significantly different from those under the termite mounds inhabited by secondary termites. Little is known on strategies of termites for selecting a site for mound construction. Nevertheless, since the soil types were not altered below the nests inhabited by primary termites, there is no indication that different soil properties below the mounds are due to a intentional selection of microsites with different properties for nest construction. The secondary inhabitants just opportunistically used the mounds erected by the primary nest builders, and hence, the secondary termites were not the ones that had actively selected the soil microsite. The different soil types below the mounds inhabited by secondary termites provide evidence that the termites' activities were responsible for the differences between soils under termite mounds and the reference soils. This termite influence on the soil was sufficiently large to even change diagnostic criteria for soil classification. The resulting soil type is an Umbrisol. It now lacks the former illuvial enrichment of clayey particles in the subsoil horizon due to physical re-allocation of soil particles by the termites. In temperate soils, a similar role of soil fauna in soil formation, for instance, was attributed to ants, which seem to promote the disappearance of bleached E and spodic B horizons below their nests (Kristiansen & Amelung, 2001).

Through selective translocation of fine soil particles by termites, the silt contents were 1.9- to 2.0-fold higher and clay contents were 1.1- to 1.2-fold higher in the topsoils below mounds than in the control topsoils. Many authors reported an enrichment of clay in termite mounds, but in most cases silt was also enriched (e.g. Holt & Lepage, 2000; Fall et al., 2001; Jouquet et al., 2002). The origin of the finer particles is unknown for *Cornitermes* mounds, but they could (partly) originate from the argic horizon, because this horizon was not only missing below secondarily inhabited termite mounds, also the clay content was lower at the respective depth below the secondarily inhabited termite mounds. The two uppermost horizons below the secondarily inhabited mounds had clay contents of 28 and 29%, respectively; while the other soils had, on average, 24% clay in the topsoil, and 32% in the argic horizon. The collection of soil materials from argic horizons was also suggested by Abe et al. (2009b) for African termites. I conclude that the termites influenced soil genesis at least directly below their mound by physical transporting soil particles. As a result, the argic horizon disappeared and the former lessivation was reversed. It is one of

the rare evidences that soil fauna may reverse end stages of soil formation, where, in this case, an argic horizon might re-develop when the termites are absent.

Higher amounts of OC, P_o and exchangeable cations (Ca^{2+} , Mg^{2+} , K^+) corresponded to the incorporation of organic matter into the mounds. It is obvious that the OC content was elevated by the introduction of organic matter, but also the cation content can be enhanced by the consumption of plants by termites as proposed by Watson (1975) and Sheikh & Kayani (1982). Higher cation contents could, in principle, also be caused by the transport of minerals or clay from deeper layers into the mound as stated above. However, if I calculate the cation content per kilogram clay, as it was also done by Watson (1975), Mg^{2+} was still enriched 51-fold in the soil under the mounds inhabited by primary, and 12-fold under those inhabited by secondary termites. Hence, the higher Mg^{2+} content was not induced by a clay transport into the nest. Such high enrichments of available Mg^{2+} in termite mounds in comparison to reference topsoils as found in my study were sparsely reported. Salick et al. (1983) and Fageria & Baligar (2004) documented enrichment factors of 10-100 and 20, respectively, for South America as well; and Lee & Wood (1971a) found factors up to 60 for Australian termite mounds. The amount of exchangeable bases could also be enhanced by a modification of exchange sites following a chemical alteration of the organic matter or the minerals by termites, which is shown by Mujinya et al. (2010). Termites can alter such materials by passage through their gut and the use of saliva and feces for nest construction (e.g. Wood et al., 1983; Bagine, 1984; Ndiaye et al., 2004b).

The mapping of similarity indices revealed the same patterns for OC and available P_i forms (Figure 3.6a & b). Hence, an alteration of incorporated organic matter likely also reflected the patterns of P, where the amount of stable P_i remained at the same level at the mound sites like in the reference soil, but the available P_i fraction was greater at the mound sites. $HCl_{conc}-P_i$ comprised 95% of total P_i in the soils and mounds of the study area (Chapter 2), and hence, the content of total P_i had an equal level in mounds and soils. Because the termites did not change the total P_i level, I suggest that available P_i was not preferentially collected but that the availability of P was changed by termite activity. Wood et al. (1983) explained the higher P availability in mounds of soil-feeding termites with a dissociation of organic and inorganic complexes in the extreme alkaline hindgut of those termites. Additionally, López-Hernández et al. (1989;); 2006 stated that the high content of organic matter in mounds influences the P sorption-desorption processes. However, the drainage water of mounds and reference soils in the same study area exhibited no significant differences of the phosphate concentration (Chapter 5).

3.4.2 Spatial extension of termite effects on adjacent soil

The termite influence is not restricted to the nesting area as termite activity or a relocation of nest material both interfere with the surrounding soil. The sites with mounds exhibited higher contents of OC and $\text{NaHCO}_3\text{-P}$ relative to the reference sites down to soil depths of 50–60 cm, i.e. a region still within the lower part of the nest (down to 30 cm depth) or directly below the nest. Different depths of termite impacts on soil properties are found throughout the literature. The reported depths are greatest for fungus-growing termites with up to 6 m (Watson, 1962; Arshad, 1981; Lal, 1987), but less deep for soil- or grass-feeding termites. The latter exhibited, similar to the grass-feeder and litter-forager termite *C. silvestrii* in my study, a general influence to 30–80 cm soil depth (Holt & Coventry, 1982; Coventry et al., 1988), although the information was sometimes limited by the sampling depth (Steinke & Nel, 1989). A similar vertical influence of the grass-feeder termites was thus found in Australia, Africa (both in former studies) and South America (this study), suggesting that these gradients are rather typical below the nests of this feeding guild.

Beside vertical effects, termite mounds also have an impact on the lateral adjoining soil. Effects of *C. silvestrii* and the secondary termite associations on the OC and $\text{NaHCO}_3\text{-P}_1$ amounts in the adjoining soil were evident approximately 20 and 60 cm away from the mound border (Figure 3.6). The effects may even reach farther out, but sampling was only done to 60 cm from the nest border. This is rather at the smaller range of lateral effects reported by Arshad (1982) (fungus-growing termites), Coventry et al. (1988) (grass- and litter-feeder termites), Park et al. (1994a) (grass-feeding termites), and Ekundayo & Aghatise (1997) (fungus-growing termites), who documented enrichments of various soil properties like OC, P, ammonium and nitrate up to a distances of 5–10 m, 40 cm, or 1 m from the mound edge, and at the mound margin, respectively. *Armitermes sp.* influenced the lateral pattern of perylene in the Cerrado also to a distance of > 1 m from the nest (Wilcke et al., 2003). On the other hand, Ndiaye et al. (2003) showed enrichments of available P, nitrate and ammonium in the mounds of African soil-feeding termites, but not at the mound edge or 40 cm away from the mound. Those results correspond with my findings for $\text{NaHCO}_3\text{-P}_0$, which was also not enriched in the lateral surroundings of termite mounds. The lateral influence noticed in the different studies was not related to nest density (Coventry et al. (1988): 283 mounds ha^{-1} ; Park et al. (1994b): 120–205 mounds ha^{-1} ; my study: 72 mounds ha^{-1} ; Ekundayo & Aghatise (1997) only 2–5 mounds ha^{-1}). Hence, I deduce that the influence on certain soil properties depends on the respective termite genera.

3.4.3 Differences between mounds inhabited by primary and secondary termites

If I interpret the mounds inhabited by secondary termites as successional stages of initial ones inhabited by primary termites, I can see a chronological development of the termite mounds. Roose-Amsaleg et al. (2005) documented the same trends for organic matter, P_i , CEC_{pot} and exchangeable Ca^{2+} in reference soils, mature and old nests of an African soil-feeding termite like in my study. The highest enrichment compared to the control soil was found in the mature or primarily inhabited nests. In older nests, the values of the chemical soil properties declined, but still remained higher than in the control soil. Very young and freshly made constructions even exhibited the highest values in the study of Roose-Amsaleg et al. (2005). In an accompanying study, I found an enrichment of lignin in the primarily as well as in the secondarily inhabited nests, whereas the former exhibited the highest lignin contents (Chapter 4). It is conspicuous that this decline of organic matter and nutrient contents occurred in still inhabited mounds.

Aside from chemical changes, the older mounds of my study had a higher bulk density. This pointed to the implications that parts of the mound were not used by secondary termite colonies and the galleries were not rebuilt, as well as that additional soil material was incorporated into the nests, as, e.g., also reflected by the loss of the argic horizon below the nests inhabited by secondary termites. Likewise, the highest contents of OC and P_o were recorded in the lower parts of the nests inhabited by secondary termites compared to upper parts in the nests inhabited by primary termites (Figure 3.4 & 3.9). This could be attributed either to the action of the secondary termite colonies or to a depletion of organic matter in the above-ground nest part. A decay of the older mounds was also supported by higher nitrate concentrations in the soil water draining from those mounds compared to younger mounds (Chapter 5). Also a higher degree of lignin oxidation in these mounds relative to that in the mounds inhabited by primary termites indicated that at least parts of the mound materials degraded (Chapter 4). Hence, I can summarize that the older mounds decayed partially despite secondary termite colonies were active.

Intriguingly, the largest changes in soil OC and P forms patterns did already occur under the mounds inhabited by primary termites and not under those inhabited by the secondary ones, whereas the largest changes observed for the basic soil properties were evident under the mounds of the secondary termites and not under those of the primary ones. I hypothesize, therefore, that the changes in soil type are not evident enough to affect soil classification below the mounds inhabited by primary termites during initial nest construction. They only alter soil properties and nutrient status in the adjoining soil. The next stage of termite effects on soil is reached at the sites with mounds inhabited by secondary termites. Those mounds start already to decay, but the argic horizon finally disappears and the soil

classification changes from Alisols and Acrisols to Umbrisols (according to IUSS Working Group WRB, 2006). However, the effects of the secondary inhabitants can not be separated from longer lasting effects of the primary termites in these older mounds.

With an average nest density of 72 mounds ha⁻¹, the areal distribution of such impacts is still small to affect soil genesis of a whole landscape within the life cycle of a few termite genera. Though such termite mounds are abundant in the Brazilian savannas. Yet, little is known on the cumulative role of such termite-induced reversion of soil genesis throughout the last millennia of landscape development, although Schaefer (2001) showed that the structure of deep weathered soils from Brazil is due to long-term termite activity. At least my study shows that even advanced stages of soil formation in the Alisol/Acrisol area of tropical highlands are not the necessarily the end stage of soil formation, but may at least temporarily be rejuvenated by termite activity, thus underlining their role not only for affecting nutrient distribution and patchiness, but also overall soil fertility in these environments.

3.5 Conclusion

I conclude from my investigations that the impact of the grass-feeder termites on soil properties and genesis might follow two steps. First the chemical properties and nutrient status of the topsoils are altered during mound construction, thus affecting organic carbon and phosphorus distributions in the soil by primary termites. Then, the major impact on soil genesis occurs during extended periods with primary termites and later eventually also by the secondary termites, extending their influence into deeper and thus diagnostic soil horizons while the original mound may already start to decay.

Furthermore, I can infer from my study that mid-infrared spectroscopy in combination with partial least squares regression provides opportunity for the fast determination of spatial distributions not only for organic carbon contents, but also for selected organic and inorganic phosphorus species within, and in the direct vicinity of termite mounds. The spatial distribution of these properties exhibited an influence of the termite activities on the lateral and vertical adjoining soil. As those patterns persisted below secondarily inhabited termite mounds, I may conclude that the termite effects on soil genesis and soil properties will remain at least for some years after the original termite colony dies.

Chapter 4

Lignin patterns in soil and termite nests of the Brazilian Cerrado¹

4.1 Introduction

Lignin is an organic macromolecule which is part of the secondary cell wall of vascular plants. Typically, 20–30% of the dry mass of wood consist of lignin. Termites feeding on wood use the easily degradable cellulose components rather than lignin as carbon and energy source (Breznak & Brune, 1994). Several studies showed that those wood-feeding termites and their symbiotic gut microorganisms could only degrade mono- or diaromatic lignin compounds; the core of larger lignin molecules resists degradation (Butler & Buckerfield, 1979; Cookson, 1987; Brune et al., 1995; Kuhnigk & König, 1997). Therefore, lignin is enriched in nests of wood-feeding termites (Hopkins et al., 1998; Amelung et al., 2002). Lignin in nests of xylophagous termites resisted also degradation when it came in contact with soil material (Cookson, 1992). In contrast to wood-feeding termites, fungus-growing termites are able to consume the lignocelluloses nearly completely, because the symbiotic *Termitomyces* fungi can degrade lignin to the same degree as other white-rot fungi (Hyodo et al., 2000; Ohkuma, 2003). Studies on other feeding guilds are scarce. It is expected that soil-feeding termites should consume lignin (as part of soil organic matter) more efficiently than wood-feeding termites, but proof is lacking (Breznak & Brune, 1994; Brune et al., 1995; Hopkins et al., 1998). Amelung et al. (2002) could explain the feeding guild of various termite species by the lignin signature of their nests, but did not find indications of different lignin breakdown pathways during food digestion.

Due to the fact that no chemical analysis can determine the lignin content in soils exactly, the analysis of phenolic CuO oxidation products has been widely used as a standard approach (Hedges & Ertel, 1982; Kögel, 1986; Amelung et al., 1997; 2008). It has the advantage that the lignin content can be estimated by the sum of oxidation products, and that lignin characteristics can be deduced from ratios of individual oxidation products. The ratio of acids to aldehydes characterizes, for example, the side chain oxidation of the soil lignin (Kögel, 1986). Additionally, the ratio of cinnamyl to vanillyl units is an indicator for lignin of herbaceous tissue (Opsahl & Brenner, 1995). However, chemical analyses

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are expensive and time consuming. Mid-infrared spectroscopy (MIRS) in combination with multivariate data analysis is a fast approach for analysis of soil organic components (Leifeld, 2006; Viscarra Rossel et al., 2006; Reeves et al., 2006; Zimmermann et al., 2007). Recent data indicated that MIRS can also be used for the determination of soil lignin (Ludwig et al., 2008; Bornemann et al., 2010), thus providing a powerful tool also for tracing lignin incorporation into termite nests and the underlying soil.

The goal of this study was to characterize the distribution and composition of lignin in termite nests and adjacent soil of the Central-Brazilian savannas using both alkaline CuO oxidation and MIRS. Younger and older nests were examined to elucidate the persistence of the termite-induced changes of the lignin content. All nests were originally built by the grass- and litter-feeding termite *Cornitermes silvestrii*, but the older ones were secondarily inhabited by inquilines, while completely abandoned nests were rare in the Brazilian savanna (Redford, 1984; Lacher et al., 1986; Domingos & Gontijo, 1996).

To follow the incorporation pathway of lignin into new termite nest constructions and to characterize the lignin alteration during incorporation into such constructions, the studies were accompanied by additional microcosm experiments with a xylophagous termite species. For this purpose, small termite nests from a rainforest were held under controlled conditions in the laboratory. During the experiment the termites were fed with corn for a natural labeling of new constructions with ^{13}C .

4.2 Materials and methods

4.2.1 Study sites and sampling

The study area for surveying the lignin distribution in epigeous termite nests and the surrounding soils was the farm of the Instituto Ecológica (10°16'S, 48°10'W, 630 m above sea level) in Taquaruçu 20 km southeast of Palmas, Tocantins, Brazil (see Figure 2.1). The site has a mean annual temperature of 24 °C and a mean annual rainfall of 1800 mm. The disturbed Cerrado (Brazilian savanna) is used as an extensive pasture after having been burnt in 2002. *Brachiaria sp.* is the dominant grass in this area. The soils (Umbric Acrisols and Umbric Alisols; IUSS Working Group WRB, 2006) are rich in organic matter, had a very low base saturation and a sandy clay loam texture. Flat dome-shaped mounds (diameter 120 cm, height 35 cm) of *Cornitermes silvestrii* (grass-feeder and litter-forager; Gontijo & Domingos, 1991; Constantino, 2002) were most abundant in the study area (see Figure 5.1). I assumed that most nests were constructed after the original Cerrado was burnt. Therefore, the termite nests should not have been older than four years at sampling in 2006. The nests were mainly built of soil material; they consisted of a dense mound wall and a nest center

with a lot of galleries. Besides those mounds existed older ones, which had been presumably constructed by *C. silvestrii*, but were now partly occupied by small termite colonies as secondary inhabitants. The mounds looked more weathered and were overgrown by mosses to some extent, suggesting that they were older than those still inhabited by *C. silvestrii*. Those secondary inhabitants were the wood- and cattle dung-feeding *Nasutitermes kemneri* (Freyman et al., 2008), which occurred in all old mounds; the grass-feeding and litter-foraging *Procornitermes araujo* (Coles de Negret & Redford, 1982); the wood- and grass-feeding *Armitermes euamignathus* (Coles de Negret & Redford, 1982; Gontijo & Domingos, 1991); as well as the soil/wood interface-feeding *Labiatermes orthocephalus* (Constantino et al., 2006) and *Embiratermes festivellus* (Gontijo & Domingos, 1991). Additional information about the nests and the study area is given in Chapters 3 & 5.

Three replicates of young nests, of old nests and of reference soils were chosen for sampling. The reference soil sites were at least situated 5 m away from termite nests and showed no evident termite influence, but some termite specimens were found during sampling. Four soil transects from the site center to the cardinal points were dug at every sampling site. Samples were taken for every transect at the widths of 0, 40, 80 and 120 cm at soil depths of 10, 30, 60 and 100 cm. Horizon boundaries were avoided and samples were taken 5 cm above or below. Termite mounds were sampled 5, 20 and 35 cm above the ground level if available. Sampling was done with five 100 cm³ cores at each sampling point. All samples were immediately air dried.

To follow the pathway of lignin incorporation into new termite nest constructions, I went to a second study site. It is a periodically flooded tropical forest at the Centro de Pesquisa Canguçu (9°58'S, 50°02'W) about 110 km northeast of Pium, Tocantins, Brazil. Mean annual temperature is about 25.5 °C and mean annual rainfall about 1750 mm. Three arboreal nests belonging to *Nasutitermes cf. minor*, which are potential wood-feeders (Martius, 1994a), were collected for the microcosm experiment. Compared to the nests of *C. silvestrii*, nests of *N. cf. minor* have the advantage that they are much easier to collect and to hold them in the laboratory. Own experiments with termites building earth nests were unsuccessful. The *N. cf. minor* nests were slightly damaged during the removal from the trees; therefore, they were exposed in the forest until the outer wall had been repaired again by the termites. Then, the nests, clay for humidity regulation, and corn cobs as food source were placed in tight stainless-steel boxes equipped with an inlet and outlet for air supply. Details of the setup were given in Bandowe et al. (2009). The corn (C₄ plant) served as a natural labeling substrate with a higher $\delta^{13}\text{C}$ value than the termite nests of an environment dominated by C₃ plants. The experiment was run for 20 days, because preliminary experiments had shown that the termite colonies could not survive for longer periods under these

conditions. Samples of nests, clay and corn were taken before and after the experiment. Additionally, freshly constructed termite sheetings (“galleries”) were observed on the clay surface and the corn after the experiment. These fresh materials were also sampled.

4.2.2 Chemical analyses

After sieving to < 2 mm and subsequent grinding with a ball mill, organic carbon (OC) was measured with an elemental analyzer (NA 2000, Fisons Instruments, Rodano, Milan, Italy). The minerals of some selected samples were characterized by X-ray diffraction (PW 1130, Philips, Almelo, The Netherlands).

Lignin contents in 28 selected samples of the savanna and all samples of the forest were estimated by the sum of phenolic oxidation products after an alkaline CuO oxidation (Hedges & Ertel, 1982; Kögel, 1986; Amelung et al., 1997). The oxidation procedure was conducted by first mixing 250–1000 mg soil material (depending on the OC content) with 400 mg CuO, 15 ml 2 N NaOH, 80 mg $\text{Fe}(\text{NH}_4)_2(\text{SO}_4)_2 \times 6 \text{H}_2\text{O}$, and 50 mg glucose; and second digestion of the mixture under N_2 atmosphere at 170 °C in a teflon pressure bomb for 2 h. The supernatant was then adjusted to pH 2 with 6 M HCl. The phenols were extracted from the acidified solution by solid-phase extraction using preconditioned octadecyl-bonded silica (Nucleodur C₁₈ ec, Macherey & Nagel, Düren, Germany), and a subsequent elution with 6 x 400 µl ethyl acetate. After drying with a rotary evaporator, the phenolic oxidation products were dissolved and derivatized with a 1:2 (v/v) mixture of pyridine and *N,O*-bis(trimethyl-silyl)trifluoroacetamide (Roth, Karlsruhe, Germany) and measured at a GC-FID (6890N, Agilent Technologies, Santa Clara, USA) equipped with a fused silica column (SPB-5, Supelco, Bellefonte, USA). Split injection with a ratio of 1:20 and a temperature of 250 °C was used. The carrier gas helium was kept at a constant flow of 1.1 ml min⁻¹. The temperature program of the oven was 3 min at 100 °C, heat to 250 °C with 10 °C min⁻¹, and finally 10 min at 250 °C. The detector was heated to 350 °C. Ethylvanillin and phenyl-acetic acid were used as first and second internal standard, and added before oxidation and before derivatization, respectively. It resulted in recoveries of ethylvanillin of better than 65%. Measurements were done in duplicate. VSC-lignin was then calculated as the sum of vanillyl (vanillin & vanillic acid), syringyl (syringaldehyde & syringic acid), and cinnamyl (p-coumaric acid & ferulic acid) phenolic oxidation products (Hedges & Ertel, 1982; Kögel, 1986; Amelung et al., 1997). Measures of the side chain oxidation of the VSC-lignin are the ratios of acids to aldehydes of the vanillyl (ac/al)_V and syringyl (ac/al)_S structures (Kögel, 1986). Also lower ratios of syringyl to vanillyl units (S/V), and cinnamyl to vanillyl units (C/V) indicate an oxidation of the lignin (Ertel & Hedges, 1984; Kögel, 1986; Opsahl & Brenner, 1995). Smaller C/V ratios are as well

markers for wood-born lignin (Opsahl & Brenner, 1995). The ketones of the vanillyl and syringyl units were not measured, because they add no information on the origin of lignin or on its degree of oxidation, and because total lignin contents remain unknown in any case.

The $^{13}\text{C}/^{12}\text{C}$ ratios in bulk samples of the microcosm experiment were determined using an elemental analyzer (FlashEA 1112, Thermo Fisher Scientific, Delft, The Netherlands) connected to an isotope ratio mass spectrometer (via ConFlo III interface; Delta V Advantage; both: Thermo Fisher Scientific, Bremen, Germany). Measurements were run in triplicate. Sucrose ($\delta^{13}\text{C} -10.449$, IAEA, Vienna, Austria) and acetanilide ($\delta^{13}\text{C} -29.52$, Arndt Schimmelmann, Bloomington, USA) were used as laboratory standards. The ratios were expressed in the common $\delta^{13}\text{C}$ -notation relative to the Vienna Pee Dee Belemnite (VPDB) international standard.

4.2.3 Mid-infrared spectroscopy

VSC-lignin and OC contents were determined in all samples of the savanna by mid-infrared spectra (MIRS) followed by partial least squares regression (PLSR). Although the VSC-lignin oxidation products are not found as monomers in soils, the sum of VSC-lignin can be quantified by means of MIRS-PLSR, while this is not possible for the VSC-lignin signature (Bornemann et al., 2010). In the following a brief description of the methods will be given, detailed information on measurements and quantifications can be found in Bornemann et al. (2008;); 2010, and Chapter 3. Five replicates of each sample were transferred to microplates and compacted with a plunger to provide a plain and dense surface. The diffuse reflectance was then recorded by 120 scans with a Bruker Tensor 27 (Bruker AXS, Madison, USA) system. Using partial least squares regression (PLS 1 algorithm; Martens & Næs 1989) within the OPUS QUANT software (2006, Bruker AXS, Madison, USA), the spectra were calibrated against the values achieved by the above described chemical methods. The calibration models were checked by a leave-one-out, full-cross validation (Efron, 2004).

As the prediction of OC had already been introduced in Chapter 3, details of the calibration models can be found there (Table 3.2, Figure 3.3). During calibration and validation of the VSC-lignin prediction it became obvious that prediction was improved if not performed across the entire range, but if the calibration was separated at 200 mg kg^{-1} to get more precise results for lower VSC-lignin contents. The calibration model for the lower VSC-lignin contents utilized 19 samples of my study with VSC-lignin contents below 340 mg kg^{-1} and also 32 samples within this range from Bornemann et al. (2010). The second calibration model comprised all 28 samples of the savanna analyzed in the laboratory, but it was

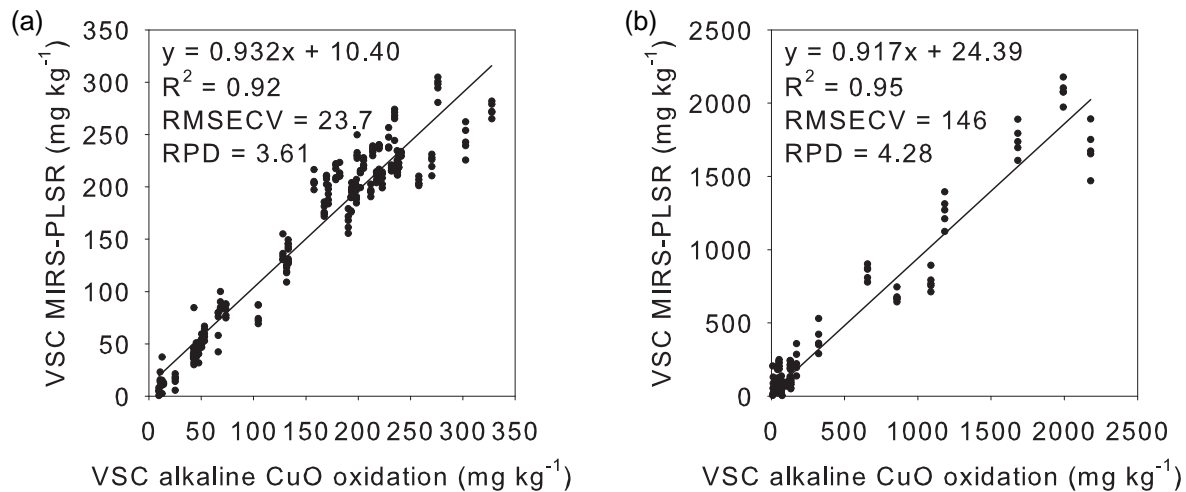


Figure 4.1 VSC-lignin predictions from mid-infrared spectroscopy and partial least squares regression (MIRS-PLSR) in comparison to the sum of phenolic oxidation products after an alkaline CuO oxidation: (a) Prediction for contents up to 200 mg kg^{-1} (51 samples), and (b) Prediction for contents above 200 mg kg^{-1} (28 samples). Five individual spectroscopic measurements are plotted per sample. (RMSECV: root mean square error of cross validation; RPD: relative percent deviation)

only used for VSC contents above 200 mg kg^{-1} . Consequently, the calibration model for lower VSC-lignin contents is similar to that used by Bornemann et al. (2010); my model included a “min-max standardization” of the spectra; spectral bands ranging from 3747–3365, 3008–2802, 2416–2287, and 2158–555; and 6 latent variables. Calibration model settings for the higher VSC-lignin contents involved “first derivative and multiplicative scatter correction” of the spectra; spectral bands ranging from 3008–2802, 2416–2285, and 2158–555; and 14 latent variables. The statistical parameters of the calibrations were given in Figure 4.1.

4.2.4 Data analyses

The spatial patterns of VSC-lignin and OC were illustrated using kriging interpolation with the standard settings of the software program Surfer 8 (Golden Software, 2002, Golden, USA). The generated maps were compared using the fuzzy numerical algorithm (neighborhood radius 15 cm, exponential decay) within the Map Comparison Kit 3.2.0 (Research Institute for Knowledge Systems, Maastricht, The Netherlands; Visser & de Nijs, 2006). Before doing this, maps with normalized (mean=0; standard deviation=1) values were constructed, which enabled me to compare maps with unequal units. The fuzzy algorithm takes neighboring values into account; therefore, the map comparison has advantages over cell-by-cell regression analyses. Additionally to an average similarity index for the whole

map, a similarity map is produced. The similarity index can get values between 0 (no similarity) and 1 (absolute similarity).

Differences between groups were examined with an analysis of variance (ANOVA), and the Scheffé test as post-hoc test for comparisons of more than two groups. The significance level was set at $P < 0.05$. The ANOVA was conducted with SPSS 14.0 (SPSS Inc., 2005, Chicago, USA).

4.3 Results

4.3.1 Soil sampling within and around savanna termite mounds

Both, OC and VSC-lignin contents were higher in termite nests than at 10 cm depth of the reference soil (Table 4.1). VSC-lignin was even more enriched than OC in termite nests inhabited by primary and secondary termites. The enrichment factor for VSC-lignin (in mg kg^{-1} soil) was about 15 for primarily inhabited nests, while the nests with secondary termites had only 7.5 times more VSC-lignin than the reference soil. VSC-lignin relative to the carbon content (g kg^{-1} C) was also enriched in the termite nests.

Elevated (ac/al)_S ratios in the nests indicated a higher degree of lignin oxidation than in the control soil (Table 4.1). The vanillyl units were more oxidized in the nests inhabited by secondary termites than in the nests of the primary ones. Also, the overall acids-to-aldehydes ratios indicated a higher degree of lignin oxidation only in the nests inhabited by secondary termites (0.36 vs. 0.26 in primarily inhabited nests, not significant at $P < 0.05$). However, the differences of the ac/al ratios between mounds and control soil can also be a consequence of higher ac/al ratios in the incorporated food or in the material collected by termites from deeper soil horizons. The C/V ratio declined in the order reference soil > primarily inhabited nests > secondarily inhabited nests (Table 4.1). This does not necessarily point to a higher decomposition of the lignin, but it can also interpret as an increasing percentage of wood tissues in the same order (Opsahl & Brenner, 1995). The S/V ratio was no sensitive indicator for differentiating the lignin status in these samples (Table 4.1).

The distributions of the OC and VSC-lignin contents in the soils transects with and without termite nests are illustrated in Figure 4.2 & 4.3. VSC-lignin showed a similar pattern when expressed in g kg^{-1} C as VSC-lignin expressed in mg kg^{-1} soil (data not shown). The patterns inside the termite nests showed that the highest contents were found above ground in nests inhabited by primary termites. In contrast, nests of secondary termites tended to have the highest contents in the lower nest center. Soils surrounding the nests inhabited by primary termites had higher VSC-lignin contents than the reference soil up to 60 cm away from the nest border (width of 120 cm) and to a depth relative to the ground level of approx-

Table 4.1 Organic carbon (OC) contents, VSC-lignin contents and characteristics in nests inhabited by primary termites, by secondary termites and in the reference soil (10 cm depth). Standard errors are given in parentheses. Within a column different letters designate significant ($P < 0.05$) differences.

	n	OC g kg ⁻¹	VSC-lignin		(ac/al) _V ^a	(ac/al) _S ^b	S/V ^c	C/V ^d
			mg kg ⁻¹ soil	g kg ⁻¹ C				
Reference soil	2	19 (1) a	131 (3) a	7 (0) a	0.32 (0.03) ab	0.22 (0.02) a	1.00 (0.01) a	0.43 (0.01) a
Primary termites	3	40 (1) b	1952 (145) b	49 (3) b	0.21 (0.02) a	0.32 (0.01) b	0.92 (0.01) a	0.32 (0.02) b
Secondary termites	3	30 (3) b	976 (162) c	33 (6) b	0.37 (0.04) b	0.34 (0.02) b	0.99 (0.08) a	0.21 (0.01) c

^a acid to aldehyde ratio of the vanillyl units; ^b acid to aldehyde ratio of the syringyl units; ^c ratio of syringyl to vanillyl units; ^d ratio of cinnamyl to vanillyl units

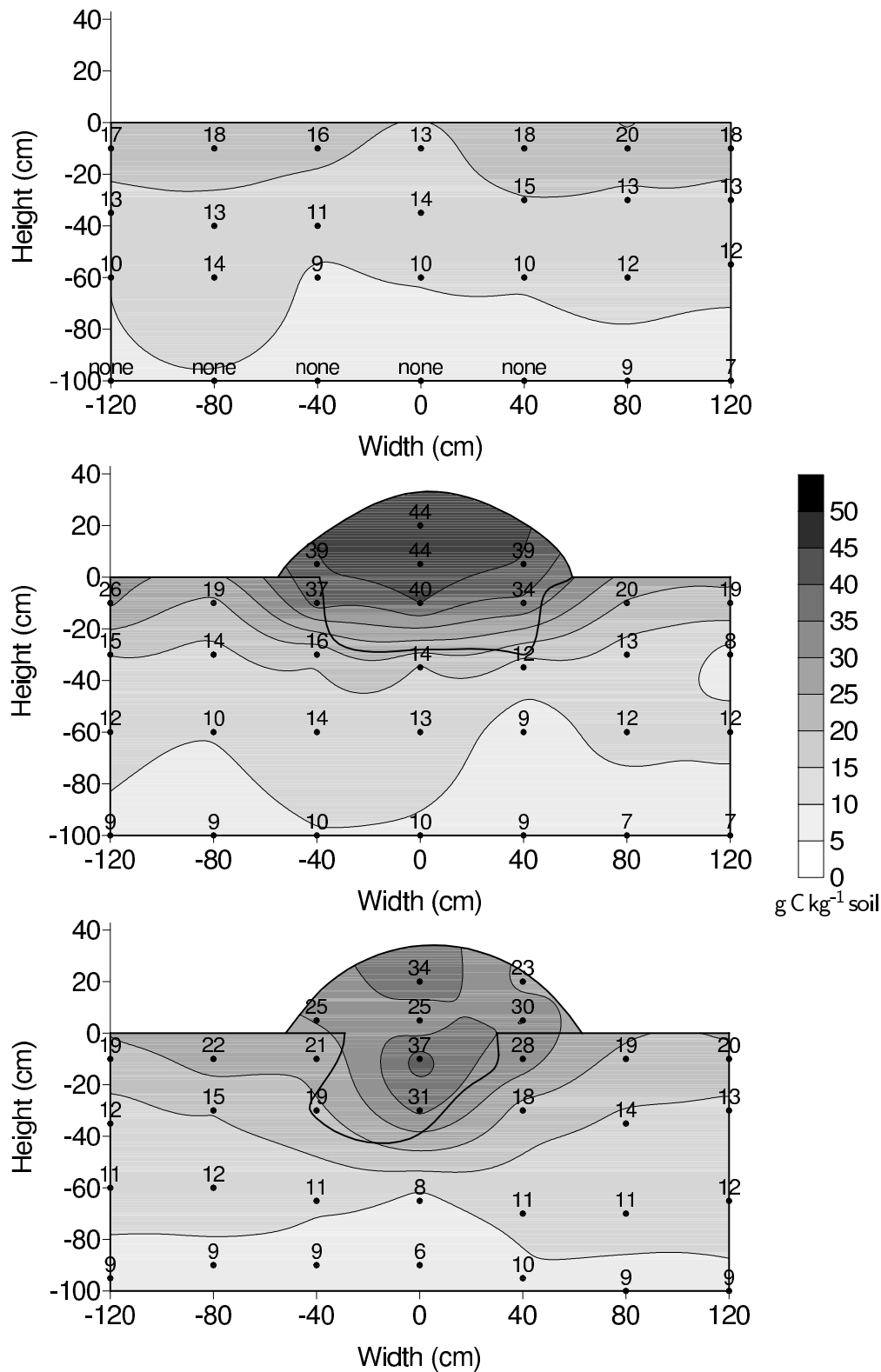


Figure 4.2 Interpolated patterns of organic carbon (predicted by MIRS-PLSR) in representative transects ($n=1$) of the reference soils (top), the mound sites inhabited by primary (center) and the ones inhabited by secondary termites (bottom). The sampling points are marked and denoted with the predicted/measured value. Lines mark the termite nest boundaries.

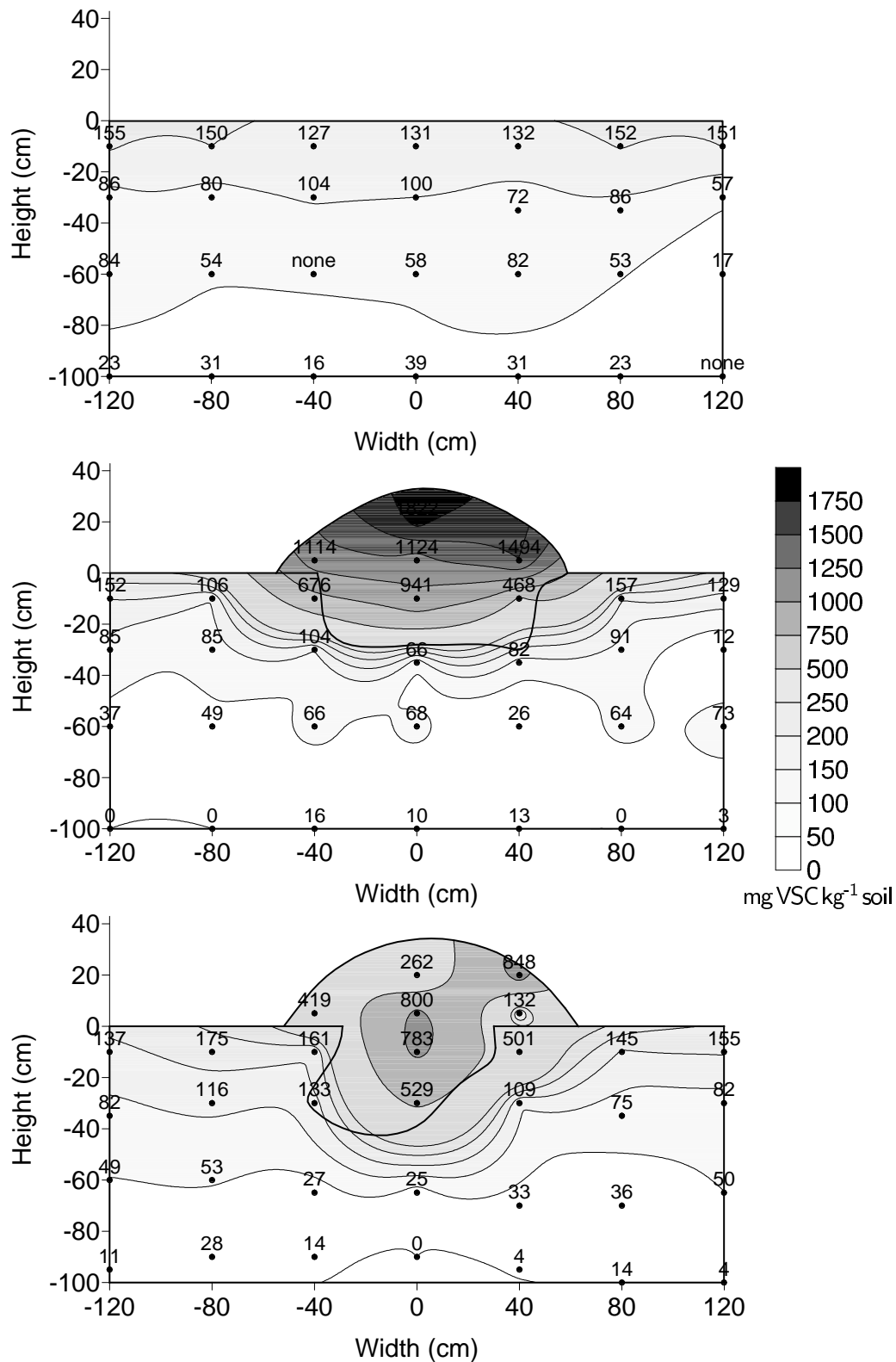


Figure 4.3 Interpolated patterns of VSC-lignin (predicted by MIRS-PLSR) in representative transects ($n = 1$) of the reference soil (top), the nest sites inhabited by primary (center) and by secondary termites (bottom). The sampling points are marked and denoted with the predicted values. Stronger lines mark the termite nest boundaries.

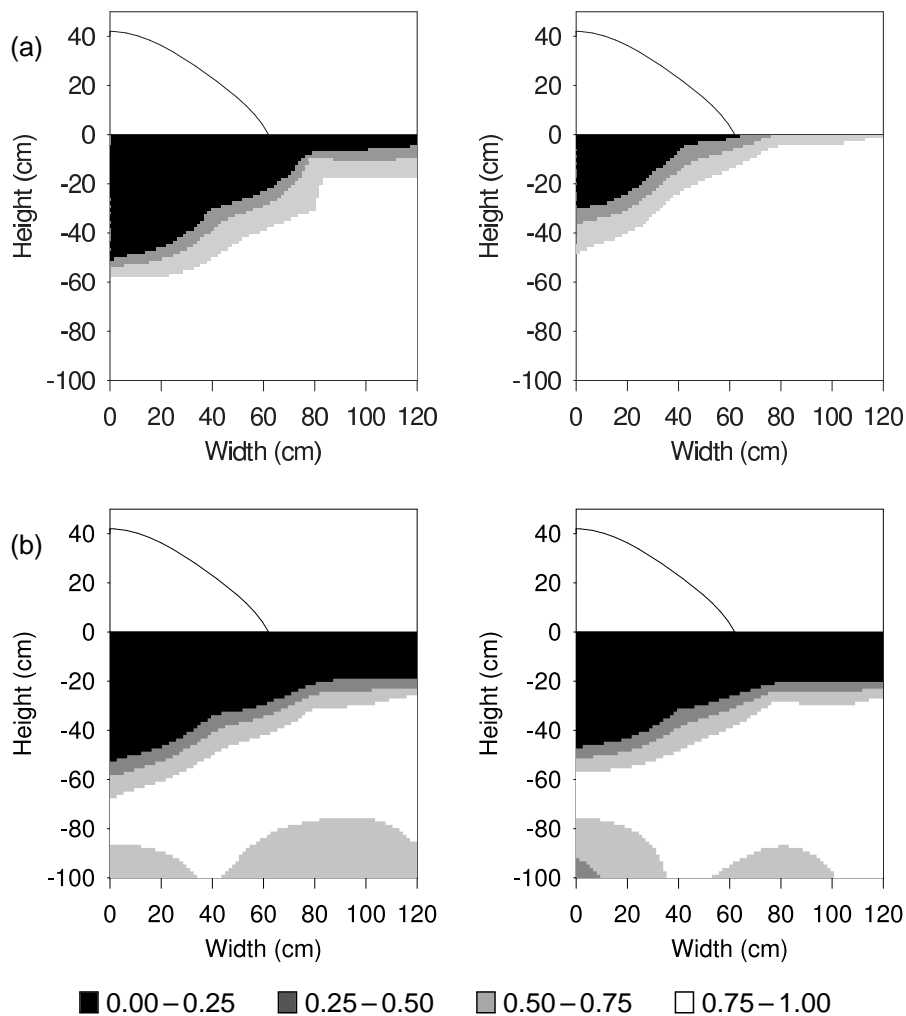


Figure 4.4 Maps of similarity indices of averaged (site center to a width of 120 cm; $n=12$, and $n=3$ for a width of 0 cm) (a) VSC-lignin contents (mg kg^{-1} soil) between the soil below primarily inhabited mounds and the reference soil (left), and between the soil below secondarily inhabited mounds and the reference soil (right). (b) shows the similarity indices of the averaged organic carbon contents between the reference soil and the primarily inhabited (left) and the secondarily inhabited mounds (right), respectively. The termite mound position is drawn above as reference.

imately 60 cm at the termite nest center (about 30 cm below the termite nest). This termite influence on the surrounding soil becomes more apparent if similarity indices between nest and reference sites are displayed for transect averages (Figure 4.4). Higher VSC-lignin contents in the soils below the secondarily inhabited mounds were more restricted to the nest parts in the soil than below primarily inhabited mounds, especially the lateral soil was less affected (Figure 4.4a). In contrast to VSC-lignin, the similarity maps for OC contents were similar below both, primarily and secondarily inhabited mounds (Figure 4.4b). Elevated carbon contents were found to vertical depths of 50–70 cm below the mounds, and laterally from the mounds also up to 30 cm soil depths. Dissimilarities at depths of 100 cm

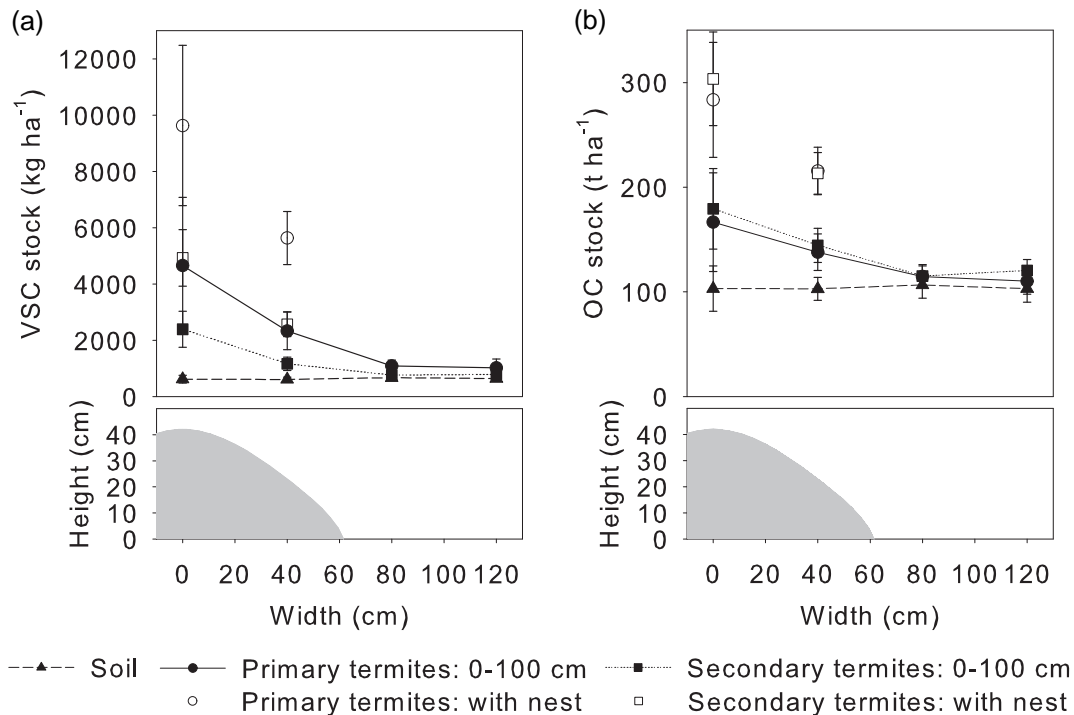


Figure 4.5 (a) VSC-lignin and (b) organic carbon stocks (0–100 cm soil depth, without and with nest parts above ground) from the site center to a width of 120 cm for the reference soil, the mound sites inhabited by primary and the ones inhabited by secondary termites. Means and standard errors of replicates and directions were shown ($n = 12$ and $n = 3$ for the site center). The connecting lines were only drawn for visualization. A mound silhouette is shown beneath as reference.

were caused by a high coefficient of variation at this depth in the reference soil. It was four times higher than at the upper sampling depths, probably reflecting variable stone contents at that depth.

The stocks of OC and VSC-lignin for 0–100 cm soil depth along the gradient from the site center to a width of 120 cm reflected the distribution of higher contents of those constituents in the soil. Higher stocks of both OC and VSC-lignin were only found below termite mounds at distances of 0 cm and 40 cm from the mound center (Figure 4.5). The highest VSC-lignin stock of $4658 \text{ kg ha}^{-1} 100 \text{ cm}^{-1}$ was recorded at the site center below mounds inhabited by primary termites. It was only the half of that below mounds inhabited by secondary termites. However, both termite-affected sites had higher VSC-lignin stocks than the reference soil, with an enrichment factor of 7.5 for the site center with primary termites, and of 3.8 for the secondary termites. When the VSC-lignin contents of mounds were included in the calculation of the stocks, these were even 15.5 and 7.9 times higher than in the reference soil (Figure 4.5a). The OC stocks were about 1.7 times (about 2.8 with mound material included) higher under both, primarily and secondarily inhabited mound centers (Figure 4.5b).

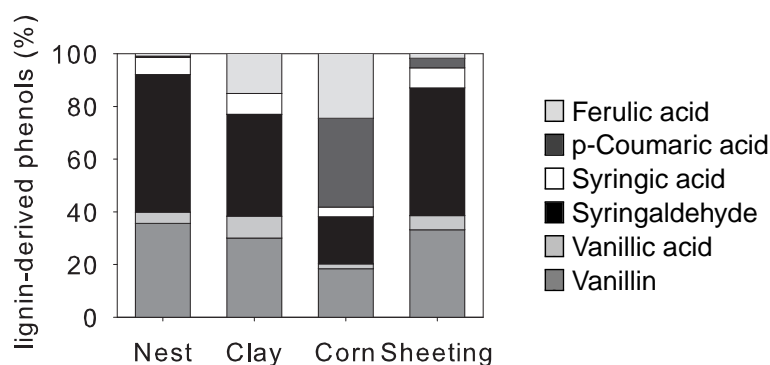


Figure 4.6 Lignin-derived phenol percentages of the VSC-lignin contents (mg kg^{-1} sample) for the *N. cf. minor* nests, clay, corn and the new constructed sheetings in the microcosm experiment.

4.3.2 Microcosm experiment with rainforest termite nests

The *N. cf. minor* used the provided corn extensively as food source. They built new sheetings on the clay and the corn for foraging. However, the chemical composition of the old nests, corn, and the clay remained the same after the experiment as before.

The contents of OC (461 g kg^{-1}) and VSC-lignin (102 g kg^{-1}) were much higher in the *N. cf. minor* nests than in the *C. silvestrii* nests found in the field, which can be attributed to the wood-feeding habit of the *N. cf. minor*. Table 4.2 shows the contents of OC and VSC-lignin in the nest, the other provided materials (clay and corn), and the freshly by termites built sheetings. Despite lower VSC-lignin contents, the new sheetings had a quite similar composition of the lignin-derived phenols like the old termite nests (Table 4.2, Figure 4.6). As expected, the corn had more cinnamyl units and less vanillyl oxidation products, which is a result of the high contents of cinnamyl units in herbaceous tissues (Table 4.2). The percentage of the cinnamyl units was a little bit higher in the sheetings than in the old nests (Figure 4.6), which indicated that some corn was used for construction of the sheetings. The clay exhibited the highest acid-to-aldehyde ratios, especially in the vanillyl units (Table 4.2), likely due to residues of highly degraded organic matter. The $\delta^{13}\text{C}$ values (Table 4.2) of the sheetings were not significantly different to those of the nest, but to those of the corn. X-ray diffraction indicated that the sheetings as well as the clay contained quartz, kaolinite, smectite and feldspar (data not shown). On the opposite, *N. cf. minor* nests contained almost no minerals, there were only hints of quartz. Altogether the results support the view that the fresh sheetings were, despite VSC-lignin contents similar to corn, mainly a mixture of former nest material and clay, while corn accounts only for a smaller portion of incorporated OC. I found no indication of lignin alteration during nest construction.

Table 4.2 Organic carbon (OC) contents, $\delta^{13}\text{C}$ values, VSC-lignin contents and VSC-lignin characteristics in samples of the microcosm experiment with rainforest termites. The values for nest, clay and corn were not changed after the experiment. Standard errors are given in parentheses ($n=3$). Within a column different letters designate significant ($P < 0.05$) differences.

Sample	OC		$\delta^{13}\text{C}$		VSC-Lignin		$(\text{ac/al})_V^a$	$(\text{ac/al})_S^b$	S/V ^c	C/V ^d						
	g kg ⁻¹		‰		mg kg ⁻¹ sample	g kg ⁻¹ C										
Nest	461	(3) a	-30.5	(0.0) a	101755	(1175) a	228	(6) a	0.14	(0.01) a	0.13	(0.01) a	1.60	(0.03) a	0.04	(0.00) a
Clay	5	(0) b	-23.4	(0.0) b	39	(0) b	7	(0) b	0.28	(0.00) b	0.20	(0.00) b	1.21	(0.01) b	0.39	(0.01) a
Corn	423	(1) a	-11.5	(0.3) c	23640	(141) c	60	(8) c	0.12	(0.01) a	0.20	(0.00) b	1.28	(0.06) b	3.04	(0.75) b
Sheetings	119	(14) c	-28.1	(0.7) a	24211	(3244) c	202	(7) a	0.16	(0.02) a	0.16	(0.01) ab	1.45	(0.03) a	0.15	(0.04) a

^a acid to aldehyde ratio of the vanillyl units; ^b acid to aldehyde ratio of the syringyl units; ^c ratio of syringyl to vanillyl units; ^d ratio of cinnamyl to vanillyl units

4.4 Discussion

Besides an accumulation of OC in nests of the savanna termites, VSC-lignin was much more enriched in these nests. This can either be attributed to a lignin-rich food or a loss of other easily degradable organic compounds during nest building and an accumulation of the remaining lignin. The former hypothesis is supported by a higher degree of wood-borne phenolic lignin units (lower C/V ratio) found in the termite nests than in the reference soil. The original nest-builder, *C. silvestrii*, is a grass- and litter-feeder, which probably also feeds on woody litter. The secondary inhabitants such as the wood-feeding *N. kemneri* may enlarge the content of the wood-borne phenolic lignin units further, because there is no evidence that the termites in my study alter the lignin to a significant amount during nest construction – a finding which was also corroborated with my microcosm study. Many earlier studies also indicated that lignin resists degradation by both, wood- and soil-feeding termites (Cookson, 1987; Breznak & Brune, 1994; Brune et al., 1995). Reasons may be that termites prefer the easily degradable cellulose as food source (Breznak & Brune, 1994), and that termites and their gut microorganisms are only able to decompose mono- or diaromatic lignin compounds (Cookson, 1987; Brune et al., 1995; Kuhnigk & König, 1997). All these processes promote the relative accumulation of lignin in termite nests, and hence, also in nests of grass- and litter-feeding *C. silvestrii*.

Depending on the different food source, the VSC-lignin content is higher in nests of the wood-feeding forest termites than in the earth nests of savanna termites. The fresh sheetings of the rainforest termites were a mixture of nest material with clay, and consequently the OC and VSC-lignin contents were in-between the values of those two substrates. The absolute contents of VSC-lignin and OC in the sheetings were depleted to a quarter relative to the nests, and accordingly, the VSC-lignin content relative to OC was similar in the sheetings as in the nests (Table 4.2). Hence, the termites in my microcosm experiment used the corn mainly as energy source and built the sheetings with old material of their nest. Maybe this behavior was related to stressful environment or the lack of right food in the microcosm. Nevertheless, the proportion of lignin relative to OC and the composition of the lignin were left unchanged during sheeting construction with re-used nest material (Figure 4.6). This supports the above-mentioned results that lignin is not attacked by the termites.

The VSC-lignin content is, like the OC content, also enhanced in the surroundings of savanna termite nests. Hence, an input of lignin into the nest surroundings must be a result of direct or indirect termite activities. However, it could not be distinguished, if it was lignin from termite nests which was transported by termites out of their nest like the *N. cf. minor* did in the microcosm experiment, or if it was collected woody food which was

lost during transportation into the nest. Leaching of lignin out of termite nests seems to be unlikely, because the flux of dissolved organic matter was reduced under termite nests (Chapter 5).

The older earth mounds inhabited by secondary termites were settled, which was shown by a higher bulk density in those nests than in the ones inhabited by primary termites (Chapter 3). As a result the OC stocks below younger and older mounds were similar, despite higher OC contents at the sites inhabited by primary termites. Yet, the VSC-lignin stock was higher below primary termites' nests, which emphasized the higher enrichment of VSC-lignin compared to OC in those nests. Obviously, VSC-lignin was lost during nest aging and colonization by secondary termites, and this effect was even sustained when the secondary termites preferred more woody food for nest construction (see above). Also the acid-to-aldehyde ratio of the vanillyl units (Table 4.1) and the one combined for vanillyl and syringyl units indicated a stronger oxidation of the VSC-lignin in the nests inhabited by secondary termites. It is important to note that this lignin degradation was probably not caused by termites recycling the nest material, but rather by soil fungi whose composition may be changed after dying of the primary termite colony (Roose-Amsaleg et al., 2004; Diouf et al., 2006). Bandowe et al. (2009) showed that the microorganisms occurring in termite nests were responsible for naphthalene production and not the termites itself.

I assume that the nests were four years old, because this was the time since last Cerrado burning. It was reported that the termites' abundance is elevated in disturbed savannas, and that especially grass- and litter-feeder termites benefit from the higher litter supply (Wood, 1996; Black & Okwakol, 1997; Brandão & de Souza, 1998). Hence, most of the lignin loss occurred within a period <4 years, thus questioning a higher recalcitrance of lignin in tropical soils or decaying termite nests. Yet, lignin losses are nowadays frequently described by two-compartment models. Rasse et al. (2006) and Marschner et al. (2008) suggested, based on published observations and their own experiments, that more than 90% of the lignin input into soil was not protected from degradation, and had turnover times of less than one year. Only the much smaller second pool of lignin had residence times of 18 to 20 years (Rasse et al., 2006; Marschner et al., 2008). The model frame fits well my observation of a rapid loss of VSC-lignin when the nests are no longer inhabited by primary termites. Due to a lack of knowledge on the lignin input and the real age of the mounds, the pool sizes and the residence time cannot be estimated reliable here. However, because the OC stocks were similar at sites with young and old nests, a transformation of lignin into other organic molecules of humified matter seems more likely than its complete conversion to CO₂.

4.5 Conclusion

The termites accumulated VSC-lignin in preference to other organic compounds in their nests as well as in the underlying and lateral adjoining soil. These lignin patterns were well detectable using MIRS as a fast screening tool for soil lignin. The lignin enrichment was favored by the inability of termites to alter lignin during nest and sheeting construction, but also to a preferential selection of woody food sources (lower C/V ratio), even for the grass- and litter-feeding termite *C. silvestrii*. Judging by the lower VSC-lignin contents and stocks at the sites with older mounds, lignin degradation occurs in the termite nests inhabited by secondary termites, however, as well as in the surrounding soil. Rainforest termites, at least in the microcosm, may use nest material to build foraging galleries and by this carry nest material into the nest surroundings. Tracing lignin in tropical soils might thus allow a better understanding of the role of active termites for the patchiness of nutrients in tropical soils, while the tracing of past termite activities may not be well indicated by lignin contents, because it is instable when the primary termites are absent.

Chapter 5

Carbon and nutrient leaching from termite mounds inhabited by primary and secondary termites¹

5.1 Introduction

Termites change soil properties through translocation, selection and ingestion of organic and inorganic materials (e. g., Lee & Wood, 1971b; Lobry de Bruyn & Conacher, 1990; Holt & Lepage, 2000; Bandeira & Martius, 2006), but how an existing mound affects its surroundings and thus causes spatial patterns of nutrients in soils has rarely been studied (Salick et al., 1983; Tongway et al., 1989; Holdo & McDowell, 2004; Obi & Ogunkunle, 2009). Termite mounds are numerous in the Brazilian savanna (Cerrado), especially in those areas converted to pastures. Given the low nutrient content in this region the numerous termites could have an important effect on soil nutrient status. Leaching of nutrients was observed in the Cerrado (Wilcke & Lilienfein, 2005), but how termite mounds influences leaching of nutrients or the infiltration of water is unknown for this region.

Nutrient transport from the mound into the soil can happen in several ways. Termites might directly relocate nest materials into the soil. Furthermore, relocation can happen when termite mounds with dying colonies decay and erode. Although intact, inhabited termite mounds often have a dense surface particularly impermeable for water (e. g., Lal, 1988; Contour-Ansel et al., 2000; Jouquet et al., 2004), partial erosion and leaching from inhabited termite mounds may add nutrients to the soil. Congdon et al. (1993, cited by Holt & Lepage, 2000) and Schwiede et al. (2005) reported leaching of nitrate and ammonium from termite nests into the surrounding soil. Additionally Barnes et al. (1992) found high nitrate contents in the hard wall of termite mounds in the Australian arid zone. They speculated that a capillary effect inside the mound during dry seasons and a subsequent transport by rain water on the mound surface caused high amounts of nitrate in groundwater. For other termites, mounds showed elevated infiltration (Ackerman et al., 2007). Also, infiltration is normally enhanced in the termites' foraging areas (Lal, 1988; Mando et al., 1996; Léonard & Rajot, 2001; Léonard et al., 2004) that are loosened by the termites' burrowing activities (e. g., Martius & Weller, 1998).

¹ This chapter was already published in a journal: Rückamp, D. et al. (2009). Carbon and nutrient leaching from termite mounds inhabited by primary and secondary termites. *Appl. Soil Ecol.* 43(1), 159–162.

Termite mounds are infrequently abandoned in the Brazilian Cerrado. Old mounds are regularly inhabited by secondary termite colonies (Redford, 1984; Lacher et al., 1986; Domingos & Gontijo, 1996), also named as inquilines. Those secondarily inhabited mounds looked weathered and had a lower carbon and available phosphorus content than the primarily inhabited ones (Chapters 2 & 3); thus, their effect on infiltration or nutrient export could be different from the primarily inhabited mounds. Consequently, the purpose of my study was to differentiate the carbon, nitrogen, and phosphorus leaching among young mounds with primary termites, old mounds with secondary termites, and a reference soil.

5.2 Materials and methods

The study was performed on the farm (10°16'S, 48°10'W) of the Instituto Ecológica in Taquaruçu, 20 km southeast of Palmas, Tocantins, Brazil, a disturbed Cerrado (savanna) site 630 m above sea level (see Figure 2.1). Mean annual temperature is about 24 °C and mean annual rainfall about 1800 mm (1920 mm in the study year) with a 5-month dry season (May – September). Soils were rich in organic material (topsoils: 20.8 g C kg⁻¹ soil), had a very low base saturation and had a sandy clay loam texture. They were classified as Umbric Acrisols (Humic, Hyperdystric, Skeletic) or Umbric Alisols (Humic, Hyperdystric, Skeletic) (IUSS Working Group WRB, 2006; see Chapter 3). Flat dome-shaped mounds of the grass-feeder and litter-forager termite *C. silvestrii* (Gontijo & Domingos, 1991; Constantino, 2002), most abundant in the study area, were selected for the study (Figure 5.1). Mounds chosen had a diameter of approximately 120 cm and a height of 23–47 cm. They consisted of a dense mound wall and a center with a lot of galleries, whereas a nursery could not be separated. The whole mound was mainly constructed from soil

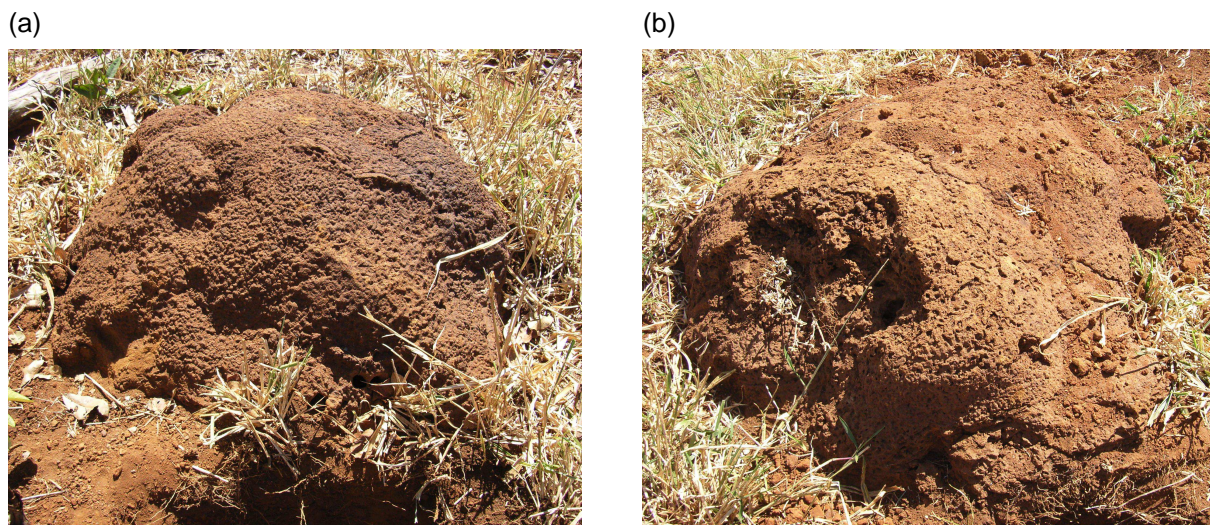


Figure 5.1 Photographs of examples of a primarily (a) and a secondarily (b) inhabited mound. In the front are hints of trenches for the lysimeter installation visible.

material. The younger mounds were still inhabited by *C. silvestrii*, while the older ones, which looked more weathered, had been constructed by *C. silvestrii*, but were now partly occupied by secondary termites which did not build dominant colonies and did not disturb the original mound structure (Figure 5.1). Those secondary inhabitants were the wood- and cattle dung-feeding *Nasutitermes kemneri* (Freyman et al., 2008), which occurred in all old mounds, the grass-feeding and litter-foraging *Procornitermes araujoi* and the wood- and grass-feeding *Armitermes euamignathus* (Coles de Negret & Redford, 1982; Gontijo & Domingos, 1991), as well as the soil/wood interface-feeding *Labiotermes orthocephalus* (Marques, 2008) and *Embiratermes festivellus* (Gontijo & Domingos, 1991).

Altogether twelve free-draining lysimeters were installed below four replicates of reference soil sites, four replicates of primarily and four replicates of secondarily inhabited mounds. During installation I paid attention to holes and macropores inside the termite wall and installed the lysimeters below an intact surface. The lysimeters consisted of a 10 cm high stainless steel frame (25 cm x 25 cm) with a bottom plate, and they were filled with a gradient of washed gravel and sand. Additionally, a 10 cm high stainless steel frame was fixed at the top to control the water flow to the lysimeter and provide good contact with the nest. The lysimeter was installed 30 cm below the soil surface from a side trench. The soil surface above the lysimeter was leveled to provide a smooth contact and then the lysimeter was pressed into position with a hydraulic car-jack (cf. Laabs et al., 2002). I assume that connection of macropores to the lysimeter was interrupted by the installation directly below the lower nest wall and the guiding frame. Soil solution was then collected in shaded bottles from July 2006 until July 2007 and sampled at least every 10 days.

The samples were immediately filtered through 0.45 µm membrane filters (Cellulose acetate, OE 67, Schleicher & Schuell, Dassel, Germany), and analyzed for pH, phosphate, ammonium, and nitrate (Clesceri, 1998). Then the samples were stored frozen until dissolved organic carbon (DOC) was measured with a total organic carbon analyzer (TOC-500, Shimadzu, Kyoto, Japan). Measured values were set to zero, when the value was below the limit of detection. Means of replicates were computed for concentrations and fluxes for each sampling date. Additionally, average concentrations and fluxes for the year studied were calculated. Differences between groups were examined with an analysis of variance (ANOVA) and the Scheffé post-hoc test using the software package SPSS 14.0 for Windows (SPSS Inc., 2005, Chicago, USA).

5.3 Results

In total, 441.51 m^{-2} of leached water was collected in the reference soil, which is about one quarter of the annual rainfall. Much less water leached through termite mounds; only about one quarter to a sixth of that of soil under primarily and secondarily inhabited mounds, respectively (Table 5.1). Leaching of measurable amounts started about one month after rainfall began, then the volume of leached water followed the rainfall distribution on a lower level (data not shown), with interruptions during drier periods. These interruptions were more pronounced below termite mounds ($P < 0.05$) due to the lower water flow. As a result, there were missing values in the chemical analyses from termite mound leachates.

Differences of element concentrations and pH (Table 5.1) were only significant ($P < 0.05$) for nitrate under secondarily inhabited termite mounds (Figure 5.2). The calculated nutri-

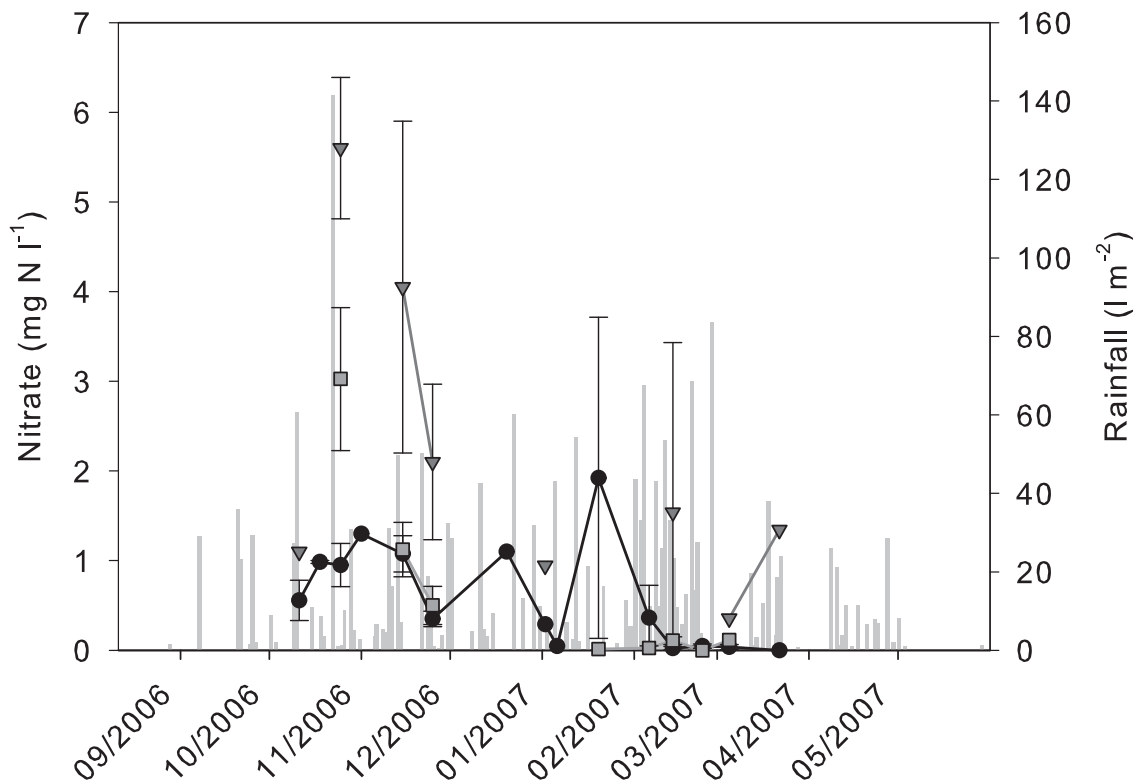


Figure 5.2 Nitrate concentrations in soil water below reference soil (●), mounds of primary (■) and of secondary termites (▼). The error bars mark the standard error ($n=4$). The sampling period takes from July 2006 until July 2007, but only during the rainy season leached water was collected. Soil water samples were inhibited by a limited water supply before October 2006 and after the end of March 2007. The grey bars show the precipitation on a daily base.

Table 5.1 Averaged concentrations and cumulative fluxes (standard error of four replicates) of DOC, phosphate, ammonium and nitrate in soil water below reference soils, and mounds of primary and secondary termites during a 1-year period. Measured concentrations of phosphate and ammonium were below the limit of detection at some dates and therefore set to zero for these dates. Within a row, different letters designate significant ($P < 0.05$) differences.

			Reference soil	Primary termites	Secondary termites
Water	Sum	l m^{-2}	441.5 (158.5) a	116.5 (59.7) b	68.2 (53.2) b
	Percent of rainfall	%	23.0 (8.3)	6.1 (3.1)	3.6 (2.8)
pH	Average		5.8 (0.1) a	5.9 (0.1) a	5.8 (0.2) a
DOC	Average concentration	mg C l^{-1}	13.8 (1.5) a	14.1 (1.9) a	16.5 (1.0) a
	Cumulative flux	$\text{mg C m}^{-2} \text{y}^{-1}$	7798 (2603) a	2365 (943) ab	1610 (1037) b
Phosphate	Average concentration	mg P l^{-1}	0.19 (0.02) a	0.19 (0.05) a	0.34 (0.06) a
	Cumulative flux	$\text{mg P m}^{-2} \text{y}^{-1}$	81.3 (2.5) a	14.4 (4.0) a	25.2 (18.0) a
Nitrate	Average concentration	mg N l^{-1}	0.60 (0.27) a	0.61 (0.28) a	2.13 (1.35) b
	Cumulative flux	$\text{mg N m}^{-2} \text{y}^{-1}$	226.0 (69.0) a	66.3 (25.0) a	200.9 (122.9) a
Ammonium	Average concentration	mg N l^{-1}	1.43 (0.07) a	1.58 (0.54) a	1.33 (0.69) a
	Cumulative flux	$\text{mg N m}^{-2} \text{y}^{-1}$	205.1 (20.6) a	15.8 (5.1) a	82.7 (4.3) a

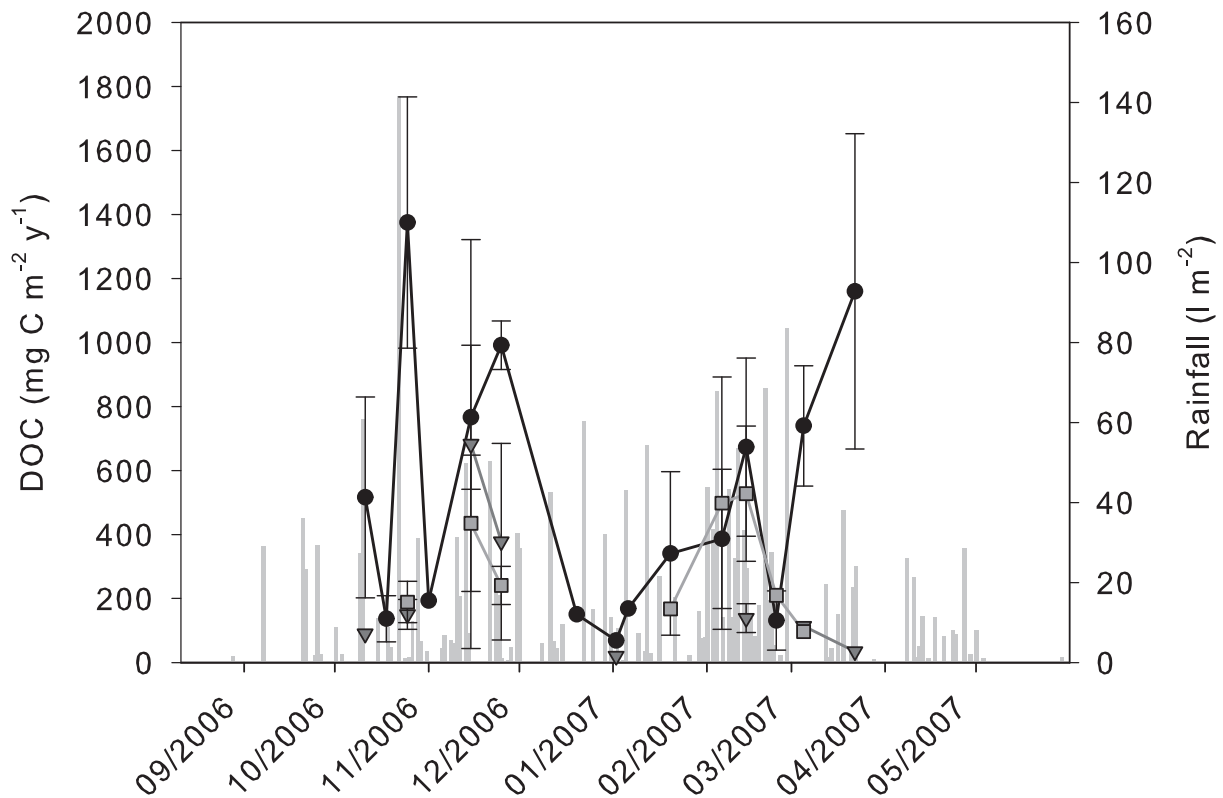


Figure 5.3 Fluxes of DOC in soil water below reference soil (●), mounds of primary (■) and of secondary termites (▼). The error bars mark the standard error ($n=4$). The sampling period takes from July 2006 until July 2007, but only during the rainy season leached water was collected. Soil water samples were inhibited by a limited water supply before October 2006 and after the end of March 2007. The grey bars show the precipitation on a daily base.

ent fluxes indicate higher exports in reference soil owing to the higher amount of drained water (Table 5.1). However, only the DOC flux was significantly ($P < 0.05$) higher below the reference soil than below the secondarily inhabited mounds (Figure 5.3).

5.4 Discussion

In general, I found higher DOC concentrations ($13.8\text{--}16.5\text{ mg C l}^{-1}$) than did Lilienfein et al. (2003) and Ciglasch et al. (2004) in an Oxisol of the Brazilian Cerrado near Uberlândia with $4.3\text{--}6.9$ and $3.3\text{--}9.1\text{ mg C l}^{-1}$, respectively. The higher C concentrations in the mound material than in the soil (reference topsoil: 20.8 g C kg^{-1} soil, primarily inhabited mound 36.5 g C kg^{-1} soil, secondarily inhabited mound 31.2 g C kg^{-1} soil; Chapter 3) could generate more DOC in the mounds, but the longer pathway for draining water from the mound top to the lysimeter could also result in increased DOC adsorption and mineraliza-

tion. This could be the reason for the lack of significant differences in DOC concentrations between mounds and reference soil. The differences in DOC fluxes were caused by less drainage water in the mounds. In contrast, brown colored leachates with supposedly much more DOC were observed below mounds of e. g., *Embiratermes sp.* and *Neocapritermes sp.* in the Brazilian rainforest (Amelung et al., unpublished data). This suggests that termite mounds with a hard mound crust, like *C. silvestrii*, which inhibits water infiltration, may have a lower effect on soil water DOC concentrations.

Besides DOC, draining water could also contain nutrients in their inorganic form or as part of the dissolved organic matter. Okello-Oloya et al. (1985) and Ndiaye et al. (2004a) showed that soil/wood- and soil-feeding termites in tropical savannas enrich in their mounds, aside from organic nitrogen, nitrate by 2–42 times and ammonium by 83 times compared to reference soil values. Such enrichments may cause elevated nitrate loadings in the leachates of termite mounds (Barnes et al., 1992), as shown here for mounds of secondary termites. I measured higher concentrations in the reference soil than Lilienfein et al. (2003) in a soil of the Brazilian Cerrado nearby Uberlândia, where nitrate was about 0.1 mg N l^{-1} and ammonium was not detected. Nevertheless, Wilcke & Lilienfein (2005) calculated much higher net fluxes of nitrate ($100\text{--}2200 \text{ mg N m}^{-2} \text{ y}^{-1}$) and similar fluxes of ammonium ($100\text{--}200 \text{ mg N m}^{-2} \text{ y}^{-1}$) at the same study site as Lilienfein et al. (2003). I attribute this finding of higher concentrations, but lower fluxes in my study to a different rain distribution at the sampling dates, because high concentrations coincided with low amounts of leached water. Furthermore, termite mounds had no significant effect on phosphate leaching, though available inorganic phosphorus was also found to be higher in these mounds (Chapters 2 & 3).

In summary, the effects on DOC and nitrate were greater below the older mounds inhabited by secondary termites than below the younger ones, inhabited by primary termites, despite lower organic matter contents in the old mounds (Chapters 2 & 3). Because age was only a qualitative classification and the real age of the mounds is unknown, it is impossible to attribute the effects to mound aging or the secondary termite species association inhabiting the mounds.

5.5 Conclusion

I conclude for this semi-humid savanna ecosystem, that the nutrients in the soil water are little influenced by recent mounds with primary termites. Old, secondarily inhabited mounds, however, have higher nitrate concentrations in their soil water and smaller DOC fluxes.

Chapter 6

Final discussion and conclusion

6.1 Summaries for the research objectives

The present work clarified the role of termites occurring in Brazil for the distribution patterns of carbon and phosphorus fractions, and the genesis of tropical soils. The availability of phosphorus is limited in most tropical soils. It was hypothesized that termites have a positive influence on phosphorus availability through the incorporation of clay and organic matter into their nests, and a chemical alteration of the organic matter. Furthermore, it was assumed that termites of different feeding guilds have distinct impacts on soil properties in general, and on phosphorus in particular. Hence, I chose a systematic approach to describe the effects of different termite species on total and plant available phosphorus. For studying the effect of termites on phosphorus forms in more detail, termite mounds of the Brazilian Cerrado were selected. In particular the spatial extension to which phosphorus forms in the soil adjacent to termite nests were modified by termites was studied. It was also expected that the termites, besides soil properties, affect soil genesis as well. To elucidate the temporal development of phosphorus forms and soil genesis, I also investigated soil below presumably older, but still inhabited mounds, because abandoned mounds are very rare in the Cerrado. Moreover, the contents and characteristics of lignin in nests, nest surroundings, and older nests were also described. It was already reported in former studies that lignin resists degradation by termites, and that it is enriched in termite nests relative to other organic compounds. On the other hand, the persistence of such lignin enrichments, and the consequences for the soil below termite nests are not studied yet. To characterize the lignin alteration during incorporation into new termite nest constructions, additional microcosm experiments with a xylophagous termite species were done. It is also unknown if there is any transport of nutrients from still inhabited nests to the surrounding soil by water flow. Actually, as there are no extensive reports on the influence of termite nests on the composition of soil solution, I analyzed soil water from termite mounds and reference soils.

Consequently, the specific objectives of my work were (i) to describe the effects of different termite feeding guilds on phosphorus forms, (ii) to elucidate the spatial and temporal

effects of termites on phosphorus in their nest and the underlying soil, (iii) to characterize the temporal development of lignin in termite mounds and the underlying soil, and (iv) to decipher the effect of termite mounds on nutrients in draining water. Considering those objectives (see also Section 1.3), I can recapitulate the following results of my work:

1. Which effects do different termite feeding guilds have on phosphorus forms?

In the first part (Chapter 2, see also Rückamp et al., 2010), the effects of wood-feeder and soil/wood interface-feeder termites (plus some grass-feeder/litter forager and lichen-feeder termites) of seven Brazilian ecosystems (Terra firme, Igapó, Várzea, Cerrado, Caatinga, Mata Atlântica, Pantanal) on phosphorus forms in their nest were studied in comparison to soil and wood used as food sources. For this purpose, different nest parts (outer wall, inner wall, central part), soils, and wood were sampled and analyzed for labile and stable P forms by using sequential extraction and liquid-state ^{31}P -NMR spectroscopy. The central part of termite nests contained between 275 and 1871 mg kg⁻¹ total P, dominated by P_i in nests of soil/wood interface-feeder termites, but with balanced P_o and P_i contents in nests of wood-feeding termites. All P_o fractions, and, in most nests, also labile P_i forms were enriched in termite mounds in comparison to soils. The P enrichment was most pronounced in nests of the Terra firme and the Igapó, where the total P contents of the soils were the lowest with 141 and 171 mg kg⁻¹. Nests of wood-feeding termites accumulated mainly highly labile resin-P_i, and partially the stable HCl_{conc}-P_i fractions, apart from P_o, which can be all attributed to the organic food source and food digestion. The soil/wood interface-feeder termites had more variations between their nests, but in general they had higher portions of P bonded to minerals. Hence, it can be concluded that (i) termite activity results in a gross enrichment of labile P forms in the nests, (ii) the P composition in termite nests reflects the major feeding guild, and (iii) the degree of this P enrichment is partly driven by the P stock in the soil.

2. What are the spatial and temporal effects of termites on their mound and the underlying soil?

The aim of Chapter 3 (see also Rückamp et al., 2012) was to characterize the changes of constitutive chemical soil properties and of the soil classification in and around termite nests in the Brazilian savanna. Two transects to a soil depth of 100 cm in each case were dug below three younger mounds of *Cornitermes silvestrii* (the primary nest builder), three older mounds in which *C. silvestrii* had died out and which were secondarily colonized mainly by *Nasutitermes kemneri*, and three reference sites in the Cerrado. Samples from the center of the transects were characterized by

standard procedures for soil classification; in addition, phosphorus extractions were conducted on selected samples using NaHCO_3 for labile P forms, and concentrated HCl for stable P forms. This data set was then used to build calibration models for the prediction of labile and stable inorganic (P_i) and organic (P_o) P forms, as well as for contents of organic carbon (OC) in the remaining samples applying mid-infrared spectroscopy in combination with partial least squares regression (MIRS-PLSR). It could be shown that the termite influence on the soil was sufficiently large to change diagnostic characteristics of the soils under termite mounds. The MIRS-PLSR predictions were suitable for quantifying organic carbon and most of the labile and stable phosphorus fractions. They showed an enrichment of OC, $\text{NaHCO}_3\text{-P}_o$ and $\text{NaHCO}_3\text{-P}_i$ contents in primarily and secondarily inhabited termite nests by factors of 1.6–2.0 and 1.4–1.5, respectively. The soils surrounding the nests had higher contents of OC and $\text{NaHCO}_3\text{-P}$ under both nest types vertically down to 30 cm below the lower nest border. At the same time OC and $\text{NaHCO}_3\text{-P}_i$ were elevated at minimum to a lateral distance of 60 cm away from the nest border. As the pattern of $\text{HCl}_{\text{conc}}\text{-P}_i$, which comprised 95% of total P, showed no variations between the sites, I conclude that the higher $\text{NaHCO}_3\text{-P}_i$ amount was formed in termite nests by changing the availability of the more stable $\text{HCl}_{\text{conc}}\text{-P}_i$. In contrast to the contents, the OC and $\text{NaHCO}_3\text{-P}$ stocks below the primarily inhabited termite mounds were comparable to those secondarily inhabited, because the bulk density of the latter ones was higher. This was due to a transport of clay-rich material from the subsurface argic horizons into the nests. Here, the secondary termites even inverted the lessivation observed in the reference soils and under mounds inhabited by primary termites, thus causing the soil types to change from Alisols and Acrisols to the properties of Umbrisols.

3. How is the temporal development of organic matter in termite mounds, which resists degradation by termites?

Chapter 4 (see also Rückamp et al., 2011) answered the questions how lignin, which is part of the organic matter not attacked by termites, was incorporated into termite mounds and how the lignin status developed from young to older termite nests, using the same data set as in Chapter 3. Lignin contents were estimated by the sum of lignin-derived phenols, and additionally by mid-infrared spectroscopy followed by a partial least squares regression. Nests inhabited by primary termites had a lignin content of 1952 mg kg^{-1} , which was 15 times higher than at 10 cm depth of the reference soils. In comparison, organic carbon was only enriched by a factor of 2 in primarily inhabited nests. My accompanying microcosm experiment showed that the lignin

composition was not changed during incorporation into termite nests. Elevated lignin contents could still be found at 60 cm lateral distance from the nest border as well as up to 60 cm soil depth beneath the mounds. The lignin content in older nests was only half that of younger nests, and the influence on the nest surroundings was less prominent. Higher acid-to-aldehyde ratios in these older nests indicated that the remaining lignin was oxidized, and thus partly degraded during nest aging. I conclude that the original mound-builder, the savanna termite *C. silvestrii* enriches lignin in its earth mounds, but that only a minor part enters the soil-protected lignin fraction when nests decay, as most of the lignin is lost during nest aging.

4. Is there any effect of termite mounds on nutrients in drainage water?

Finally, Chapter 5 (see also Rückamp et al., 2009) clarified the role of *C. silvestrii* mounds in the Cerrado for leaching of nutrients into deeper soil horizons. Free-draining lysimeters were installed below termite mounds and into the reference soil in the same study area as described in the former chapters. The soil solution was regularly collected during one year, and analyzed for dissolved organic carbon (DOC), phosphate, nitrate, ammonium and pH. Due to the hard outer nest wall, the volume of drainage water was significantly lower under the nests, and so was the flux of DOC and nutrients. Only nitrate concentrations were significantly enhanced under secondarily inhabited termite mounds. Hence, a small effect of the termite mounds on mosaic-like patterns of soil nutrients through leaching is evident, but only from secondarily inhabited (i.e. degrading) mounds.

All in all, the data showed a clear effect of termites on the properties of their nest and the surrounding soil. It was shown that most termite species enhance the phosphorus availability, and that the grass-feeding termites accumulate lignin in their nests. The surrounding soil was influenced by termites lateral adjacent and directly under their nests, by which the land surface affected by termites was extended. Not only single soil properties, but also soil genesis was changed by termites through an upwards transport of clay. Those changes of the soil were relatively stable under older termite mounds and the export of nutrients from older mounds was not elevated, which suggests that termites at least have a long-term effect on tropical soils by changing the soil type.

6.2 Synthesis

6.2.1 Processes driven by Cerrado termites and their classification

Cornitermes species are dominant termite species in the Brazilian Cerrado (*C. cumulans* in the southern part, and *C. silvestrii* in the northern part (Araujo, 1970; Constantino, 2002)). Hence, the studied termites are the dominant termite species living in and on the soil in the disturbed Cerrado in Northern Brazil. The overall mound density in this area was 72 ha⁻¹ with an occupied area of 22 m² ha⁻¹. The mounds originally built by *C. silvestrii* accounted for about 60% of the total number and for more than 60% of the total occupied area, since those mounds were larger than the others occurring in this area. Even though the studied mounds were conspicuous in the Cerrado, much higher earth mound densities were reported in the literature (Table 6.1). In Australia, mound densities up to 587 ha⁻¹ for a single species were found (Spain et al., 1983b). For Africa, extremely variable mound densities from 4 to 1239 ha⁻¹ were reported (Table 6.1). Nevertheless, the occupied areas were larger with up to 10% (or 20% as an outlier) of the total area in each study of Australia and Africa than in the Brazilian Cerrado studied here (0.1%). Those high numbers were, among others, due to the large mounds of fungus-growing termites in Africa. This indicates that the actual proportion of land which is affected by *C. silvestrii* activities is small compared to other termite species. However, it was also shown that *C. silvestrii* affect the surrounding soil to a lateral distance of at least 60 cm from the mound border. Therefore, the area which is actually affected by *C. silvestrii* or their nest inquilines, accounts for 1.1%. In addition, it can be assumed that the active mound sites are shifting over the land and that, consequently, the soil area altered by termites will be larger after a few years.

In general, termites are important soil engineers which transport a lot of soil material (Table 6.2). Excluding the outliers in Table 6.2, which were estimated from short-term measurements, it can be generalized that termites transport about 1000 kg ha⁻¹ a⁻¹ soil material from deeper horizons to the ground level. For example, Brossard et al. (2007) measured 1200 kg ha⁻¹ a⁻¹ brought to the soil surface, the mounds grew with 400 kg ha⁻¹ a⁻¹, and 800 kg ha⁻¹ a⁻¹ were immediately eroded and returned to the soil. The annual growth of mounds referred to in the literature covered a range from 105 to 1250 kg ha⁻¹ a⁻¹. The study of Lobry de Bruyn & Conacher (1995) gives comparable values for mound density and the occupied land area to my work (Table 6.1). Therefore, I assume that the *C. silvestrii* mounds in my study grow in the same order like the mounds in their study do. This fairly moderate estimate¹ of 100 kg ha⁻¹ a⁻¹ still ignores the annual masses transported to the sur-

¹ In this calculation, the existing mound mass per hectare of this approximately four years old mounds was not considered.

Table 6.1 Termite earth mound densities and areas occupied by termite mounds referenced in the literature for various termite species and savanna ecosystems.

Country	Ecosystem	Termite species	Mound status	Mound density ^a ha ⁻¹	Area occupied ^a m ² ha ⁻¹	Reference
Africa						
Burkina Faso	woodland savanna ^b	various	alive or dead	783	1068.2	Traore & Lepage (2008)
Côte D'Ivoire	shrubland	various	alive or dead	13	910.0	Abbadie et al. (1992)
South Africa	shrubland	various	intact mounds	4	895.1	Moore & Picker (1991)
Zimbabwe	woodland	<i>Macrotermes michaelseni</i>	good to poor	6	707.6	Holdo & McDowell (2004)
Burkina Faso	woodland savanna ^c	various	alive or dead	390	706.0	Traore & Lepage (2008)
Burkina Faso	woodland savanna ^d	various	alive or dead	1239	333.0	Traore & Lepage (2008)
Côte D'Ivoire	shrubby savanna	various	not reported	16	330.0	Konaté et al. (1999)
Burkina Faso	woodland savanna ^e	various	alive or dead	381	218.9	Traore & Lepage (2008)
Nigeria	savanna	<i>Macrotermes bellicosus</i>	not reported	7	52.8	Abe et al. (2009a)
Australia						
Australia	savanna ^f	<i>Drepanotermes perniger</i> , <i>Drepanotermes rubriceps</i>	not reported	350	2000.0	Watson & Gay (1970)
Australia	woodland	<i>Amitermes vitosus</i>	alive or dead	197	128.0	Spain et al. (1983b)
Australia	woodland	various	alive or dead	283	90.0	Holt et al. (1980)
Australia	open woodland ^g	<i>Amitermes vitosus</i>	alive or dead	587	89.4	Spain et al. (1983b)
Australia	open woodland	various	not reported	459	88.8	Spain et al. (1983a)
Australia	open woodland ^h	<i>Amitermes vitosus</i>	alive or dead	473	61.9	Spain et al. (1983b)
Australia	woodland	<i>Drepanotermes tamminensis</i>	alive or dead	113	57.6	Park et al. (1994b)
Australia	shrubland	<i>Drepanotermes tamminensis</i>	alive or dead	126	37.8	Park et al. (1994b)
Australia	heathland	<i>Drepanotermes tamminensis</i>	good to poor	20	36.0	Lobry de Bruyn & Conacher (1995)
Australia	open woodland	<i>Drepanotermes tamminensis</i>	good to poor	70	28.0	Lobry de Bruyn & Conacher (1995)
South America						
Brazil	savanna	various	alive	72	21.9	present work

^a some values were newly calculated; ^b with grazing, but without fire; ^c with grazing and fire; ^d without grazing and fire; ^e without grazing, but with fire; ^f "outbreak" of *Drepanotermes*; ^g yellow earth; ^h red earth

face. When I calculate the organic matter and available phosphorus masses incorporated into the mounds, I come to the conclusion that the accumulated organic carbon accounts for about $4 \text{ kg ha}^{-1} \text{ a}^{-1}$, $\text{NaHCO}_3\text{-P}_i$ for $1.8 \text{ g ha}^{-1} \text{ a}^{-1}$, and $\text{NaHCO}_3\text{-P}_o$ for $4.0 \text{ g ha}^{-1} \text{ a}^{-1}$. These values are very low compared to stocks present in this area (OC: $100 \text{ t ha}^{-1} 100 \text{ cm}^{-1}$; $\text{NaHCO}_3\text{-P}_i$: $70 \text{ kg ha}^{-1} 100 \text{ cm}^{-1}$; $\text{NaHCO}_3\text{-P}_o$: $140 \text{ kg ha}^{-1} 100 \text{ cm}^{-1}$; see also Figure 3.7). Notably, these accumulated masses are mostly concentrated in $< 0.1\%$ of the area.

It can be speculated that a lot of soil material brought to their mounds by Cerrado termites was immediately returned to the topsoil as described in the study of Brossard et al. (2007). This can be a reason for higher contents of carbon and phosphorus in the soils adjacent to the mounds. However, the rate of erosion from termite mounds could not be estimated. Nevertheless, the nutrient fluxes in soil water were reduced under termite mounds in comparison to reference soils (Chapter 5; see also Rückamp et al., 2009). It will take, therefore, more than 300 years^2 to remove the $\text{NaHCO}_3\text{-P}_i$ contents of older secondarily inhabited nests by drainage water if the hard termite wall persists for such a long time (which is unlikely). Thus, the removal will be by far faster when the mound persists only for approximately ten years. Additionally, it was shown in the microcosm experiment (Chapter 4) that termites transport material out of their nest for the construction of new buildings. Therefore, the removal of elevated contents in the nests can be even faster by the activity of (secondary) termites.

It was shown that termites in the *Nasutitermes* genus in general enriched the easily plant available $\text{NaHCO}_3\text{-P}$ at least as strongly as did the *C. silvestrii* (Chapter 2; see also Rückamp et al., 2010). However, *Nasutitermes* (*N. surinamensis*, *N. ephratae*, *N. corniger*) studied feed on wood, whereas *N. kemneri* occurring in the Cerrado also feed on dung (Freymann et al., 2008). Cattle dung is rich in phosphorus (Haynes & Williams, 1993; McDowell & Stewart, 2005); therefore, also the constructions made by *N. kemneri* should be rich in P. In fact, $\text{NaHCO}_3\text{-P}_i$ and $\text{NaHCO}_3\text{-P}_o$ were depleted in the older mounds inhabited by *N. kemneri* compared to the younger ones. Also the lignin content in older mounds of the Cerrado was lower than in primarily inhabited mounds, despite the occurrence of wood-feeding termites, like *N. kemneri* and *Armitermes euamignathus*, in those older mounds. For this reason, a large influence of the dung-, wood- and grass-feeding secondary termites on constructions in the older mounds is not probable. On the other hand, a depletion at least of lignin can be promoted by soil-feeding termites like *Embriatermes festivellus* and *Labiotermes orthocephalus* which inhabited one replicate of the old mounds. Nevertheless, in Chapter 3 (see also Rückamp et al., 2012) it has been already concluded that the effect of inquilines on the properties of older mounds is negligible, because they occupy only parts

² According to a rough calculation with a phosphate flux of $25.2 \text{ mg P m}^{-2} \text{ y}^{-1}$.

Table 6.2 Turnover and soil brought up by termite activities as well as growth and erosion of termite mounds referenced in the literature for various termite species and savanna ecosystems.

Country	Ecosystem	Termite species	Soil turnover kg ha ⁻¹ a ⁻¹	Soil brought up ^{a, b}	Growth of mounds ^a	Erosion of living mounds ^a	Reference
Africa							
Kenya	pasture	<i>Pseudacanthotermes spiniger</i>		1300			Kooyman & Onck (1987)
Nigeria	woodland	<i>Macrotermes nigeriensis</i>			1250		Nye (1955)
Namibia	grassland	<i>Hodotermes mossambicus</i>			895		Grube (2001)
Uganda	pastoral	<i>Macrotermes subhyalinus</i>				7167	Pomeroy (1976)
Uganda	grassland	<i>Macrotermes</i>				3575	Pomeroy (1976)
Uganda	garden	<i>Macrotermes bellicosus</i>				1263	Pomeroy (1976)
Uganda	garden	<i>Pseudacanthotermes</i> sp				918	Pomeroy (1976)
Burkina Faso	savanna	<i>Trinervitermes geminatus</i>		1200	400	810	Brossard et al. (2007)
Kenya	open bushland	<i>Odontotermes</i>		1059			Bagine (1984)
South Africa	savanna	<i>Hodotermes mossambicus</i>		700			Hewitt et al. (1990)
Uganda	grassland	<i>Macrotermes subhyalinus</i>				426	Pomeroy (1976)
Asia							
India	grassland	<i>Odontotermes gurdaspurensis</i>		19080			Gupta et al. (1981) ^c
Australia							
Australia	open woodland	<i>Amitermes vitosus</i>	350				Coventry et al. (1988)
Australia	woodland	<i>Tumulitermes hastilis</i>			1175		Williams (1968)
Australia	open woodland	<i>Amitermes vitosus</i>			400		Holt et al. (1980)
Australia	open woodland	<i>Drepanotermes tamminensis</i>			105		Lobry de Bruyn & Conacher (1995)
Australia	open woodland ^d	<i>Amitermes vitosus</i>				194	Bonell et al. (1986) and Holt et al. (1980)
Australia	open woodland ^e	<i>Amitermes vitosus</i>				147	Bonell et al. (1986) and Holt et al. (1980)
North America							
USA	shrub/grass	<i>Gnathamitermes tubiformans</i>		5268			MackKay & Whitford (1988) ^c
USA	grassland	<i>Gnathamitermes tubiformans</i>		1248			MackKay & Whitford (1988) ^c
USA	shrubland	<i>Gnathamitermes tubiformans</i>		996			MackKay & Whitford (1988) ^c
USA	desert grassland	<i>Gnathamitermes perplexus</i>		575			Nutting et al. (1987)
USA	desert grassland	<i>Heterotermes aureus</i>		70			Nutting et al. (1987)

^a some values were newly calculated; ^b soil for mounds and sheetings; ^c extrapolated from short-term measurements; ^d red earth; ^e yellow earth

of those mounds, and they do not rebuild collapsed galleries; as a consequence, the bulk density of the older mounds was higher (Figure 3.1c). Figure 6.1 underlines the assumption that older mounds were degrading, at least in the central part of the mound, in spite of termite presence. The core of this mound had been collapsed, and the new cavity was potentially used by other animals like snakes; though, the outer mound wall still existed and though the water flow into the soil was as small, and comparable to that observed for younger mounds (Chapter 5; see also Rückamp et al., 2009). The persistence of the outer mound wall implies that the wall has a different composition than the mound center. A different chemical composition of the outer wall was documented in Chapter 2 for C and P contents, whereas Amelung et al. (2002) found no differences for C contents between outer wall, inner wall and nursery of various termite nests in Brazilian Amazonia. Such hard outer walls still protect the mounds after the death of the colony, and consequently they are the reason for the use of those mounds by inquilines (Redford, 1984). Altogether it points to the implication that the changed properties still visible in older mounds were caused by activities of the primary inhabitant *C. silvestrii*. If it is true that the effect of secondary termites on mound characteristics was small and that the still elevated contents of carbon, lignin, and available P were a consequence of the primary termites' activities, it is also likely that the primary termites were responsible for the changed soil types below old mounds. In fact, the higher clay content in the topsoil corroborated with lower clay content in the underlying argic horizon, strongly indicating that there was rather an upward transport of clays than a downward transport in consequence of mound erosion. However, the assumption that the primary termites cause the soil type to change can not be verified, because only very young, fresh looking primarily inhabited mounds as well as older, more weathered secondarily inhabited ones were chosen for the study, whereas older mounds inhabited by *C. silvestrii* were missing in this study design.

6.2.2 Summary of the life of a *Cornitermes* mound

The results of my work enable me to generalize the effects of mound growth and mound decaying on soil properties in the disturbed Cerrado of Northern Brazil. Additionally, the life of the dominant mounds in this area can be summarized. In this regard, the effects of the *C. silvestrii* and inquilines can be described as follows:

1. The original mound-builders *C. silvestrii* are founding their colonies at suitable microsites, but my results indicate that they do not have a prerequisite of an optimal soil type (Chapter 3).



Figure 6.1 Photograph of the interior of an old termite nest, which had a hard outer wall, but a cavity inside.

2. The large supply of litter and grass in the extensive pasture sustains the growth of the *C. silvestrii* colonies. This may be a reason for the dominance of *C. silvestrii* and their mounds in such areas.
3. Their food-collecting and mound-constructing activities cause an enrichment of organic carbon, lignin, $\text{NaHCO}_3\text{-P}$, and exchangeable cations in their nests and its surroundings. During ingestion, lignin is preferentially enriched relative to other organic constituents, because lignin resists degradation as commonly observed for grass-feeding termites, and documented for wood-feeding termites in the microcosm experiment of Chapter 4. The increase of easily plant available phosphorus contents is caused by changes in P availability during nest construction rather than by a accumulation of those P forms by termites.
4. The construction of mounds with hard outer walls reduces the drainage of water. Therefore, the fluxes of nutrients leached out of the mounds are reduced in compar-

ison to reference soils, despite higher or similar nutrient concentrations in the soil water at the mound sites.

5. After a few years secondary termites colonize *C. silvestrii* mounds, which are either still inhabited by *C. silvestrii* like nest no. 1 with primary termites in Table 3.1, or the original colony is already dead when the mound is being occupied by inquilines. The inquilines colonize only parts of the mounds, thus other parts are decaying.
6. During occupation of the mound by termites, the soil type directly below the mound is changed from Alisols and Acrisols to Umbrisols, which is a consequence of an upwards transport of clay by termites. The inquilines can contribute to these changes, but as the secondary termites only have a small influence on mound and soil properties, it is more likely that the clay transport has been done by the *C. silvestrii*.
7. The outer mound wall is conserved at the time of colonization with inquilines, either by its inherent chemical composition or by the work of secondary inhabitants. As a consequence, the water flow under secondarily inhabited mounds is even lower than in reference soils.
8. The secondary inhabitants are active in some parts of the mounds, but the contents of organic matter and nutrients decline from the highest level in mounds inhabited by primary termites, although nutrient contents remain higher than in the reference soil. Especially lignin is quickly degraded when it comes in contact with mound material.
9. The question of what happens to the mounds when the secondary colonies die could not be answered.

6.2.3 Relevance of the termites in the Brazilian Cerrado

Clear effects of the *C. silvestrii* on the accumulation and availability of phosphorus, the enrichment of lignin, and an upward transport of clay were observed in my studies. Nevertheless, it was shown that these termites had a low impact on changes of P contents compared to other termite species occurring in Brazil, and that the observed enrichments were small compared to the soil nutrient stocks. Therefore, I agree with Black & Okwakol (1997) that farming practices may have a greater influence on plants and soil nutrients than the termites. On the other hand, the termites and their mounds are no obstacle for the use of the studied land as an extensive pasture. Termite mounds are, indeed, a problem for the use of machinery in agriculture (Constantino, 2002), and *C. silvestrii*, *Procornitermes*

araujoi as well as *Armitermes euamignathus* are listed as pests for sugarcane and pastures, for eucalyptus and rice, and for eucalyptus, respectively (Constantino, 2002). However, Constantino (2002) qualified his statements and cited Fernandes et al. (1998): “at least in pastures, *Cornitermes spp.* are best defined as aesthetic pests, because farmers dislike their presence but they cause little or no real damage to grass production“. Wood (1996) added “the harvester termites merely remove the little forage that livestock have not consumed”. Summarizing, it can be said that the studied Cerrado termites may be a potential source for agricultural damages, but as long as the area is used as an extensive pasture, the potential damages will be small.

Elevated contents of phosphorus fractions and lignin are, at a lower level, also persistent below older mounds. However, especially as the $\text{NaHCO}_3\text{-P}$ fractions are not belonging to the very stable ones in soil, it must be questioned, therefore, that this nutrient patchiness will prevail for decades and above the live cycles of the termite mounds. In contrast, the disappearance of the argic horizon below such mounds is remarkable as it reverts a soil formation which otherwise would be unidirectional, and which likely lasted for millennia before it is changed by termite activity. In these very long cycles of soil formation, even a coverage of $<0.1\%$ soil surface can have a great influence on overall landscape development, depending on the frequency at which new mounds establish or disappear.

6.3 Research perspectives

As shown above, my work has been successful in answering the objectives, but some further specific questions had arisen during my work. To quantify the influence of the Cerrado termites for soil and nutrient accumulation and relocation, it will be necessary for further studies to know the real age of the individual mounds. A better knowledge of the mound age will also help to clarify the roles of primary and secondary termites for soil property changes and soil genesis. However, the most important point for assessing the termites' impact on Cerrado soils is to study the development of the secondarily inhabited mounds, because it remains unclear in my study whether and when the elevated nutrient content in those mounds will reach the level of the contents in the reference soil. Considering this point, it is also interesting to know whether the nutrient pattern in the topsoil reflects a former spatial distribution of the mounds. Further studies should also focus on the stability and the long-term development of the outer wall, because this part is very stable as its composition is presumably different from the mound center composition. **The questions listed above can be summarized under the question of turnover and temporal development of mound material.**

In addition, it was underlined above that the Cerrado termites have an effect on soil properties, but it is probable that other termites like the wood-feeding *Nasutitermes* and *Constrictotermes* or the soil/wood interface feeder *Termes* and *Embiratermes* of Brazil have a much larger impact on soil properties (see Chapter 2). Therefore, it will be suitable for upcoming studies to judge the results presented here for *C. silvestrii* against the effects of other termite species. This is especially true for the incorporation and temporal development of lignin as well as for the nutrients and dissolved organic matter in the draining soil solution. The latter for example was observed by Amelung et al. (unpublished data), who reported much more dissolved organic matter in the soil water below mounds of *Embiratermes sp.* and *Neocapritermes sp.* in the Brazilian rainforest. **Consequently, those questions address the generalization of the documented impacts of the Cerrado termites for other termite species.**

Finally, I raise the question of the relevance of termites for tropical pastures. It is well known that the abundance of termite mounds in Brazilian pastures is high, especially in those areas most heavily grazed by cattle (Redford, 1984). The questions are what factors lead to variation in the abundance of the mounds and what long-term impacts mounds have on the suitability of the soil for land use. Maybe the termites even slow the rate of land degradation?

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