Soil-plant dynamics of water, nitrogen and sulfur: A study on indigenous and exotic tree species in Munessa Forest, Ethiopia

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Dedicated to
Seyoum
Kebede
Miriam

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According to the different priority rules in naming, I address Ethiopians by their first name, while the Non-Ethiopians retain their dichotomous names in the following list of references.

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Summary

Forest plantations are necessary to counteract the destruction of tropical montane forests. Sustainable forestry requires comprehensive knowledge of tree effects on site conditions and nutrient cycling, but substantial information is lacking even for widely-planted species. In my work, I aimed at identifying such plant effects on ecosystem dynamics, focussing on water, nitrogen (N) and sulfur (S), which included the development of a stable-isotope methodology for S.

Based on a characterization of the soils of the study area at the Main Ethiopian Rift Valley escarpment, experimental plots were set up in neighbouring stands of a natural forest dominated by *Podocarpus falcatus* and in plantations of *Cupressus lusitanica* and *Eucalyptus globulus*. All investigations on the ecology of these trees were conducted on the same single-tree centred plots in a combination of time series of natural parameters with isotope tracer experiments, employing inorganic ^{15}N tracers and litter labelled with ^{34}S. Soils of the region reflected the influence of climate and relief, while the homogeneous bedrock caused no influence throughout the region. Methodological work to improve $\delta^{34}S$ analysis was a precondition for the ecological study on S dynamics. Technical adjustments to the analytical system including a liquid-nitrogen trap reduced the amount of S required for reliable $\delta^{34}S$ determination by a factor of six compared to the conventional procedure.

Soil-plant water dynamics were strongly related to the root system. *P. falcatus* with high fine root biomass to below 1 m depth appeared active in redistributing soil water. Its physiological response to changing soil moisture with a marked reduction in transpiration (by a factor of six) at dry conditions had a further balancing effect. *P. falcatus* and *C. lusitanica* expanded their root systems substantially in the dry season, shifting to deeper layers. Seasonality was very weakly expressed for root biomass and depth of water uptake under *E. globulus*. It mainly relied on deep water resources tapped by its low-biomass root system, supporting physiological activity in the dry season, when transpiration was increased by a factor of five.

Soil labelling with ^{15}N showed similar patterns of root activity. It also revealed the dominance of *C. lusitanica* near the surface, with its roots effectively intercepting nutrients. However, this had negative impacts on deeper soil layers by reducing

biological transformations and increasing leaching losses. In the natural forest, phosphate-extractable soil N and low natural-abundance $\delta^{15}N$ indicated an intense, conservative N cycling in the upper 60 cm, which was also evenly exploited by the roots of *P. falcatus*. Nitrogen uptake by *E. globulus* was concentrated in the deeper layers. A preferential stabilization of N was observed in the topsoil, while losses were indicated by high natural-abundance $\delta^{15}N$ values, which probably reflected recent processes. As for the trees, species-specific N uptake strategies were observed for the understorey.

Litter for the S mineralization experiment was successfully labelled with ^{34}S, opening a way to elucidate soil processes as well as plant uptake and recirculation. Different regimes of decomposition resulted in increasing extractability of S in the topsoil with depth under *P. falcatus* and *C. lusitanica*, whereas a decrease was noticed in the *E. globulus* stand. Seasonality of both bulk and extractable S were minimal. Isotope labelling showed rapid incorporation of litter into the topsoil of *E. globulus*, while S from litter of *C. lusitanica* was susceptible to leaching. Plant uptake by *P. falcatus* and *E. globulus* led to a steady increase of $\delta^{34}S$ values. In contrast, isotope enrichment in *C. lusitanica* leaves peaked after the first rainy season, thereby indicating recirculation of S.

The different approaches of my work complemented one another, revealing a consistent pattern of plant traits. *P. falcatus* had a balancing influence on the ecosystem and appeared to promote soil life. *C. lusitanica* confined biological transformations to the topsoil and raised the risk of leaching losses. *E. globulus* was largely independent of superficial resources, giving space to understory growth. This strategy may lead to depletion of groundwater and structural deterioration of the soil.

Zusammenfassung

Forstplantagen können helfen, der Zerstörung tropischer Bergwälder entgegen zu wirken. Ihre nachhaltige Bewirtschaftung erfordert umfassende Kenntnisse über die Auswirkungen der gepflanzten Baumarten auf Standortsbedingungen und Nährstoffkreisläufe. Allerdings bestehen selbst über die verbreitetsten Baumarten erhebliche Wissensdefizite. Meine Arbeit zielte darauf ab, die Dynamik von Wasser, Stickstoff (N) und Schwefel (S) in Abhängigkeit von der Baumart aufzuklären.

Aufbauend auf eine bodengeografische Charakterisierung des Untersuchungsgebiets wurden Einzelbaum-gewichtete Dauerversuchsflächen in benachbarten Beständen eingerichtet, einem Naturwald mit Dominanz von *Podocarpus falcatus* sowie Plantagen von *Cupressus lusitanica* und *Eucalyptus globulus*. Auf diesen Flächen wurde die Messung von Zeitreihen natürlicher Parameter mit Stabilisotopen-Markierungsexperimenten kombiniert (^{15}N in anorganischer Form, ^{34}S in Blattstreu).

Die bodengeografische Beschreibung des petrografisch homogenen Untersuchungsgebiets zeigte den dominierenden Einfluss von Klima und Relief auf die Bodeneigenschaften. Technische Vorarbeiten waren für die Anwendung des Isotopen-Tracers ^{34}S im Gelände erforderlich. Durch apparative Veränderungen im isotopen-massenspektrometrischen Messsystem - vor allem eine Tauchkühlfalle - konnte die für eine zuverlässige δ^{34}S-Bestimmung erforderliche Probenmenge um den Faktor sechs gesenkt werden.

Die Wasserdynamik im System Boden-Pflanze spiegelte Einflüsse des Wurzelsystems wider. *P. falcatus* hatte eine hohe Feinwurzelbiomasse bis unterhalb 1 m Tiefe. Wurzeln schienen aktiv zur Umverteilung von Bodenwasser beizutragen. Auf veränderte Bodenfeuchte reagierte diese Baumart stark, indem sie die Transpiration bei Trockenheit um den Faktor sechs senkte, was zusätzlich zu einem gleichmäßigeren Bodenmilieu beitrug. *P. falcatus* und *C. lusitanica* passten ihr Wurzelsystem trockeneren Bedingungen an, sowohl durch Erhöhung der Biomasse als auch durch räumliche Expansion, vor allem in tiefere Lagen. Die saisonale Anpassung von *E. globulus* war wesentlich schwächer ausgeprägt, was gleichermaßen für Feinwurzelbiomasse und Wasseraufnahmetiefe galt. Diese Baumart mit geringer Wurzelbiomasse nahm Wasser vor allem aus größeren Tiefen auf und erhöhte ihre Transpiration in der Trockenzeit auf das Fünffache.

Die Markierung von zwei Bodentiefen mit ^{15}N zeigte ein ähnliches Muster der Wurzelaktivität bei der Nährstoffaufnahme. Das oberflächlich dichte Wurzelwerk von *C. lusitanica* war effektiv bei der N-Aufnahme, schien aber auch das Bodenleben im Unterboden zu unterdrücken. Dies hatte ein geringeres Ausmaß von biologischen Umsetzungen zur Folge und begünstigte Nährstoffauswaschung. Im Naturwald deutete das Muster der phosphat-extrahierbaren N-Spezies in Verbindung mit niedrigen $\delta^{15}N$-Werten (natürliche Häufigkeit) auf geringe N-Verluste bei einem intensiven N-Umsatz in den oberen 60 cm hin, aus denen eine gleichmäßige Aufnahme von N durch *P. falcatus* zu beobachten war. *E. globulus* nahm N vorwiegend aus größerer Tiefe auf. Im Oberboden war eine bevorzugte N-Stabilisierung zu beobachten. Hohe $\delta^{15}N$-Werte (natürliche Häufigkeit) spiegelten vermutlich aktuelle Prozesse wider, was auf einen offenen Nährstoffkreislauf deutet. Ebenso wie die Baumarten verfolgten Pflanzen des Unterwuchses unterschiedliche Strategien bei der N-Aufnahme.

Der neuartige Ansatz der Markierung von Laubstreu mit ^{34}S erlaubte es, den S-Kreislauf im Boden, die Aufnahme durch Pflanzen und die pflanzeninterne Rezirkurlation zu verfolgen. Unterschiede bei der Streuzersetzung führten zu einem Konzentrationsanstieg des phosphat-extrahierbaren S mit der Tiefe bei *P. falcatus* und *C. lusitanica*, während unter *E. globulus* eine Abnahme zu beobachten war. Saisonale Effekte auf beide S-Pools waren minimal. Die Isotopenmarkierung zeigte eine rasche Einarbeitung der Streu in den Mineralboden des *E. globulus*-Bestandes. Schwefelauswaschung betraf vor allem die Streu von *C. lusitanica.* Die S-Aufnahme durch *P. falcatus* und *E. globulus* manifestierte sich in einem stetigen Anstieg der $\delta^{34}S$-Werte in den Blattproben. Im Laub von *C. lusitanica* hingegen sanken die $\delta^{34}S$-Werte nach der ersten Regenzeit, was als Hinweis auf Rezirkulation und eine verminderte Verfügbarkeit von tracerbürtigem S gewertet wurde.

Die Kombination der genannten Versuchsansätze ergab ein in sich stimmiges Bild von charakteristischen Eigenschaften der untersuchten Baumarten. *P. falcatus* zeichnete sich durch seinen ausgleichenden Einfluss auf die Lebensbedingungen im Boden aus und förderte damit das Bodenleben. *C. lusitanica* hingegen reduzierte die biologische Aktivität auf eine dünne, oberflächliche Lage, was erhöhte Nährstoffauswaschung mit sich brachte. *E. globulus* beschränkte sich in seiner unterirdischen Aktivität weitgehend auf den Unterboden. Trotz Vorteilen für den

Unterwuchs birgt dies auch die Gefahr verminderter Grundwasserneubildung und einer Verschlechterung der Bodenstruktur.

Extended Summary

Research problem: sustainable forest management in the tropics

Tropical montane forests are generally acknowledged for their wide range of environmental services (FAO 2003). They ensure hydrological stability of river basins by balancing discharge at low sediment yield and keep water quality high, they are known as biodiversity hotspots, and they are of global relevance in the budget of CO_2 and trace gases. And besides their cultural value, they can supply locals of low economic capacity with fuelwood, building materials, medicines and food. Nevertheless, the destruction and degradation of these ecosystems is progressing at high rates (FAO 2003). This is largely due to the demand of a growing population for land and the over-utilization of remaining forests by extracting timber, fuelwood and non-wood forest products.

To guarantee the benefits from tropical montane forests for the future, this resource needs to be managed in a sustainable manner, and degraded areas need to be rehabilitated. Sustainable forest management has to integrate the aspects production, conservation of nutrients, water, soil and biodiversity, as well as cultural qualities. This requires sound scientific knowledge about the state of these ecosystems, about ecological processes and about socio-economic and socio-cultural interference, both threats and potentials (FAO 2005).

The integration of plantation forestry appears imperative for sustainable forest management. It can practically mitigate the pressure on the remaining natural forests by satisfying the demand for timber and fuelwood, and it can help to rehabilitate degraded lands. However, most large-scale afforestation schemes rely entirely on a few fast-growing species, which are frequently exotic to these environments. This raises questions about their adaptation and long-term impact on the environment, which may be detrimental to soil and biodiversity. Yet in many cases scientific knowledge on the various aspects of this topics is still insufficient to provide a solid basis for practical recommendations.

The problems of forest over-utilization are exemplified by the situation in Ethiopia, where a long history of sedentary agriculture by a large population has led to comprehensive destruction of montane forests and concomitantly severe shortages of fuelwood and timber as well as soil erosion (Nyssen et al. 2004). Afforestation efforts with exotics species, mainly eucalypts, date back 100 years and are also popular among smallholders. Modern forest plantations encompass large schemes of several exotic species, mainly eucalypts, *Cupressus lusitanica* and pines, but indigenous species have more recently moved into the focus of interest. The dominance of homogeneous volcanic substrates and the systematic pattern of environmental settings in combination with a mosaic of land use systems make the Ethiopian highlands a suitable research area to work on both the effects of different forest types as well as those of ecological gradients.

Motivated by the wide knowledge gaps on the ecology of tropical montane forests and driven by the great interest from the Ethiopian side in a perspective of sustainable forestry, we commenced an interdisciplinary research project on forest ecology in the Central Ethiopia. In a holistic approach, we address aspects of ecosystem state and basic research on ecosystem dynamics in the context of silviculture and socio-economy. The work constituting this dissertation contributes a description of soils in the different geo-ecological zones of the study area as well as detailed studies on the dynamics of water and organically associated nutrients in different forest types.

Nutrient cycling and ecosystem sustainability

The conservative management of nutrients is one prerequisite for sustainable forestry, even more as losses of many nutrients may be irreversible. Once degraded, site rehabilitation is additionally impeded by the fact that nutrient replenishment through fertilization is rarely viable in tropical forests due to technical and economic constraints. To attain a conservative cycling of nutrients, net nutrient fluxes need to be known on the one hand for a rating of sustainability, which is tackled in our project by Yeshanew Ashagrie in form of a nutrient balance.

On the other hand, studies on nutrient availability and processes of nutrient cycling are required to identify potential leaks and internal degradation of the nutrient cycle. This knowledge is essential to finally adjust the system with the aim of an active and closed nutrient cycle. The internal cycling is particularly important with nutrients that strongly interact with the mineral phase or soil organic matter. Above all, this refers to the organically associated macro-nutrients nitrogen (N), phosphorus (P) and sulfur (S), which commonly occur in concentrations limiting to plant growth. Their chemical nature can also give insight into the dynamics of the associated soil organic matter, which to a large extent determines fertility of tropical soils. Unlike the rather immobile P, whose cycling is largely confined to the topsoil and vegetation (Jobbagy and Jackson 2001; Solomon et al. 2002), the cycling of N and S regularly extends into the atmosphere and the subsoil (Schroth et al. 1999). The intimate association of N and S with biological materials (Novak et al. 2003) in combination with their susceptibility to chemical transformations and leaching lends them qualities as proxies for ecosystem nutrient sustainability. Vegetation effects on the P and S status of the soils under study have been investigated on topsoil samples by Solomon et al. (2001; 2002; 2003). In the work for my dissertation, I aimed at describing and linking the dynamics of water, nitrogen (N) and sulfur (S) in the ecosystem as affected by different tree species.

Water dominates ecosystem fluxes in quantity, and it plays a most prominent role in the exchange of energy, nutrients and gas in the soil-vegetation-atmosphere system. As a polar solvent, it is essential in all kind of biological processes and living structures. It is also needed as a reactant in biological key processes like photosynthesis, and water availability greatly affects ecosystem nutrient cycling by determining the activity of plants and micro-organisms, including their physiological pathways.

Nitrogen and S are much more confined to ecosystem boundaries. The studies of their dynamics are somehow complementary, as both elements show a largely similar behaviour, but also important differences. Both elements are subject to high turnover in active biological structures such as proteins or enzymes and play a major part in metabolic key processes like photosynthesis. Both elements occur in several oxidation states, in organic and inorganic forms, interacting with the mineral phase. Frequently, organic forms play a major role in losses from the ecosystem. Both elements can be taken up by plants in several forms and are of high plant-internal mobility, facilitating the redistribution to current sinks. Nevertheless, the nutrient cycle of N is more open to the atmosphere under the given conditions of low air pollution than that of S, which cannot be extracted from the atmosphere on demand. Furthermore, inorganic S is subject to strong adsorption on sesqui-oxides, reducing its downward mobility in tropical soils.

These similarities and differences make N and S a good couple to study ecosystem sustainability. Experimental power is added by the occurrence of several stable isotopes, the ratios of which in natural samples can give direct clues on ecosystem sustainability (Högberg 1997). Isotope labelling techniques can be used to trace these elements through different ecosystem pools, which allows to elucidate gross internal cycling and processes involved in transformation and translocation.

Objectives

The general objectives of the interdisciplinary research project in Munessa Forest were to conduct a geo-ecological inventory of the region in the socio-economic context, to work out interactions between soil and vegetation, and to provide the comprehensive ecological and eco-physiological information needed to finally develop sustainable silvicultural systems.

The specific objectives for my work were:

- to characterize typical soils of the escarpment of the Main Ethiopian Rift Valley as a basis for ecological in-depth studies, facilitating the transferability of scientific findings (Study 1)
- to establish a stable-isotope methodology to study S dynamics of the soil-plant system *in situ* (Studies 2 & 5)
- to identify effects of the indigenous tree species *Podocarpus falcatus* and the widely-planted exotics *Cupressus lusitanica* and *Eucalyptus globulus* on the dynamics of water, N and S, including nutrient recycling from soil and leaf litter (Studies 3 - 5)

The regional context (Study 1)

All ecological experiments included in this dissertation were conducted in the Munessa-Shashemene Forest of the Central Ethiopian Rift Valley Lakes region. The study area with a forest cover of about 23000 ha comprises natural forests of different altitudinal belts, plantations of various tree species (mainly *C. lusitanica*, eucalypts, pines), agricultural plots and pasture land (Silvanova 1996).

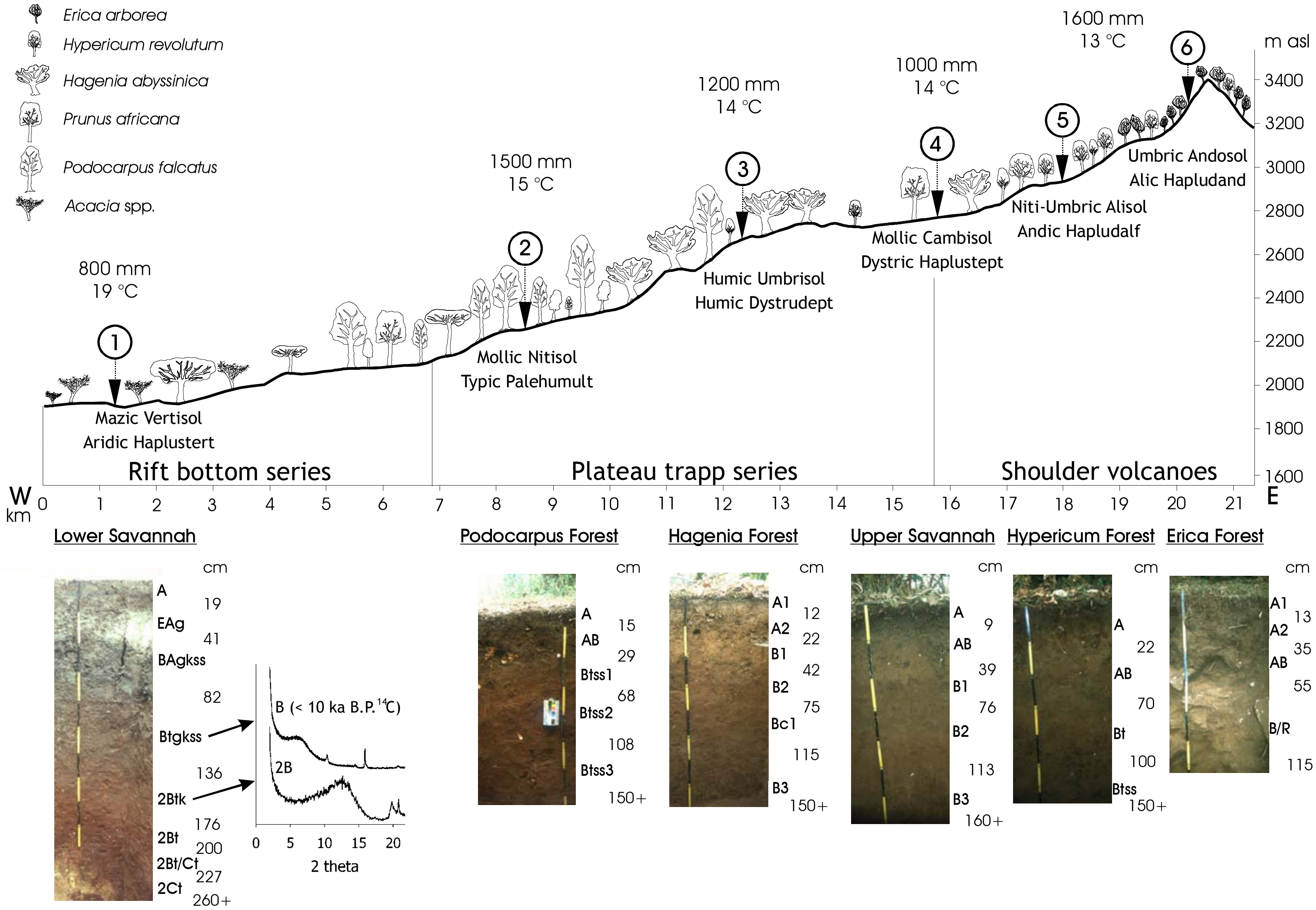

Fig. I: Geo-ecological transect through the study area with 6 soil profiles classified according to WRB and Soil Taxonomy. XRD spectra are included for two horizons of the lowermost, polygenetic profile (dominant clay minerals: B - smectite, 2B - kaolinite).

The geo-ecological characterization of a research area is imperative for the in-depth investigations on ecosystems or their components. Information about spatial heterogeneity and geo-ecological gradients facilitates the selection of appropriate, representative research sites and opens a way to extrapolate findings from small-scale experiments to adjacent environments. Although several studies on land use effects have been conducted in the region, a detailed description of soils including their classification had been missing. My work thus started with an investigation on the soil conditions under natural vegetation of six altitudinal belts.

The geomorphic setting of the study area is the Main Ethiopian Rift Valley, which stretches with a NNE trend all through Ethiopia (Benvenuti et al. 2002). The arid Rift bottom at 1600 m asl is occupied by the Ziway-Shalla lake basin with various lacustrine deposits resting on the volcanic bedrock, while the marginal volcanoes of the Rift shoulder reach more than 4200 m asl. Six profiles of the volcanic complex were sampled in the forest zone from 1900 m asl to 3200 m asl, covering a wide range of soil climates and vegetation types (Fig. I). These pedons were described in the field and characterized by standard procedures of soil chemistry and mineralogy.

Soils of the Rift bottom series at 1900 m asl were dominated by the influence of the level terrain, making rainy-season waterlogging a common phenomenon in the semi-arid *Acacia* woodlands. This water regime together with the accumulation of basic cations led to the formation of characteristic Mazic Vertisols / Aridic Haplusterts, according to the WRB (FAO et al. 1998) and Soil Taxonomy (Soil Survey Staff 2003) classification systems, respectively. Pedogenesis in this landscape unit appeared controlled by slope and also by climate history (Chalie and Gasse 2002), as in the sampled pedon smectitic horizons of Holocene origin were underlain by kaolinitic material from the more arid Late Pleistocene (Fig. I).

Kaolinite was dominant in the upper five, well-drained profiles of the transect, which exhibited a systematic transition of soil characteristics with climate and relief. Mollic Nitisols / Typic Palehumults with considerable accumulation of pedogenic oxides and a favourable soil structure were typical of the *P. falcatus* dominated forest at 2300 m asl with 1500 mm rainfall. In the *Hagenia abyssinica* dominated forest of the Rift shoulder (2600 m asl), soil structure was less well developed, base depletion was more progressed, and chlorites indicated high Al availability in these acidic soils (Humic Umbrisols / Humic Dystrudepts). Mollic Cambisols / Dystric Haplustepts were characteristic of the drier upper plain (2670 m asl), where less rainfall was also reflected in a lower degree of weathering. With rainfall increasing to about 1600 mm on the midslopes of the marginal volcanoes, clay illuvation and cation leaching were typical of the Niti-umbric Alisols / Andic Hapludalfs of the *Hypericum revolutum* forest around 2900 m asl. In the *Erica arborea* forest at 3200 m asl, influence of the parent material was stronger, and shallower profiles with rock fragments and a loamy texture were signs of less progressed pedogenesis in the sampled Umbric Andosol / alic Hapludand.

Soil carbon stocks increased with altitude from 147 to 362 Mg ha^{-1}. C/N ratios were similar along the transect, C/S ratios widened with increasing elevation from 56 to 99. Potential cation exchange capacity was generally high, but the effective positive charge was reduced with elevation by decreasing topsoil pH values. While the slopes showed neither signs of erosion nor sedimentation, the two profiles in level terrain (1 and 4) pointed towards in influence of Early Holocene volcanic activity reported for the region (Le Turdu et al. 1999).

Ecosystem dynamics: experimental approach

Based on the soil-geographic study, the mid-altitude, sub-humid *P. falcatus* forest belt was selected for the in-depth investigations on nutrient cycling. Homogeneous site conditions and the close neighbourhood of remnant natural forests and plantations provided an opportunity to work out species-specific characteristics, as well as differences between tree species. We established permanent experimental plots at 2280 m asl (7°26’ N 38°52’ E) in the degraded natural forest and nearby plantations of *C. lusitanica* and *E. globulus* within a distance of 1 km. In each forest type, three single-tree-centred plots (Fig. II) within a range of 200 m were equipped with instruments to measure ecosystem fluxes within the "single-tree influence circle” (Amiotti et al. 2000). The solution samples obtained by these equipment are dealt with in an ecosystem balance of the ongoing work by Yeshanew Ashagrie. The investigations of my dissertation are essentially based on tensiometer records and destructive sampling of soil and vegetation, meteorological data and sap flow measurements.

Fig. II: Permanent experimental plot in the *C. lusitanica* plantation, equipped with rain collectors, sap flow probes, litter collectors, litter lysimeters, 4 clusters of tensiometers and three clusters of suction cups, protected by fence.

Soil-plant-atmosphere water transfers were studied in an interdisciplinary manner, combining tensiometry, transpiration measurements, a quantitative description of the root system and $\delta^{18}O$ gradients in soil and xylem water. Nutrient dynamics of N and S were investigated on the same plots to finally obtain information on the linkage between these ecosystem cycles (Fig. III).

As a large proportion of these nutrients is rather inactive, soil was extracted with a neutral phosphate solution to obtain biologically available fractions with higher turnover than bulk N and S, thus primarily reflecting recent processes and responding sensitively to shifts in equilibria. In order to assess pool-internal cycling and to elucidate processes that lead to the patterns of the parameters accessible to classical chemistry, stable-isotope tracers (^{15}N and ^{34}S) were introduced into the ecosystem nutrient cycle. These tracer experiments on organically associated nutrients complemented each other, as they started in different ecosystem compartments: Inorganic ^{15}N labelling of topsoil and subsoil, respectively, and of the organic layer with ^{34}S-labelled litter opened an opportunity to relate the recycling from plant material to the translocation and transformation of a fraction of high initial availability.

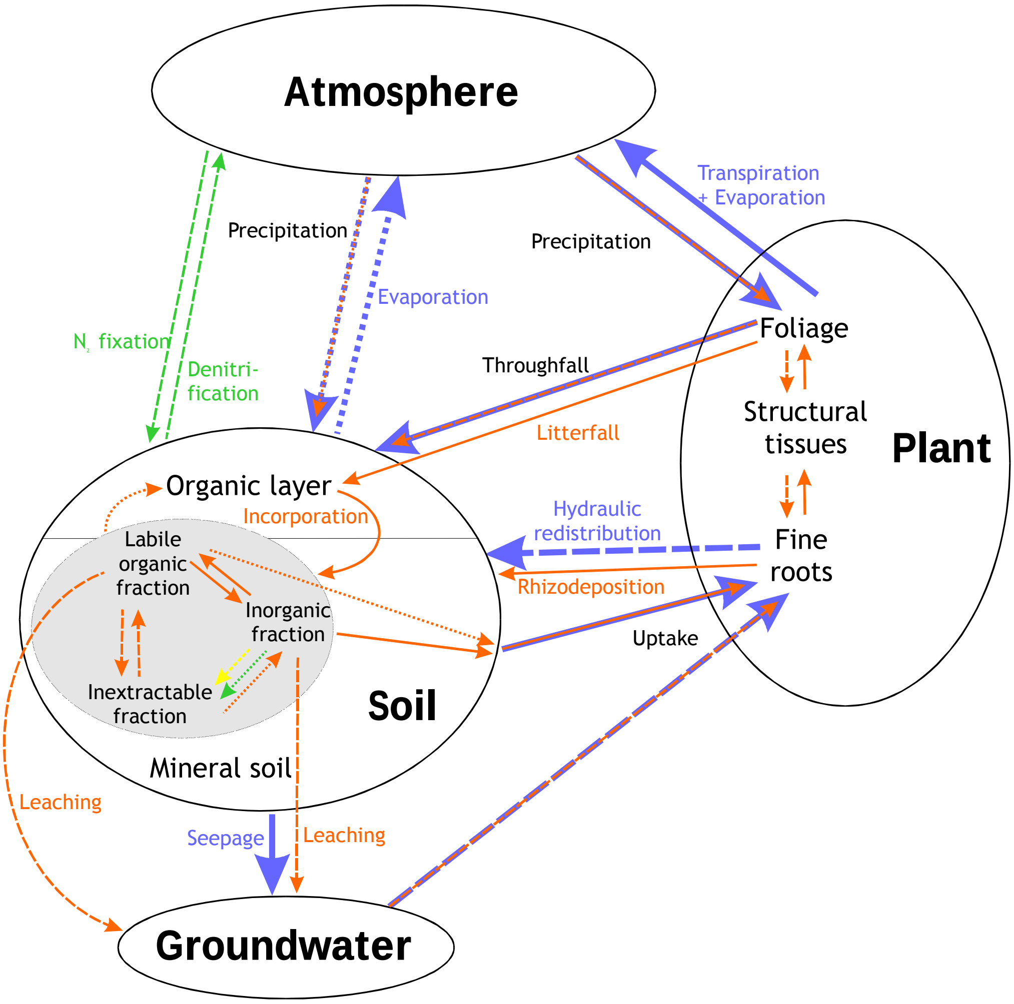

Fig. III: Simplified sketch of ecosystem dynamics of water, N and S in closed forests with low air pollution. Soil fraction technically defined (KH_2PO_4 extraction), with the "Inorganic fraction" comprising extractable SO_4^{2-}, NO_3^- and NH_4^+. Different fluxes by colour: blue – water; orange – N and S; green – N; yellow – S. Quantitative relevance by pattern: solid – major; dashed – in some cases major; dotted – minor.

Isotope labelling

For the S recycling experiment, $K_2{}^{34}SO_4$ generated from dry combustion of elemental ^{34}S was injected into the stems of individuals (Fig. IVa) from the respective trees growing distantly from the permanent plots, as described for ^{15}N by Horwath et al. (1992). One week after finishing the injection, the trees were wrapped in gas-tight plastic sheets (Fig. IVb) and treated with ethene for another week to induce senescence of the foliage (Abeles et al. 1992). Leaves that had not had fallen down due to abscission were harvested manually. After drying and quantification, this litter was evenly distributed on one plot of each forest type in July 2002 prior to the large rainy season. Similar amounts of litter were obtained (1.5 to 1.7 kg), yet with differing isotope enrichment (5.34 – 12.08 at%ex ^{34}S). The input of ^{34}S tracer with the litter was equivalent to 22, 9 and 13 mg m^{-2} under *C. lusitanica*, *P. falcatus* and *E. globulus*, respectively. For a better comparison of the forest types, the corrected $\delta^{34}S$ values ($\delta^{34}S^{*}$) were calculated by normalizing tracer enrichment to the input under *P. falcatus* (9 mg m^{-2}), termed $\delta^{34}S^{*}$.

Fig. IV: Litter labelling with ^{34}S: (a) Tracer injection into *E. globulus*; (b) *P. falcatus* wrapped for ethene gassing.

After the rainy season of 2002, a tracer solution of $^{15}NH_4Cl$ was injected around the trees in the centre of the plots at 120 points of an orthogonal grid, covering about 20 m² (1.0 kg ^{15}N ha^{-1}). Of each forest type, one plot was labelled beneath the litter layer (0 cm depth) and one at 40 cm depth; the third plot served as an unlabelled control.

In-situ measurements and sampling

Water-related parameters and roots

Meteorological data (rainfall, wind speed, temperature, vapour pressure deficit, solar radiation) and soil matric potentials (20, 50, 100, 200 cm depth) are included in this work, recorded on an hourly and weekly/biweekly basis, respectively, from May 2001 through October 2003. Transpiration was measured as xylem sap flow by the thermal heat dissipation method of Granier (1987) during several campaigns in different seasons covered by the hydrological record. Macroscopic architecture of the root systems was studied by excavation (Böhm 1979). Samples for live fine root biomass (LFR) in five layers were taken with a root auger at the end of the long dry season in April 2002 and during the main rainy season in August 2002. Roots were separated by washing and identified in the laboratory prior to quantification (Abate 2004). In order to elucidate the response in root activity to declining soil water availability, auger samples from 20, 50, 100 and 200 cm depth as well as non-green twigs from the crowns of the central trees of two plots each were collected on seven occasions from October 2002 to December 2002. These samples were immediately transferred into gas-tight containers for direct equilibration with 1 % CO_2 in Helium (Scrimgeour 1995).

Nutrient cycling

Sampling for the ^{34}S litter decomposition study included the organic layer and the upper 20 cm of the mineral soil, divided by 5 cm steps (3 cores), as well as composite leaf samples. The first samples were taken prior to the labelling on 11 July 2002, with four other sampling dates following until October 2003, the last three of which coincided with the sampling dates for the N study.

Sampling for the study on N dynamics was started on 01 Oct 2002 preceding the soil labelling. Soil samples were taken from 0 – 30 cm and 30 – 60 cm depth with an auger (4 points per plot) on 5 dates according to the seasonality of rainfall until October 2003. Composite leaf samples were collected on the same and additional dates from the central trees, understorey plants and neighbour trees. The material obtained for this experiment was in part used for the ^{34}S study as well.

Analytical methods

Soil extraction

Soil and organic layer were extracted with a neutral 0.1 M KH_2PO_4 solution to quantify and characterize the mineral and mineralizable nutrient pools of N and S (Kowalenko 1993). This fraction has been shown to be well defined, comprising mainly bacterially-derived N of labile protein-like structures (Matsumoto et al. 2000) and yielding best agreement with the potentially plant-available S (Watkinson and Kear 1996). A rather high salt concentration was chosen in order to obtain an approximately complete extraction (Kowalenko 1993), which is important in isotope tracer studies.

Chemical analyses

Bulk contents of C, N and S of soil and plant samples were measured automatically by elemental analysis (dry combustion). Total extractable N, NH_4^+ and NO_3^- of the extractable fraction were quantified using a flow injection analyzer; extractable organic N was calculated as the difference between the total extractable N and the inorganic species. Total extractable S was analyzed by inductively coupled plasma – atomic emission spectrometry (ICP-AES).

Isotope analyses

The $\delta^{18}O$ signature of soil and tree xylem water samples was determined by continuous-flow isotope ratio mass spectrometry (CF-IRMS) after direct equilibration with CO_2 (1 % CO_2 in Helium) in gas-tight sample containers (Scrimgeour 1995), as this method provides best precision for clay-rich samples (Kelln et al. 2001) at a good applicability in the field.

Nitrogen isotopic composition ($\delta^{15}N$) was analysed of the bulk samples as well as the extractable inorganic soil N. Prior to analysis, inorganic N was transferred into filter discs by micro-diffusion after reduction of NO_3^- with Devarda's alloy (Stark and Hart 1996). Nitrogen in plant samples, soil and filter discs was combusted to N_2 in an elemental analyzer and directly measured by CF-IRMS (EA-CF-IRMS).

The novel approach of *in-situ* ^{34}S labelling required major analytical improvements (Study 2). Whereas in principle EA-CF-IRMS is the method of choice for measuring the isotope signature of large sample sets, the common procedures are not suited for the direct determination of δ^{34}S after combustion of material with low S contents embedded in an organic matrix. This is on the one hand a consequence of the maximum amount of sample that can be combusted. On the other hand, the generated CO_2 in organic materials dilutes the SO_2 peak, reducing signal intensity in the IRMS to unreliable levels. Applicability of off-line sample preparation commonly employed for δ^{34}S analysis of soil samples (e. g. Giesemann et al. 1994; Novak et al. 2003) was restricted by the large sample set of c. 700 samples and low sample masses. The construction of an automatic, time-programmed cold-trapping device allowed the exact δ^{34}S determination on small samples largely irrespective of the embedding matrix (Fig. V). This was achieved by freezing the SO_2 separated from CO_2 by gas chromatography in a liquid-nitrogen bath with subsequent controlled thawing and peak dispersion. The implemented method proved to maintain the accuracy of established methods (± 0.3 ‰ δ^{34}S), while requiring only 15 % (in our case 6 µg) of the sample mass (Fig. VI). Plant and soil samples as well as the freeze-dried soil extracts were all analyzed in a CF-IRMS system involving this concentration-adjustment step after dry combustion.

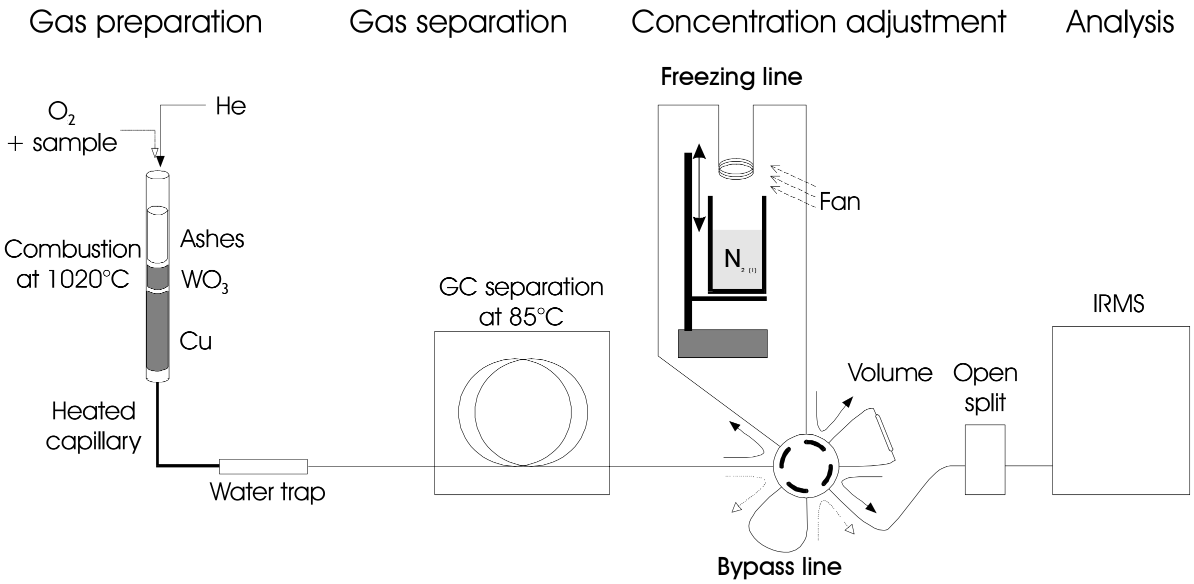

Fig. V: Sketch draw of the analytical setup for δ^{34}S analysis with concentration adjustment employing a liquid-nitrogen trap.

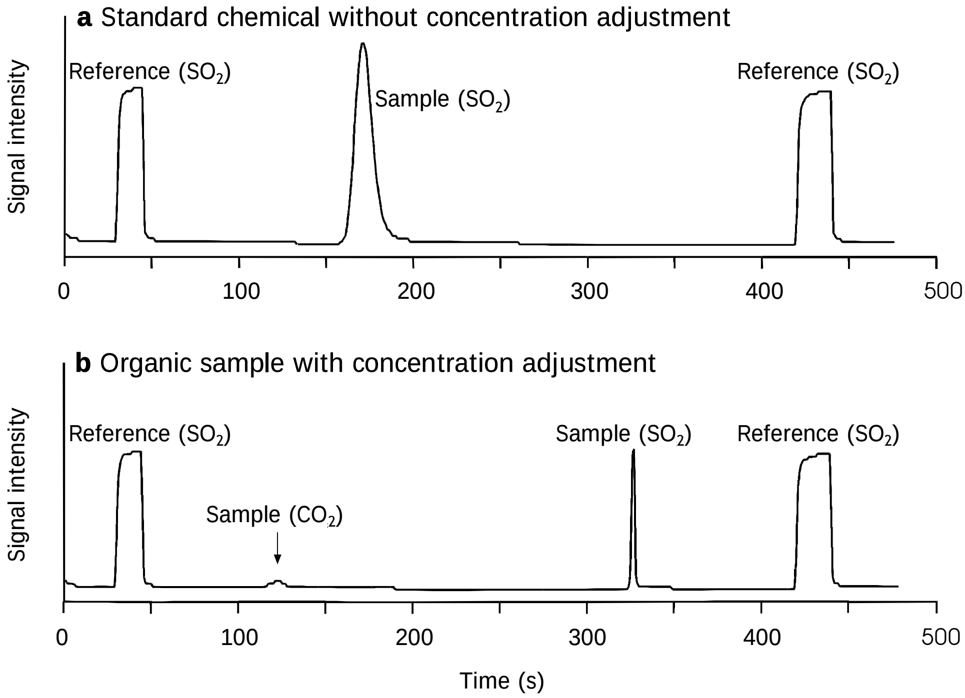

Fig. VI: Ion current of the IRMS detector (a) with standard procedure (43.7 µg S as Ag_2S, with buffer volume) and (b) employing concentration adjustment (6.2 µg S).

Water dynamics (Study 3)

The combination of a 2.5-years record of climate and soil water availability with natural-abundance $\delta^{18}O$ profiles of soil and xylem water, seasonal data on root distribution and transpiration yielded a comprehensive picture of soil-plant hydrology over temporal scales, linking soil water with physiological responses.

Although rainfall events were recorded throughout the year, seasonality of climate was pronounced, with about 75 % of the rain falling between May and September, and a strongly elevated vapour pressure deficit during the rest of the year. Soil water was close to saturation in the peak rainy season in July and August, but even in the dry season matric potential did not reach critical values (Fig. VII). Interannual variability of rainfall was considerable (c. 350 mm), with 2002 being an exceptionally dry year.

P. falcatus in the natural forest emerged as well adapted to varying soil moisture. After rainfall events, water was fast to reach greater depths in the well structured soil than in the other forests. Yet balanced conditions were quickly restored, presumably due to the strong positive response of transpiration to improved water availability (factor six), and hydraulic redistribution by the dense root system.

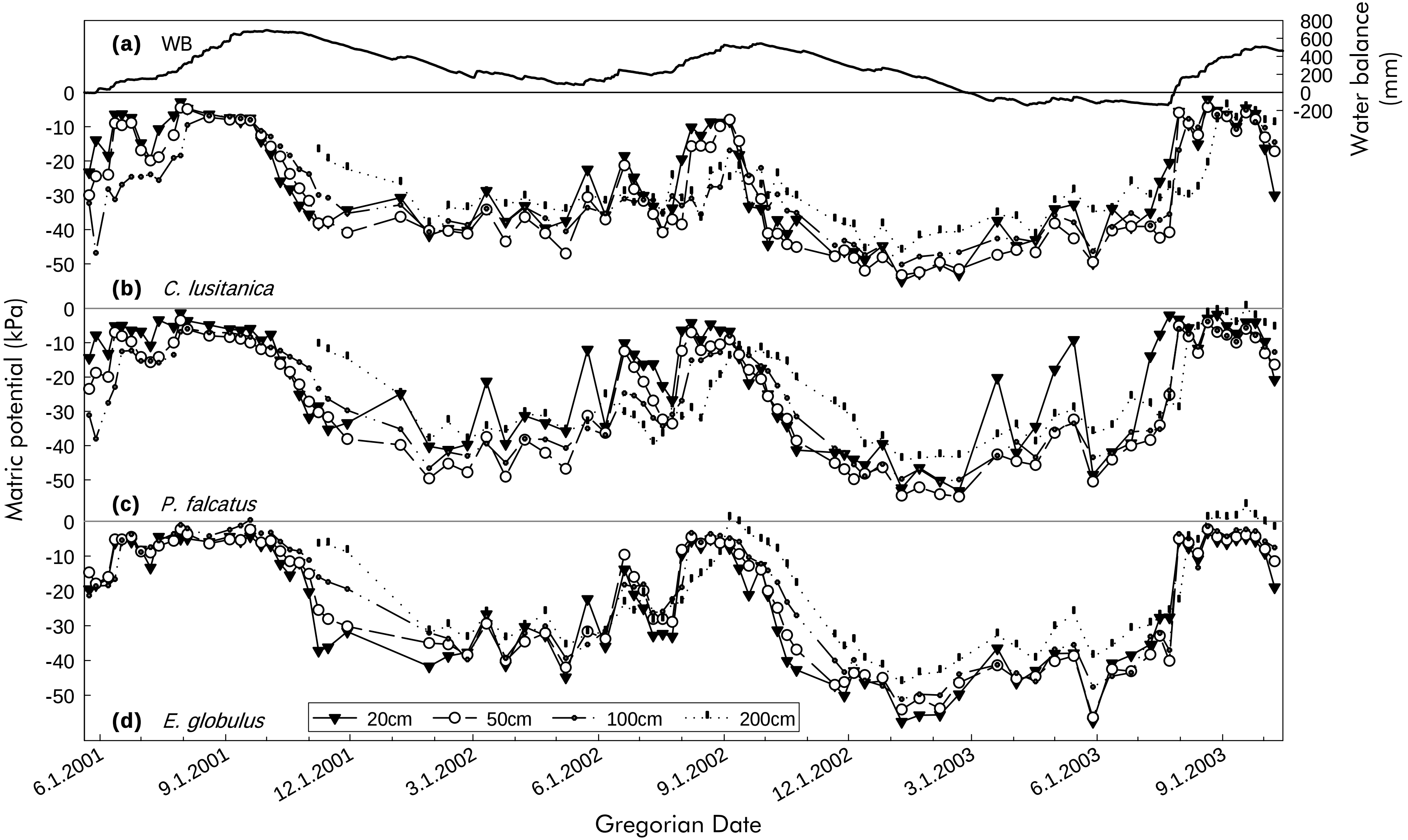

Fig. VII: Course of atmospheric water balance (a, rainfall - potential evapotranspiration) and matric potential at 20, 50, 100 and 200 cm soil depth under (b) *C. lusitanica*, (c) *P. falcatus* and (d) *E. globulus*.

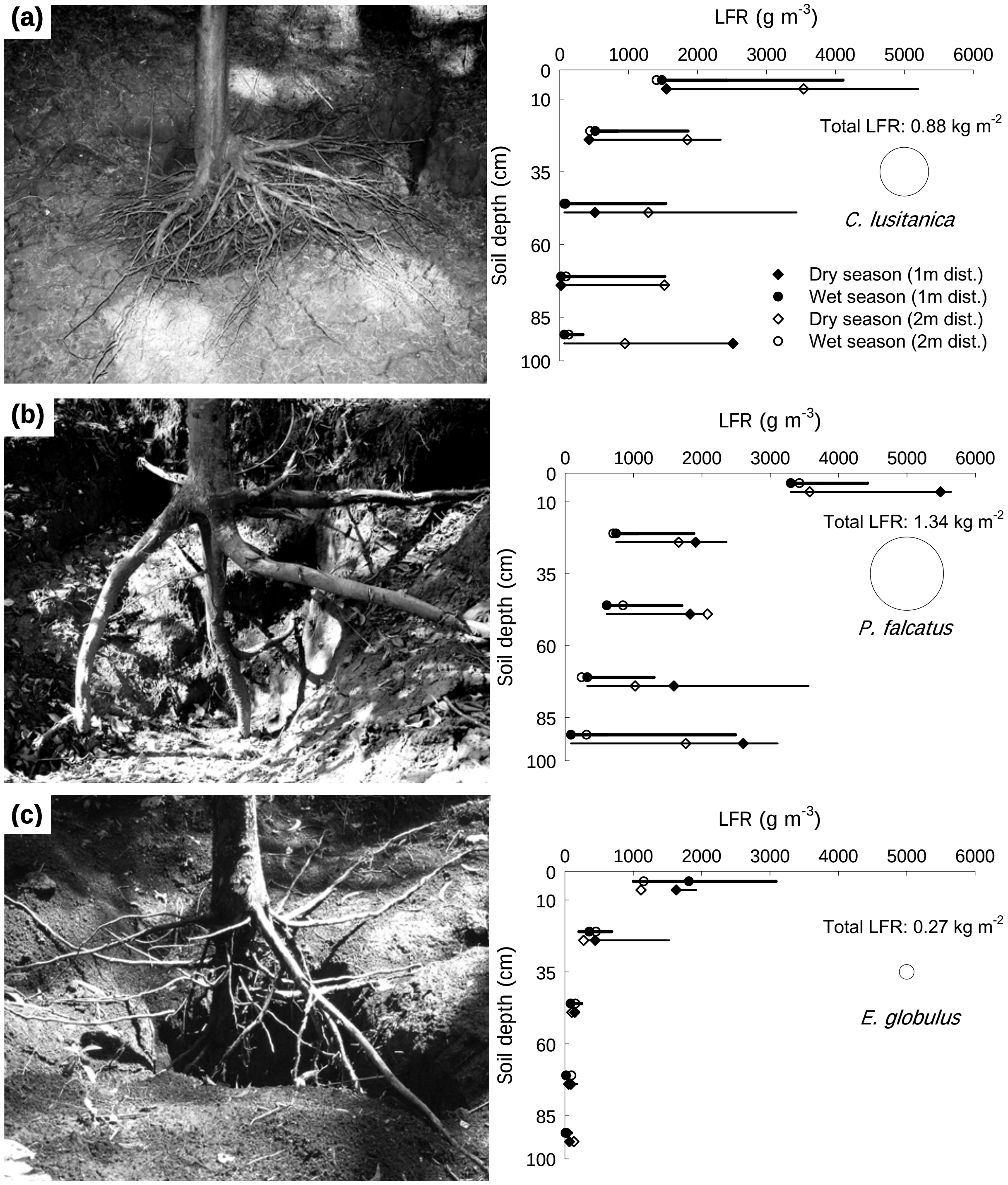

Fig. VIII: Root systems of the three species under study: (a) *C. lusitanica*; (b) *P. falcatus*; (c); *E. globulus*. Left row: root architecture by excavation. Right row: Live fine root biomass (LFR) down to 100 cm (bubbles) and spatial distribution for the wet and dry seasons (Median and range for 1 m distance from the bole, means for 2 m distance; n =3).

Life fine root biomass (LFR) of *P. falcatus* was high (1.34 kg m^{-2}) and extended into the subsoil (Fig. VIII). The hypothesis of redistribution processes to the topsoil was supported by the δ^{18}O data of soil and xylem water that indicated uplift of lighter groundwater at the onset of the dry season and by the minor gradient in soil water δ^{18}O. In the dry season, LFR of *P. falcatus* markedly increased, with roots expanding to deeper layers and greater distance. The plantation of *C. lusitanica* with its dense canopy and the root system concentrated in the topsoil had the consistently lowest soil moisture, which was particularly striking in a dry year (Fig. IX).

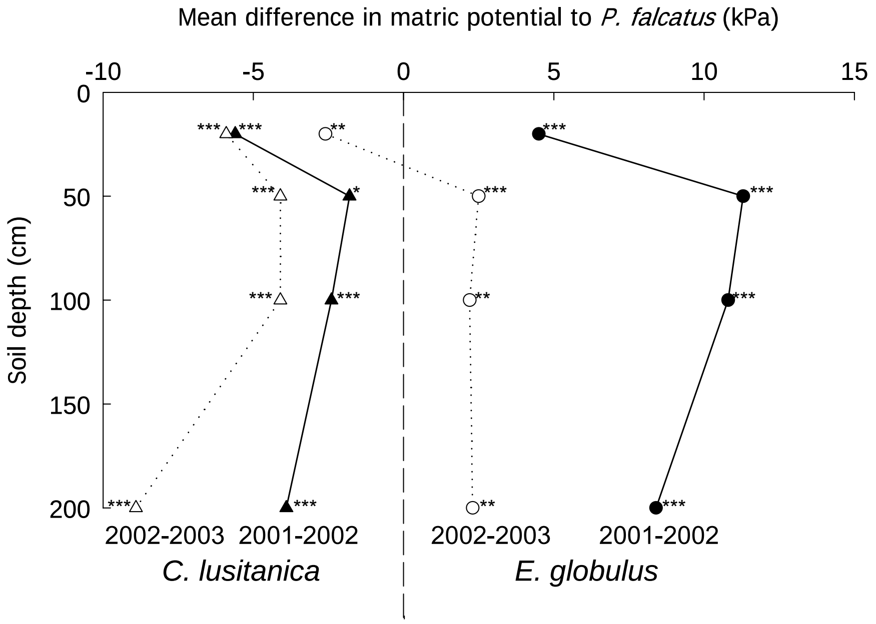

Fig. IX: Difference in soil matric potential relative to *P. falcatus* during the dry season of 2002 (Oct 01 to Feb 02) and 2003 (Sept 02 to Oct 03), respectively (t-test for differences from 0; *P < 0.05; **P < 0.01; ***P < 0.01).

Seasonality of LFR (0.88 kg m^{-2}) was similar to *P. falcatus*. Dry season transpiration was also reduced, but only by a factor of two. The seasonal root biomass allocation was mirrored by the δ^{18}O of soil and xylem water indicating a steady trend to water uptake from deeper layers at declining soil moisture. In the *E. globulus* plantation, soil was wettest throughout the year. Total LFR in the upper meter was just one fifth that of *P. falcatus*. In contrast to the other species, dry season transpiration was increased by a factor of five. This was facilitated by uptake of groundwater through the well-developed tap roots, as reflected in the δ^{18}O ratios showing a permanently deeper depth of water uptake. At the same time, seasonal shift in root allocation was minimal.

Plant effects on N cycling (Study 4)

The experiment on soil-plant N dynamics covered one complete seasonal cycle (13 months) from the end of the 2002 rainy season. Seasonality was clearly expressed in all soil N pools (bulk and inorganic N, phosphate-extractable organic N) and in the foliage of trees and understorey. This was reflected in concentrations and the stable isotope signature, both at natural abundance and after ^{15}N labelling.

Concentrations of bulk N were similar among the forest types in 30 – 60 cm soil depth, appearing widely unaffected by the conversion into plantations. Bulk N concentrations in the upper 30 cm tended to be lowest in the natural forest and highest in the plantation of *E. globulus*. At the same time, the natural forest had the highest amounts and proportions of extractable N in both layers (Table I), with strong correlations of bulk and extractable N indicating a large active N pool.

Table I: Contribution of N_{eo} and N_{ei} (= NH_4^+ + NO_3^-), respectively, to bulk N of two soil layers, including the ratio of these layers (SE in parenthesis, n = 112 for *C. lusitanica*, n = 110 for *P. falcatus*, n = 111 for *E. globulus*, total n = 333).

	C. lusitanica		*P. falcatus*		*E. globulus*		**All forests**	
	$\%N_{eo}$	$\%N_{ei}$	$\%N_{eo}$	$\%N_{ei}$	$\%N_{eo}$	$\%N_{ei}$	$\%N_{eo}$	$\%N_{ei}$
0 - 30 cm	4.56^{ab*} (0.33)	1.48^{AB} (0.09)	5.34^{a} (0.23)	1.77^{A} (0.09)	3.93^{b} (0.15)	1.44^{B} (0.06)	4.60 (0.15)	1.46 (0.09)
30 - 60 cm	5.38^{b} (0.31)	1.76 (0.12)	7.09^{a} (0.29)	1.93 (0.09)	5.52^{b} (0.31)	1.79 (0.12)	6.00 (0.18)	1.75 (0.07)
layer ratio lower/upper	1.18 (0.09)	1.19 (0.09)	1.33 (0.06)	1.09 (0.07)	1.41 (0.07)	1.24 (0.08)	1.30 (0.04)	1.20 (0.07)

[*] Different superscripts in one row indicate significant differences ($P < 0.05$) between the forest types for one parameter.

Minimum concentrations of extractable organic N were found at the end of the dry season in all three forest types, being stronger expressed in the topsoil. Inorganic N constituted constantly around 25 % of the total extractable N, with slightly lower values in the subsoil. The highest topsoil concentrations of bulk N under *E. globulus* in combination with the low extractability were a sign of preferential N stabilization, which was corroborated by a concomitant *in-situ* incubation study of ^{15}N-labelled litter (Johann 2004). Under *C. lusitanica,* high mobility of the different extractable N species was indicated by strong correlations between the topsoil and the subsoil, while an increase in the proportion of inorganic species with depth and the lack of correlations between bulk N and extractable N implied low biological N turnover in the subsoil.

Natural-abundance $\delta^{15}N$ in the *E. globulus* stand was higher by c. 3 ‰ $\delta^{15}N$ than under *P. falcatus*. Constant differences of soil and foliage pointed towards recent processes like leaching and denitrification instead of an effect inherited from the conversion phase. The effect of soil labelling with ^{15}N at two depths (0 and 40 cm) on the inorganic fraction exceeded the bulk fraction by roughly a factor of ten (Fig. X). The tracer signal was higher from the superficial label in all treatments, so was tracer recovery in the sampled ecosystem compartments, reaching c. 80 % under *C. lusitanica*, 50 % in the natural forest and 35 % in the *E. globulus* plantation.

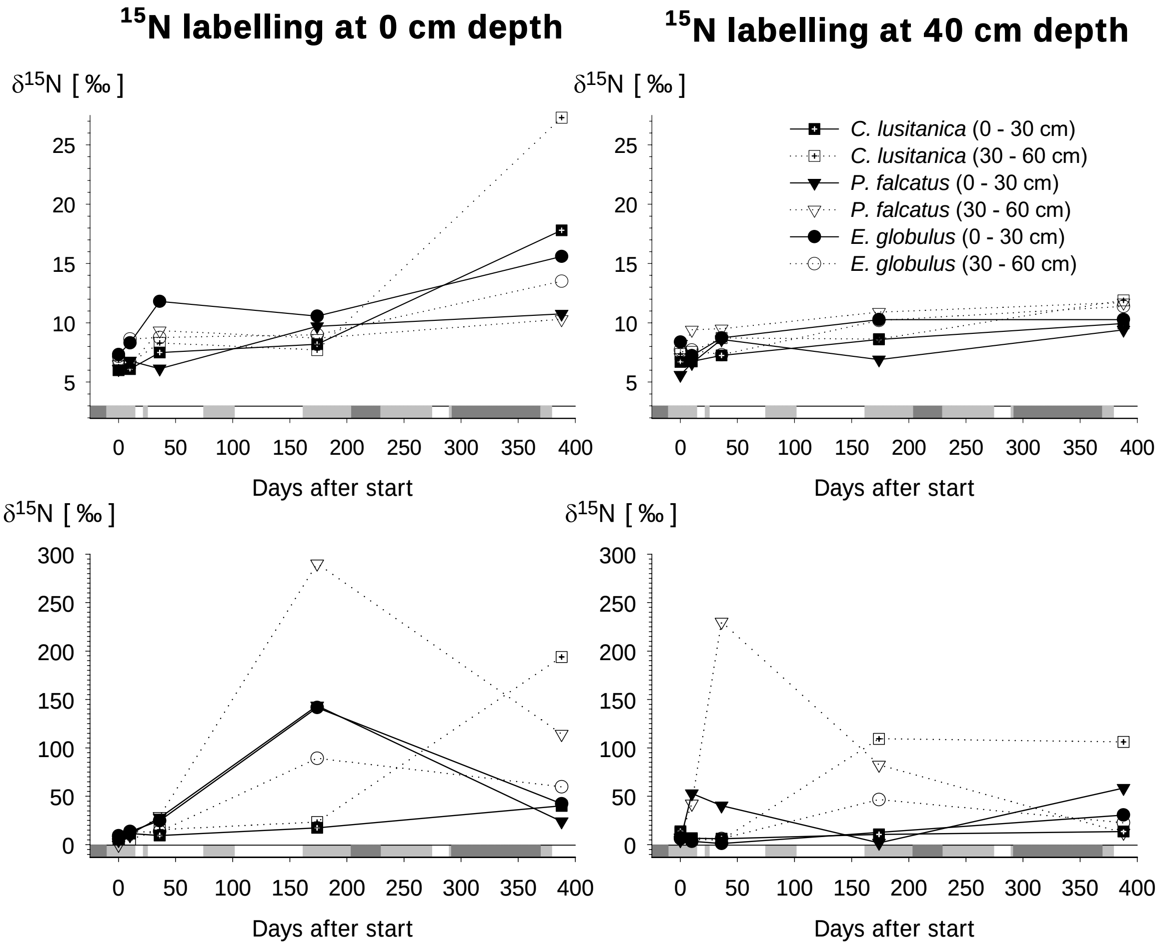

Fig. X: Time series of $\delta^{15}N$ values of bulk N (upper row) and extractable inorganic N (lower row) in two soil layers after tracer application to 0 (left) and 40 cm depth (right). Grey shading near the time axis indicates rains, with dark grey for periods of heavy and continuous rain.

Tracer dynamics in the soil were in line with the findings from the pool fractionation, indicating highest N turnover in the natural forest. In most cases, maximum $\delta^{15}N$ values were only achieved at the end of the study period of 13 months, which was attributed to plant uptake and later recirculation to fine roots and soil (Fig. XI).

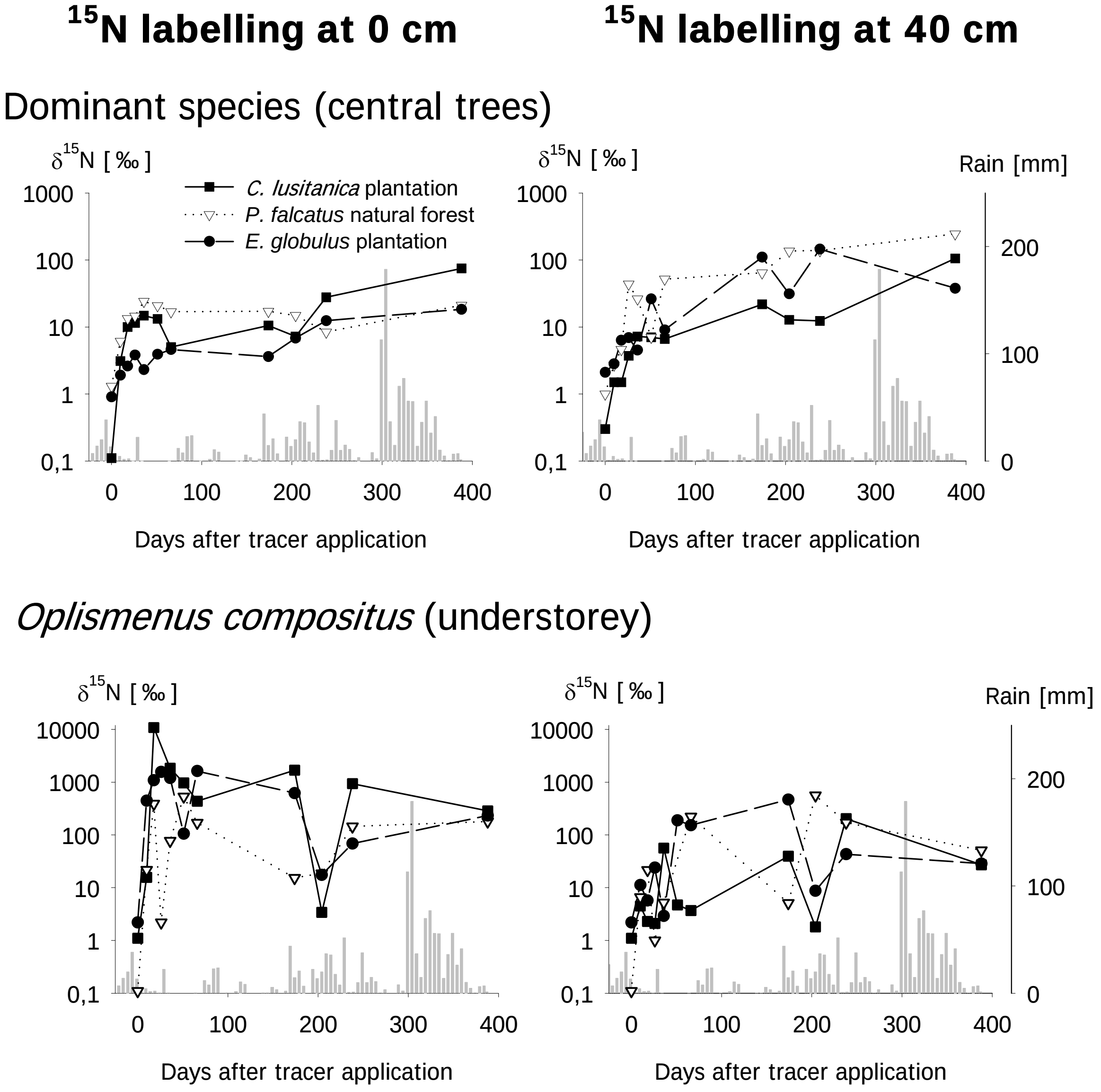

Fig. XI: Plant uptake of ^{15}N tracer applied to 0 and 40 cm soil depth for the respective dominant tree species (upper row) and the understorey grass *Oplismenus compositus* (lower row) in three forest types.

Plant uptake of the ^{15}N label was detected in leaves from the first sampling date. It reflected the root architecture, being fastest but largely confined to the topsoil for *C. lusitanica*. Roots of *P. falcatus* were active in both layers, while *E. globulus* mainly tapped the subsoil (Fig. XII). Uptake by the understorey grass *Oplismenus* *compositus* was concentrated in the topsoil and strongly influenced by competition of tree roots, forcing its roots to the surface in the plantation of *C. lusitanica*. In contrast, *Rubus steudneri* was very effective in subsoil N uptake, underlining the importance of species traits. Neighbouring trees of the dominant species showed the expected lower tracer accumulation with the same seasonal pattern as the central trees, thus supporting the experimental concept to study single-tree influences. The pioneer tree *Croton macrostachys* proved highly competitive in N uptake. Seasonality of tracer uptake was strongly expressed in leaves of the understorey, indicating a close coupling to the available soil N pool.

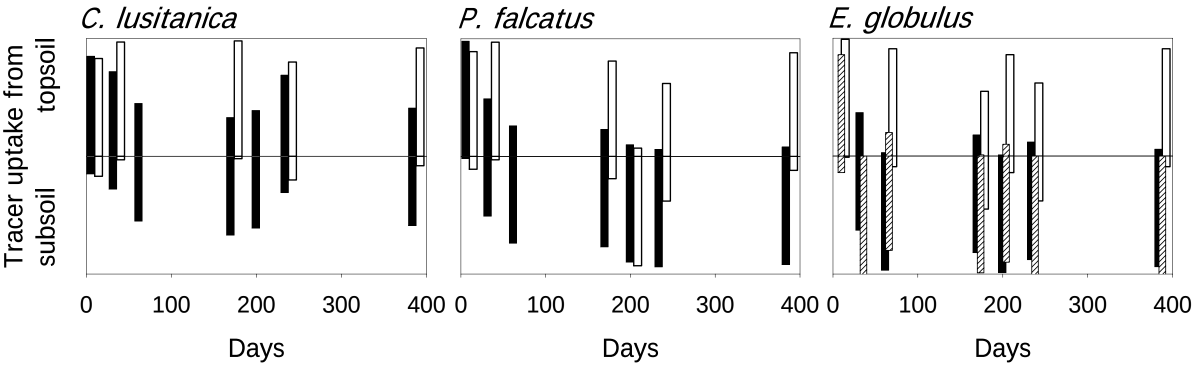

Fig. XII: Relative root activity of the dominant trees (filled bars) as well as understorey *Oplismenus compositus* (open bars) and Rubus *steudneri* (hatched bars, only under *E. globulus*) from 0 cm and 40 cm soil depth.

Recycling of S from litter (Study 5)

The novel approach of ^{34}S labelling was successfully employed to study S recycling from litter for 14 months, covering two main rainy seasons. Seasonality of both bulk and extractable soil S concentrations was very low. Bulk S concentration in the upper 15 cm of the mineral soil was significantly higher under *E. globulus* than in the other forest types (Fig. XIII), probably due to the rapid incorporation of the litter into the topsoil, which was also visible in soil fractions (Johann 2004). Differences between the forest types were striking for the profiles of extractable S. While concentrations were increasing with depth under *P. falcatus* and *C. lusitanica*, a significant decrease from high values in the organic layer was noticed under *E. globulus*, leading to a rather constant proportion of extractable S and indicating a decline in size of the available, biologically active pool with increasing depth within the upper 20 cm.

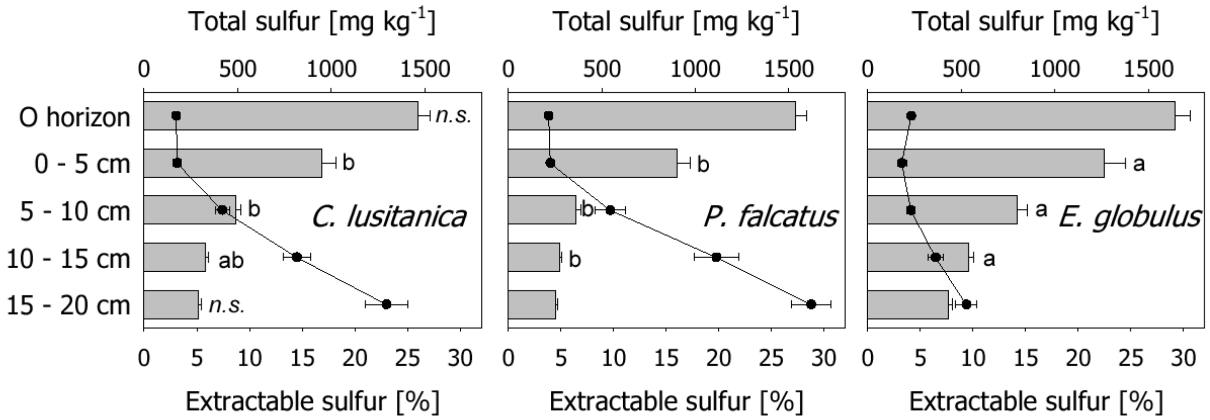

Fig. XIII: Sulfur in the topsoil in the three forest types: Total S (bars) and proportion of S extractable by KH_2PO_4 (lines). Error bars represent standard errors; significant differences by different letters (Tukey's HSD test, $P < 0.05$, $n = 15$; n.s.: not significant).

Natural-abundance $\delta^{34}S$ values were similar for all forest types, covering a range of 9 – 14 ‰ $\delta^{34}S$ with plant material slightly depleted. Application of ^{34}S labelled litter brought about a strong isotope signal (Fig. XIV). The litter mass calculated from isotope dilution after 120 days exceeded the mass determined gravimetrically by a factor of 2.2 (*P. falcatus*) to 3.0 (*C. lusitanica*), which was in the range to be expected from the effects decay and litterfall. The soil extracts generally yielded less variable patterns then the bulk soil, attributable to the greater chemical homogeneity of this fraction. The highest enrichment of c. 200 ‰ $\delta^{34}S$ occurred in the extracts from the organic layer of the *C. lusitanica* plantation. The corresponding $\delta^{34}S$ value of bulk S was only half, indicating a high susceptibility of S in litterfall to solute transport and leaching, which was also expressed in the small $\delta^{34}S$ increase in the mineral soil and in line with the high overestimation of the litter mass. The tracer enrichment as well as the ratio of $\delta^{34}S$ values for the two S fractions was much less under the other species. Under *E. globulus*, incorporation into soil and immobilization in the upper mineral soil were rapid. S turnover was highest under *P. falcatus*, visible from a high proportion of extractable S and its $\delta^{34}S$ values resembling those of the bulk fraction. The central trees from *P. falcatus* and *E. globulus* steadily accumulated S from the applied litter during the period of investigation (Fig. XV). In contrast, leaf $\delta^{34}S$ of *C. lusitanica* peaked after the first rainy season, indicating plant-internal recirculation and S losses from the available pool.

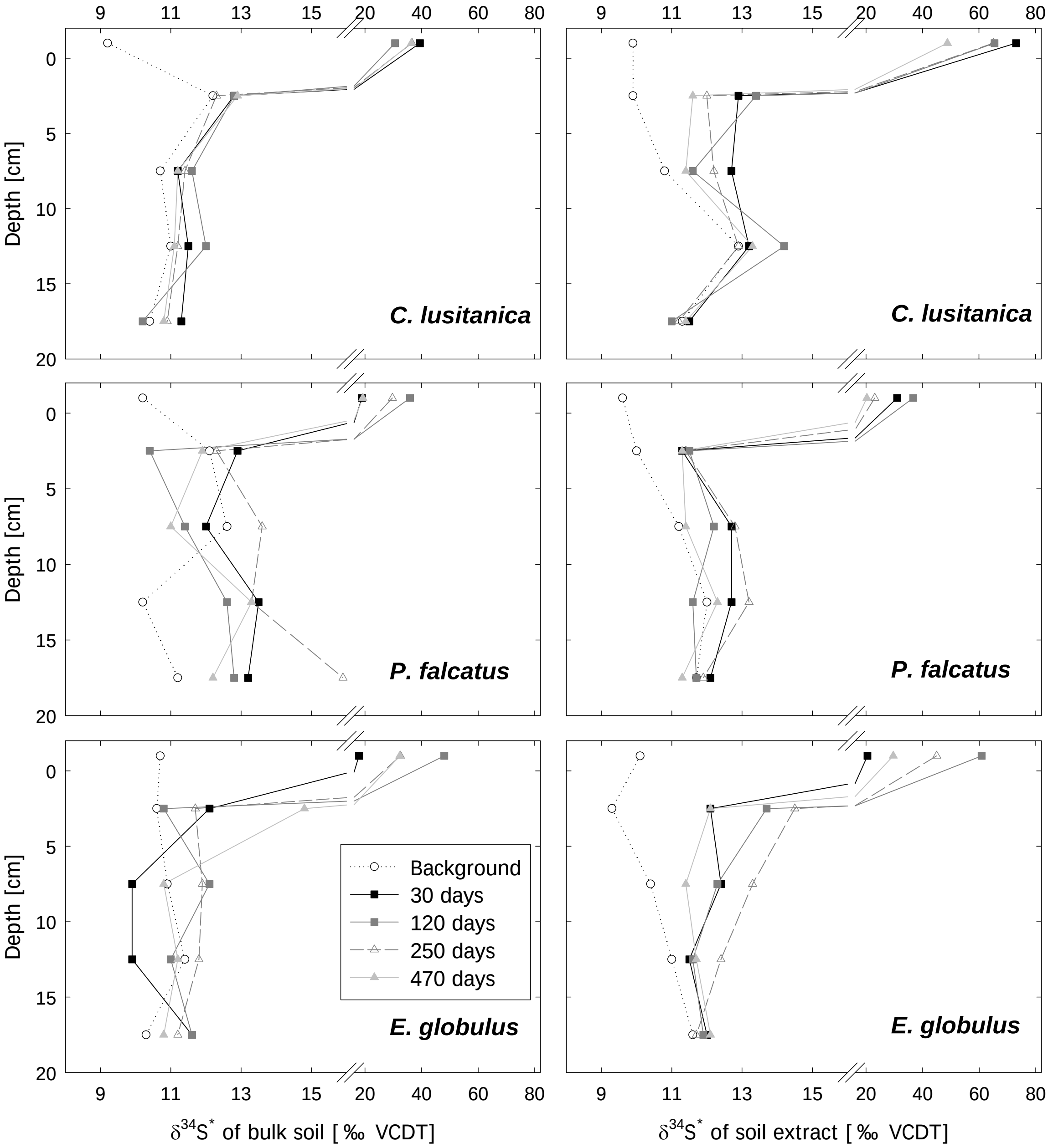

Fig. XIV: Time series of $\delta^{34}S$ depth profiles (normalized) after labelling in the respective forest stands (median values, n = 3): bulk soil (left column) and soil extracts (right column).

Uptake patterns of neighbouring trees and the understorey varied by species, regarding both extent and seasonality. *Rubus steudneri* took up less tracer than the shallow-rooted *Oplismenus compositus*. Uptake from deeper layers by this grass was visible from declining $\delta^{34}S$ values during the dry season. The herb with the relatively highest $\delta^{34}S$ enrichment, *Bothriocline schimperi* in the *E. globulus* stand, occurred only during the wet season and was thus able to rely on superficial resources.

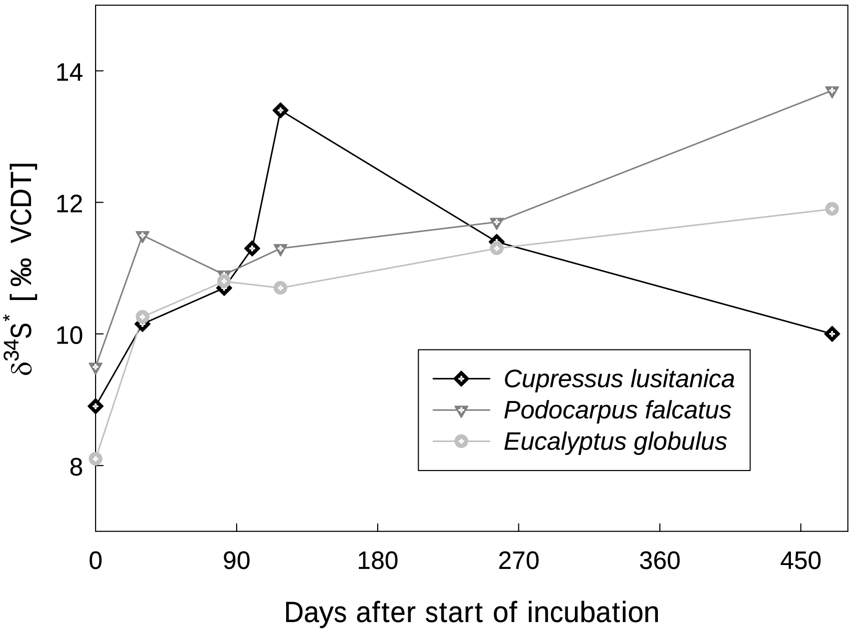

Fig. XV: Plant uptake of mineralized ^{34}S tracer: Time series of normalized $\delta^{34}S$ values for the respective species (central trees).

Synthesis on ecosystem dynamics of water, N and S

The plot studies yielded a broad picture of plant-affected ecosystem processes by linking the dynamics of water and soil N with the recycling of S from organic matter. The different approaches to water dynamics and the widely overlapping cycles of the two applied isotope tracers added to the validity of these findings. Distinct influences of tree species and understorey vegetation were revealed on all three aspects.

Besides the aboveground canopy structure, root distribution, the "belowground canopy", appeared to largely control ecosystem dynamics. Its influence on water uptake and redistribution, the pore system, competition in the topsoil and nutrient recovery from deeper layers has important consequences for sustainability. This concerns above all the understorey vegetation, which emerged to play an important part in buffering the high-turnover soil nutrient pools through rapid retention and recirculation, thereby contributing to nutrient conservation. Chemical characteristics of the litter and their specific effects on the microbial community also exert strong control on nutrient availability by facilitating leaching (under *C. lusitanica*) or internal sequestration (*E. globulus*).

The evidence from the comparative experiments presents the natural forest as a system with high biological activity and internal cycling. Dynamics of water and different nutrients appeared closely coupled with an intense feedback by *P. falcatus* on water availability. The higher diversity in species and plant functional types may be one reason for the strong nutrient cycling in the mineral soil (Hiremath and Ewel 2001). Leaf litter seemed to consist of rather stable structures, reflected in the accumulation of an organic layer and the lack of preferential S losses from freshly added litter. Still the large active fraction of nutrients may make this forest vulnerable to nutrient losses after disturbances.

The *C. lusitanica* plantation emerged as dominated by the shallow root system of these trees, which is capable to exploit the topsoil effectively, but weak in recovering nutrients from the subsoil. This superficial dominance together with the only moderate reduction in transpiration as a response to drier conditions also led to imbalanced moisture conditions. Moreover, it suppressed understorey plants and apparently confined microbial activity largely to the surface. In spite of the driest soil conditions, leaching losses are likely to be highest in this plantation due to the lack of biological transformation in the subsoil together with reduced root activity. This is aggravated by the low cover by understorey plants, which otherwise scavenge highly available nutrients. Chemical composition of the leaf litter appeared quite heterogeneous, as visible from the high availability of S from the fresh litter and the accumulation of an organic layer on the same time.

The deep root system of *E. globulus* brought about distinctly different effects on ecosystem dynamics. Water uptake from the subsoil made this species widely independent of seasonal soil water availability. Consequently, it was able to enhance transpiration at increased vapour pressure deficit - positive for production but aggravating dry-season groundwater shortage. Deep roots were the main players in nutrient uptake as well and may even recover nutrients from deep layers. The characteristic root activity leaves the topsoil largely to the understorey, promoting natural regeneration but also compaction of the less rooted upper soil and denitrification due to higher soil moisture. Incorporation of *E. globulus* litter into the mineral soil was rapid, and topsoil N cycling in part resembled the natural forest. However, the active fraction was much smaller and internal sequestration of N and S was observed, probably a chemical effect of litter quality on microbial transformations.

Conclusions and outlook

Methodological aspects

The characterization of the study area adds one fundamental element to the variety of geological, geographical and ecological work performed in the Rift Valley Lakes region, which helps to clear up a certain degree of confusion on soil description. Study 1 also strengthens the basis to extension of the findings from the plot studies, together with the spatial investigations by Alemu (1998) and by Rückamp and Abate (Rückamp 2004), but in contrast to these studies, further research must also include dynamic parameters to elucidate site-related differences in plant effects.

The technical contribution to $\delta^{34}S$ analysis may have high value for a wide range of scientists working in inorganic and organic geochemistry, in ecology and biology, as it provides a fast and precise procedure to determine $\delta^{34}S$ on small sample quantities in a wide range of matrices. This paves the way for a wider application of S isotope tracers with a high potential to extend knowledge on a nutrient that has been in the focus of environmental sciences for its role as a pollutant. Whereas this study has demonstrated the general applicability of S isotope tracers in the field, the four stable isotopes of this element (32, 33, 34, 36) open further chances to separate effects of natural fractionation from tracer signals and to identify different sources of S. While this is not possible for C and N, their close association with S may allow to extend evidence from the biogeochemical cycling of S to these elements (Novak et al. 2003).

The single-tree centred plot design allowed to identify specific effects of the three tree species in their typical environment. Plant uptake of the ^{15}N tracer unmistakably confirmed the assumption that this design puts the principal weight on the central trees, while it provides additional information on interactions with other vegetation elements. The similar tree size and comparable stocking density of the different forests were positive for its applicability. In my opinion, the single-tree centred plot design was also the best way to cope with the challenges of the floristic and structural diversity of the natural forest. The high and differing degree of degradation due to selective logging and grazing in virtually all forests of Ethiopia makes it highly problematic to implement an area-representative plot design, the final outcomes of which are likely to be of little transferability. Moreover, processes on plot scale can be expected to greatly vary, when the trees are established in plantations or mixed with other species, including natural regeneration. However, multiple plant traits will stay basically the same under different conditions and can thus be expected to explain a great share of variability (Eviner and Chapin 2003). Nevertheless, the constraints from the implemented design must be borne in mind, particularly in considerations of transpiration.

The comparative approach pursued allows to relate results and boosts transferability, as extensive literature is available on *E. globulus* and similar *Eucalyptus* species, while the other species have hardly been studied.

While the advantage of a multidisciplinary approach to ecology is commonsense, the benefits from integration of the seasonality of live fine root biomass and transpiration for all three plot studies deserve special emphasis.

Outlook on sustainable forest management

Cupressus lusitanica and *Eucalyptus globulus* are the prime tree species in Ethiopian forestry, but also of high global relevance. Moreover, the selected species can be taken as model trees for forestry systems, as they pursue greatly differing strategies in water and nutrient acquisition and investment, which finally result in different seasonal patterns, growth rates and timber quality.

There is trend to assign a greater role to indigenous species in forestry, which are well adapted to their habitat and valuable for conserving biodiversity. Besides its relevance for conserving the montane forests of Ethiopia, conservation aspects are vital for *P. falcatus* itself, which has already disappeared from wide regions (Negash 2003). While it cannot compete in growth with *E. globulus*, the rehabilitation of *P. falcatus* with its balancing influence on soil hydrology might bring other regional economic benefits like a constant flow of high-quality water (Legesse et al. 2004).

In my dissertation, I tried to integrate some traits of three tree species, yet these investigations need to be put into a larger context. This extends on the one hand to plant effects on other nutrients. One crucial point will be to relate the processes identified in this study to gross fluxes from the input-output balance of the same plots currently under way. But also the mechanisms involved need to be addressed in detail. Rhizodeposition is one sticking point for soil microbial activity (Grayston et al. 1997) with virtually no information on these forests. Another critical ecosystem process is nutrient uptake through mycorrhizal associations, which may finally be decisive for the survival of seedlings and trees (Michelsen 1992, 1993). The success of forest rehabilitation may thus depend on their presence, complicating the regeneration through seeds. On the other hand, mixing with other species may make stand more valuable concerning biodiversity and enhance their productivity. However, research is needed on the interaction between different species to attain these goals (Forrester et al. 2005). Natural regeneration of indigenous species (Feyera et al. 2002) is one key process to be promoted for sustainable forestry, which will also positively affect water and nutrient cycling.

Contributions to the included manuscripts

I contributed to the five studies of this thesis by preparing all manuscripts and artwork, putting the results in the scientific context and discussing their implications. All data were gathered in my own work, except the data on root architecture and live fine root biomass (Asferachew Abate) as well as the transpiration measurements (Masresha Fetene). The experiment on N dynamics was handled in the Diplomarbeit of Holger Fischer, who performed the laboratory analyses and most of the data processing, while I was responsible for the experimental design as well as the sampling. Holger Fischer and I conducted the experiment and its evaluation in close collaboration, which was the reason to somehow share the responsibility for primary authorship for the resulting manuscript. I also contributed significantly to the field work and supervision of the Diplomarbeit by Anne Johann, which is cited several times when discussing N and S dynamics.

The authors listed on the different manuscripts contributed as follows:

Study 1:

F. Fritzsche:	90 % (field work, laboratory analyses, manuscript preparation)
W. Zech:	5 % (experimental design, discussion of results)
G. Guggenberger:	5 % (discussion of results, comments to improve manuscript)

Study 2:

F. Fritzsche: 90 % (technical concept and implementation, analytical work, manuscript preparation)
M. Tichomirowa: 10 % (concept of manuscript, discussions on laboratory procedure, comments to improve manuscript)

Study 3:

F. Fritzsche: 65 % (experimental design, installation of instruments, tensiometry, meteorology, δ^{18}O analyses, manuscript preparation)
A. Abate: 14 % (root architecture, sampling and quantification of live fine root biomass, comments to improve manuscript)
M. Fetene: 10% (transpiration measurements, comments to improve manuscript)
E. Beck: 4 % (discussion of results, comments to improve manuscript)
S. Weise: 4 % (methodological aspects of δ^{18}O analyses, comments to improve manuscript)
G. Guggenberger: 3 % (discussions on experimental design, comments to improve manuscript)

Study 4:

H. Fischer: 45 % (field labelling, laboratory work, data analyses, comments to improve manuscript)
F. Fritzsche: 45 % (experimental design, field labelling, field sampling, supervision of analytical work and data analyses, manuscript preparation)
W. Zech: 4 % (discussions on experimental design, supervision of work performed by the primary author)
G. Guggenberger: 6 % (discussions on experimental design, comments to improve manuscript)

Study 5:

F. Fritzsche: 85 % (experimental design, field work, analytical work, manuscript preparation)

D. Solomon: 5 % (discussions on experimental design, comments to improve manuscript)

M. Tichomirowa: 5 % (contributions to laboratory work, comments to improve manuscript)

G. Guggenberger: 5 % (discussions on experimental design, comments to improve manuscript)

References

Abate A (2004) Biomass and nutrient studies of selected tree species of natural and plantation forests: Implications for a sustainable management of the Munessa-Shashemene Forest, Ethiopia. PhD dissertation. Faculty of Biology, Chemistry and Geosciences. University of Bayreuth, Bayreuth, Germany, 163 p

Abeles FB, Morgan PW, Saltweit MEJ (1992) Ethylene in plant biology, 2nd edn. Academic Press, New York

Alemu B (1998) Spatial study of soil nutrient status after natural forest conversion to plantation and secondary forests at Munessa Montane Forest, Ethiopia. M.Sc. Thesis. Swedish University of Agricultural Sciences, Debre Zeit, 77 p

Amiotti NM, Zalba P, Sanchez LF, Peinemann N (2000) The impact of single trees on properties of loess-derived grassland soils in Argentina. Ecol 81:3283-3290

Benvenuti M, Carnicelli S, Belluomini G, Dainelli N, Di Grazia S, Ferrari GA, Iasio C, Sagri M, Ventra D, Atnafu B, Kebede S (2002) The Ziway-Shala lake basin (Main Ethiopian Rift, Ethiopia): a revision of basin evolution with special reference to the Late Quaternary. J Afr Earth Sci 35:247-269

Böhm W (1979) Methods of studying root systems. Springer, Berlin, Germany

Chalie F, Gasse F (2002) Late Glacial-Holocene diatom record of water chemistry and lake level change from the tropical East African Rift Lake Abiyata (Ethiopia). Palaeogeogr Palaeocl 187:259-283

Eviner VT, Chapin FS (2003) Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. Annu Rev Ecol Evol S 34:455-485

FAO, ISRIC, ISSS (1998) World reference base for soil resources. Food and Agriculture Organization of the United Nations, Rome, Italy

FAO (2003) State of the world's forests, 2003. Food and Agriculture Organization of the United Nations, Rome

FAO (2005) State of the world's forests, 2005. Food and Agriculture Organization of the United Nations, Rome, Italy

Feyera S, Beck E, Lüttge U (2002) Exotic trees as nurse-trees for the regeneration of natural tropical forests. Trees-Struct Funct 16:245-249

Forrester DI, Bauhus J, Cowie A (2005) On the success and failure of mixed-species tree plantations: lessons learned from a model system of *Eucalyptus globulus* and *Acacia mearnsii*. For Ecol Manage 209:147-155

Giesemann A, Jäger HJ, Norman AL, Krouse HR, Brand WA (1994) On-line sulfur-isotope determination using an elemental analyzer coupled to a mass spectrometer. Anal Chem 66:2816-2819

Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol 3:309-320

Grayston SJ, Vaughan D, Jones D (1997) Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. Appl Soil Ecol 5:29-56

Hiremath AJ, Ewel JJ (2001) Ecosystem nutrient use efficiency, productivity, and nutrient accrual in model tropical communities. Ecosystems 4:669-682

Högberg P (1997) ^{15}N natural abundance in soil-plant systems. New Phytol 137:179-203

Horwath WR, Paul EA, Pregitzer KS (1992) Injection of ^{15}N into trees to study nitrogen cycling in soil. Soil Sci Soc Am J 56:316-319

Jobbagy EG, Jackson RB (2001) The distribution of soil nutrients with depth: global patterns and the imprint of plants. Biogeochemistry 53:51-77

Johann AC (2004) *In-situ*-Inkubation ^{15}N^{34}S-markierter Zuckerrohrstreu in Waldbeständen entlang eines Höhentransekts im äthiopischen Hochland. Diplomarbeit. Institute of Soil Science and Soil Geography. University of Bayreuth, Bayreuth, Germany, 145 p

Kelln CJ, Wassenaar LI, Hendry MJ (2001) Stable isotopes (δ^{18}O, δ^{2}H) of pore water in clay-rich aquitards: a comparison of measurement techniques. Ground Water Monit R 21:108-116

Kowalenko CG (1993) Extraction of available sulfur. In: Carter MR (ed) Soil sampling and methods of soil analysis. Lewis Publishers, Boca Raton, FL, pp 65-74

Le Turdu C, Tiercelin JJ, Gibert E, Travi Y, Lezzar KE, Richert JP, Massault M, Gasse F, Bonnefille R, Decobert M, Gensous B, Jeudy V, Tamrat E, Mohammed MU, Martens K, Atnafu B, Chernet T, Williamson D, Taieb M (1999) The Ziway-Shala lake basin system, Main Ethiopian Rift: influence of volcanism, tectonics, and climatic forcing on basin formation and sedimentation. Palaeogeogr Palaeocl 150:135-177

Legesse D, Vallet-Coulomb C, Gasse F (2004) Analysis of the hydrological response of a tropical terminal lake, Lake Abiyata (Main Ethiopian Rift Valley) to changes in climate and human activities. Hydrol Process 18:487-504

Matsumoto S, Ae N, Yamagata M (2000) Extraction of mineralizable organic nitrogen from soils by a neutral phosphate buffer solution. Soil Biol Biochem 32:1293-1299

Michelsen A (1992) Mycorrhiza and root nodulation in tree seedlings from 5 nurseries in Ethiopia and Somalia. For Ecol Manage 48:335-344

Michelsen A (1993) Growth improvement of Ethiopian acacias by addition of vesicular-arbuscular mycorrhizal fungi or roots of native plants to nonsterile nursery soil. For Ecol Manage 59:193-206

Negash L (2003) In situ fertility decline and provenance differences in the East African Yellow Wood (*Podocarpus falcatus*) measured through in vitro seed germination. For Ecol Manage 174:127-138

Novak M, Buzek F, Harrison AF, Prechova E, Jackova I, Fottova D (2003) Similarity between C, N and S stable isotope profiles in European spruce forest soils: implications for the use of δ^{34}S as a tracer. Appl Geochem 18:765-779

Nyssen J, Poesen J, Moeyersons J, Deckers J, Haile M, Lang A (2004) Human impact on the environment in the Ethiopian and Eritrean highlands - a state of the art. Earth-Sci Rev 64:273-320

Rückamp D (2004) Rasterbasierte Untersuchung von Zusammenhängen zwischen Böden und Vegetation im Umfeld des Munessa-Waldes (Äthiopien). Diploma. Institute of Soil Science and Soil Geography. University of Bayreuth, Bayreuth, Germany, 132 p

Schroth G, da Silva LF, Seixas R, Teixeira WG, Macedo JLV, Zech W (1999) Subsoil accumulation of mineral nitrogen under polyculture and monoculture plantations, fallow and primary forest in a ferralitic Amazonian upland soil. Agric Ecosyst Environ 75:109-120

Scrimgeour CM (1995) Measurement of plant and soil water isotope composition by direct equilibration methods. J Hydrol 172:261-274

Silvanova (1996) Enterprise formations of the Munessa-Shashemene State Forestry Project. Oromia Bureau of Agriculture Development, Addis Ababa, Ethiopia

Soil Survey Staff (2003) Keys to Soil Taxonomy, Ninth edn. United States Department of Agriculture, Natural Resources Service, Washington, USA

Solomon D, Lehmann J, Tekalign M, Fritzsche F, Zech W (2001) Sulfur fractions in particle-size separates of the sub-humid Ethiopian highlands as influenced by land use changes. Geoderma 102:41-59

Solomon D, Lehmann J, Mamo T, Fritzsche F, Zech W (2002) Phosphorus forms and dynamics as influenced by land use changes in the sub-humid Ethiopian highlands. Geoderma 105:21-48

Solomon D, Lehmann J, Martinez CE (2003) Sulfur K-edge XANES spectroscopy as a tool for understanding sulfur dynamics in soil organic matter. Soil Sci Soc Am J 67:1721-1731

Stark JM, Hart SC (1996) Diffusion technique for preparing salt solutions, Kjeldahl digests, and persulfate digests for nitrogen-15 analysis. Soil Sci Soc Am J 60:1846-1855

Watkinson JH, Kear MJ (1996) Sulfate and mineralisable organic sulfur in pastoral soils of New Zealand. II. A soil test for mineralisable organic sulfur. Aust J Soil Res 34:405-412

General introduction

Research Background

The destruction of tropical lowland forests, above all in the Amazon has been an issue of great public interest for some two decades, whereas other areas have come into the spotlight only later and to a far lesser extent. This holds particularly true for tropical highland forests, which frequently appear on maps only as narrow fringes in marginal regions - the importance of which is only becoming clear to the general public, when deforestation leads to devastating runoff peaks flooding densely populated areas. As tropical montane forests grow in a highly vulnerable environment and as they are vanishing at an alarming rate, they have emerged more recently as a matter of particular interest in scientific research and land use planning.

However, runoff regulation is only one important function of tropical montane forests (Bruijnzeel and Proctor 1995; Bonell and Molicova 2003). They also stabilise slopes and help to conserve soil and nutrients, water quality and biodiversity (Myers et al. 2000). And sustainable forest utilization can yield direct economic benefits from timber, non-wood forest products, eco-tourism or carbon emissions accounting according to the Kyoto Protocol, which may make it on balance the most profitable land use in marginal regions (Crook and Clapp 1998; Reddy and Price 1999; Jagger and Pender 2003).

Protection of forests is a complex issue in countries where a rural structure and poverty drive people to encroach more and more marginal environments. Ethiopian forests, for instance, have reportedly declined from over 30 % at the end 19th century to an actual cover of less than 3 % (Environmental Protection Agency 1998). With an estimated 83 % of rural population (FAO 2003), fuelwood is still the outstanding energy source, and the large majority of houses for the growing population are constructed of wood. In fact, Ethiopia is the largest consumer of fuelwood in Africa (FAO 2003). The high pressure on the remaining forest resources can only be countered by strict conservation measures (Crook and Clapp 1998), backed by a policy to increase awareness, economic incentives (Barbier and Burgess 2001) and, practically most important, by plantation forestry to secure the supply (Cairns and Meganck 1994; Bawa and Seidler 1998).

Yet plantations require careful species selection and silvicultural management (Kanowski et al. 2005), in order to avoid negative effects on the biogeochemical equilibrium (Montagnini and Porras 1998; Binkley and Resh 1999) and to retain an option to rehabilitate natural vegetation (Michelsen et al. 1996; Teketay 1997; Carnevale and Montagnini 2002). Moreover has to be borne in mind that traditional forest utilization goes well beyond timber and fuelwood extraction (e. g. Girma 1998; Geldenhuys 2004). People around the Munessa Forest, for instance, keep bees in the forest, and they appreciate the presence of climbers used as ropes and the medicinal agents of e. g. *Hagenia abyssinica* or *Prunus africana*.

The Munessa Forest as a study area

The Munessa-Shashemene Forest is located between 1900 m and 3200 m asl at the eastern escarpment of the Central Ethiopian Rift Valley and covers an area of 23000 ha (Silvanova 1996). It comprises large remnant natural forests and plantations of *Cupressus lusitanica*, eucalypts and pines established in the lower parts up to 2600 m asl (Chaffey 1980) starting from the 1970s. The neighbourhood of different forest types and the homogeneous site conditions of the volcanic bedrock make this area ideal for the identification of site-vegetation interactions.

Scientific work can build on a number of investigations in the region, starting from geology and geohistory (Le Turdu et al. 1999; Benvenuti et al. 2002; Chalie and Gasse 2002; Hailemichael et al. 2002; Legesse et al. 2002), which include the hydrological impacts of land use change (Chernet et al. 2001; Legesse et al. 2004). The effects of land use changes were also in the focus of studies on soil quality (Alemu 1998; Eshetu and Högberg 2000a; Solomon et al. 2001; Solomon et al. 2002a; Solomon et al. 2002b; Solomon et al. 2002c; Ashagrie et al. 2003; Solomon et al. 2003; Lemenih et al. 2004b; Ashagrie et al. 2005; Lemenih et al. 2005; Solomon et al. 2005), while other investigations concentrated on natural soil conditions (Lundgren 1971; Lemenih and Itanna 2004). Physiologic characteristics of different forest trees have been described (Lüttge et al. 2003; Fetene and Beck 2004), as well as their biomass allocation (Abate 2004) and growth performance (Teshome and Petty 2000). Data on vegetation (Lundgren 1971; Chaffey 1980; Abate 2004), vegetation changes (Eshetu and Högberg 2000b) and regeneration of indigenous plants are available (Teketay and Granstrom 1995; Yirdaw 2001; Feyera et al. 2002; Senbeta et al. 2002; Yirdaw and Leinonen 2002; Lemenih et al. 2004a; Yirdaw and Luukkanen 2004), and research has been started on functional parameters of trees, by comparing leaf litter quality (Gindaba et al. 2004) and characterizing mycorrhizal communities(Wubet et al. 2003; Wubet et al. 2004).

All these studies provide a valuable foundation for further ecological research. However, the lack of a detailed description and classification of the soils complicates the identification of appropriate locations as well as a judgement about their implications at landscape level. Equally important, process-oriented studies on the ecosystem dynamics are missing so far.

Research objectives and experimental approach

The lack of integrated data on ecosystem processes was the motivation for commencing the interdisciplinary research, part of which resulted in the presented thesis. These activities aim at linking evidence from geobotany, plant physiology, soil science, mycology and silviculture across different scales from the single plant to landscape level, in order to finally reach to practical, transferable recommendations for sustainable forest use.

Important aspects of ecosystem sustainability are nutrient conservation and a balanced water regime. This is obvious when dealing with plant growth, but also includes off-site effects, which may affect larger regions. This has been stressed for the study area by Chernet et al. (2001) and Legesse et al. (2004), who reported a decline in water quality in the endorheic Rift Valley following land use changes.

In our studies on water and element dynamics, we focussed on three tree species of high regional importance: *Podocarpus falcatus* is the dominant indigenous species in Munessa like in many other Ethiopian forests (Abate 2004), and is highly valued for its timber quality (Negash 2003). *Eucalyptus globulus* has been introduced to Ethiopia more than 100 years ago and is the most important plantation species due to its fast growth and easy establishment (Pohjonen and

Pukkala 1990). It is particularly useful for construction poles and very popular among peasants (Jagger and Pender 2003). *Cupressus lusitanica* is the most important conifer in Ethiopian plantation forestry, grown in the country since the 1930s (Pohjonen and Pukkala 1992) and making up more than 60 % of the plantations in Munessa Forest (Teshome and Petty 2000). Apart from their practical importance in Ethiopia, East Africa and on a global scale (Maro et al. 1992; FAO 2001; Whitehead and Beadle 2004), the three selected species can be taken as model trees for contrasting plant architecture and physiology. These characteristics lead to different canopy environments and have thus a great influence on nutrient cycling by the understorey and natural regeneration of indigenous species (Michelsen et al. 1996; Prescott 2002).

As we aimed at the identification of species characteristics of the three species under study, we conducted all these comparative experiments on the same identical plots in three neighbouring forest stands of the *P. falcatus* belt with uniform site conditions. This approach was guided by a notion described by Eviner and Chapin (2003):

> „Most plant-effect studies focus on one type of ecosystem process and often on a subset of the key traits involved in that process. It is vital to consider the overall impact of a plant species on its ecosystem. In order to do this, it is crucial to understand how these traits and multiple effects interact."

To identify such plant effects in a canopy, the influences of different species have to be separated. This is particularly hard in mixed stands like the natural forest, which was the reason to implement a single-tree centred design by conducting experiments within a certain "single-tree influence circle" (Rhoades 1997; Amiotti et al. 2000).

In my thesis, I pursued different complementary approaches in order to obtain an integrated, transferable view of the dynamics of water, nitrogen and sulfur as affected by the three timber species under study, working out the mutual dependency as well as differences between these biogeochemical cycles.

Water was chosen for its prominent roles in biological activity and nutrient leaching, by which it exerts a strong control on ecosystem nutrient fluxes, production and degradation. Nitrogen is a highly mobile nutrient with a high turnover and an open cycle, which is also susceptible to leaching. Like N, S is largely associated with organic matter, but has stronger interactions with the mineral phase in oxide-rich soils. Leaf contents of S are low in Munessa Forest (Abate 2004), and little is known about its cycling.

The specific objectives addressed in my dissertation were:

1) to characterize the spatial pattern of soils in the study area, including their genesis and fertility, by sampling representative units of a geo-ecological gradient from the Rift bottom series at 1900 m asl to the volcanoes of the Rift shoulder at 3200 m asl

2) to develop a methodology to trace ecosystem S dynamics, comprising a procedure for stable-isotope analysis of ^{34}S in organic samples and the ^{34}S labelling of tree leaves for ecological experiments *in situ*

3) to identify and link specific characteristics of the tree species *P. falcatus*, *C. lusitanica* and *E. globulus* in their respective canopies, divided into the single aspects
    a. soil-plant-atmosphere water dynamics by integrating meteorological conditions and soil moisture, as well as the characteristic adaptation to and regulation of these parameters through physiologic responses and root adaptation
    b. the seasonal pattern of N in soil pools of different availability, as well as N turnover and transfers in the soil-plant system by stable-isotope methods (natural abundance and ^{15}N labelling)
    c. recycling of S from litter labelled with ^{34}S, applying a novel method to study S mineralization, its leaching, its uptake and its recirculation by plants

References

Abate A (2004) Biomass and nutrient studies of selected tree species of natural and plantation forests: Implications for a sustainable management of the Munessa-Shashemene Forest, Ethiopia. PhD dissertation. Faculty of Biology, Chemistry and Geosciences. University of Bayreuth, Bayreuth, Germany, 163 p

Alemu B (1998) Spatial study of soil nutrient status after natural forest conversion to plantation and secondary forests at Munessa Montane Forest, Ethiopia. M.Sc. Thesis. Swedish University of Agricultural Sciences, Debre Zeit, 77 p

Amiotti NM, Zalba P, Sanchez LF, Peinemann N (2000) The impact of single trees on properties of loess-derived grassland soils in Argentina. Ecology 81:3283-3290

Ashagrie Y, Zech W, Guggenberger G, Teketay D (2003) Changes in soil organic carbon, nitrogen and sulphur stocks due to the conversion of natural forest into tree plantations (*Pinus patula* and *Eucalyptus globulus*) in the highlands of Ethiopia. World Resource Review 15:462-482

Ashagrie Y, Zech W, Guggenberger G (2005) Transformation of a *Podocarpus falcatus* dominated natural forest into a monoculture *Eucalyptus globulus* plantation at Munesa, Ethiopia: soil organic C, N and S dynamics in primary particle and aggregate-size frations. Agriculture, Ecosystems and Environment 106:89-98

Barbier EB, Burgess JC (2001) Tropical deforestation, tenure insecurity, and unsustainability. Forest Science 47:497-509

Bawa KS, Seidler R (1998) Natural forest management and conservation of biodiversity in tropical forests. Conservation Biology 12:46-55

Benvenuti M, Carnicelli S, Belluomini G, Dainelli N, Di Grazia S, Ferrari GA, Iasio C, Sagri M, Ventra D, Atnafu B, Kebede S (2002) The Ziway-Shala lake basin (main Ethiopian rift, Ethiopia): a revision of basin evolution with special reference to the Late Quaternary. Journal of African Earth Sciences 35:247-269

Binkley D, Resh SC (1999) Rapid changes in soils following *Eucalyptus* afforestation in Hawaii. Soil Science Society of America Journal 63:222-225

Bonell M, Molicova H (2003) A hydrological approach to tropical forestation: Controversial issues and possible applications of topographic-wetness models. Journal of Tropical Forest Science 15:411-431

Bruijnzeel LA, Proctor J (1995) Hydrology and biogeochemistry of tropical montane cloud forests: What do we really know? In: Hamilton LS, Juvic JO, Scatena FN (eds) Tropical montane cloud forests, vol 110. Springer, Berlin, pp 38-78

Cairns MA, Meganck RA (1994) Carbon sequestration, biological diversity, and sustainable development - Integrated forest management. Environ Manage 18:13-22

Carnevale NJ, Montagnini F (2002) Facilitating regeneration of secondary forests with the use of mixed and pure plantations of indigenous tree species. Forest Ecol Manag 163:217-227

Chaffey DR (1980) South-west Ethiopia forest inventory project: an inventory of forest at Munessa and Shashemene. In. Ministry of Overseas Development, Land Resource Division, London

Chalie F, Gasse F (2002) Late Glacial-Holocene diatom record of water chemistry and lake level change from the tropical East African Rift Lake Abiyata (Ethiopia). Palaeogeogr Palaeocl 187:259-283

Chernet T, Travi Y, Valles V (2001) Mechanism of degradation of the quality of natural water in the Lakes Region of the Ethiopian rift valley. Water Res 35:2819-2832

Crook C, Clapp RA (1998) Is market-oriented forest conservation a contradiction in terms? Environmental Conservation 25:131-145

Environmental Protection Agency (1998) Background information on drought and desertification in Ethiopia, Addis Ababa, Ethiopia

Eshetu Z, Högberg P (2000a) Effects of land use on ^{15}N natural abundance of soils in Ethiopian highlands. Plant and Soil 222:109-117

Eshetu Z, Högberg P (2000b) Reconstruction of forest site history in Ethiopian highlands based on ^{13}C natural abundance of soils. Ambio 29:83-89

Eviner VT, Chapin FS (2003) Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. Annual Review of Ecology Evolution and Systematics 34:455-485

FAO (2001) State of the world's forests, 2001. In. Food and Agriculture Organization of the United Nations, Rome

FAO (2003) State of the world's forests, 2003. In. Food and Agriculture Organization of the United Nations, Rome

Fetene M, Beck EH (2004) Water relations of indigenous versus exotic tree species, growing at the same site in a tropical montane forest in southern Ethiopia. Trees - Structure and Function 18:428-435

Feyera S, Beck E, Lüttge U (2002) Exotic trees as nurse-trees for the regeneration of natural tropical forests. Trees - Structure and Function 16:245-249

Geldenhuys CJ (2004) Bark harvesting for traditional medicine: From illegal resource degradation to participatory management. Scandinavian Journal of Forest Research 19:103-115

Gindaba J, Olsson M, Itanna F (2004) Nutrient composition and short-term release from *Croton macrostachyus* Del. and *Milletti a ferruginea* (Hochst.) Baker leaves. Biology and Fertility of Soils 40:393-397

Girma D (1998) Non-wood products in Ethiopia. In. EC-FAO partnership programme, Addis Ababa

Hailemichael M, Aronson JL, Savin S, Tevesz MJS, Carter JG (2002) δ^{18}O in mollusk shells from Pliocene Lake Hadar and modern Ethiopian lakes: implications for history of the Ethiopian monsoon. Palaeogeogr Palaeocl 186:81-99

Jagger P, Pender J (2003) The role of trees for sustainable management of less-favored lands: the case of eucalyptus in Ethiopia. Forest Policy and Economics 5:83-95

Kanowski J, Catterall CP, Wardell-Johnson GW (2005) Consequences of broadscale timber plantations for biodiversity in cleared rainforest landscapes of tropical and subtropical Australia. Forest Ecol Manag 208:359-372

Le Turdu C, Tiercelin JJ, Gibert E, Travi Y, Lezzar KE, Richert JP, Massault M, Gasse F, Bonnefille R, Decobert M, Gensous B, Jeudy V, Tamrat E, Mohammed MU, Martens K, Atnafu B, Chernet T, Williamson D, Taieb M (1999) The Ziway-Shala lake basin system, Main Ethiopian Rift: influence of volcanism, tectonics, and climatic forcing on basin formation and sedimentation. Palaeogeogr Palaeocl 150:135-177

Legesse D, Gasse F, Radakovitch O, Vallet-Coulomb C, Bonnefille R, Verschuren D, Gibert E, Barker P (2002) Environmental changes in a tropical lake (Lake Abiyata, Ethiopia) during recent centuries. Palaeogeogr Palaeocl 187:233-258

Legesse D, Vallet-Coulomb C, Gasse F (2004) Analysis of the hydrological response of a tropical terminal lake, Lake Abiyata (Main Ethiopian Rift Valley) to changes in climate and human activities. Hydrol Process 18:487-504

Lemenih M, Gidyelew T, Teketay D (2004a) Effects of canopy cover and understory environment of tree plantations on richness, density and size of colonizing woody species in southern Ethiopia. Forest Ecol Manag 194:1-10

Lemenih M, Itanna F (2004) Soil carbon stocks and turnovers in various vegetation types and arable lands along an elevation gradient in southern Ethiopia. Geoderma 123:177-188

Lemenih M, Olsson M, Karltun E (2004b) Comparison of soil attributes under *Cupressus lusitanica* and *Eucalyptus saligna* established on abandoned farmlands with continuously cropped farmlands and natural forest in Ethiopia. Forest Ecol Manag 195:57-67

Lemenih M, Karltun E, Olsson M (2005) Assessing soil chemical and physical property responses to deforestation and subsequent cultivation in smallholders farming system in Ethiopia. Agriculture, Ecosystems and Environment 105:373-386

Lundgren B (1971) Soil studies in a montane forest in Ethiopia. In. Royal College of Forestry, Department of Forest Ecology and Forest Soils, Research Notes No.11, Stockholm

Lüttge U, Berg A, Fetene M, Nauke P, Peter D, Beck E (2003) Comparative characterization of photosynthetic performance and water relations of native trees and exotic plantation trees in an Ethiopian forest. Trees - Structure and Function 17:40-50

Maro RS, Chamshama SAO, Nsolomo VR, Maliondo SM (1992) Soil chemical characteristics in a natural forest and a *Cupressus lusitanica* plantation at West Kilimanjaro, Tanzania. Journal of Tropical Forest Science 5:465-472

Michelsen A, Lisanework N, Friis I, Holst N (1996) Comparisons of understorey vegetation and soil fertility in plantations and adjacent natural forests in the Ethiopian highlands. J Appl Ecol 33:627-642

Montagnini F, Porras C (1998) Evaluating the role of plantations as carbon sinks: An example of an integrative approach from the humid tropics. Environ Manage 22:459-470

Myers N, Mittermaier RA, Mittermaier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853-858

Negash L (2003) In situ fertility decline and provenance differences in the East African Yellow Wood (*Podocarpus falcatus*) measured through in vitro seed germination. Forest Ecol Manag 174:127-138

Pohjonen V, Pukkala T (1990) *Eucalyptus globulus* in Ethiopian forestry. Forest Ecol Manag 36:19-31

Pohjonen V, Pukkala T (1992) *Juniperus procera* Hocht. ex. Endl. in Ethiopian forestry. Forest Ecol Manag 49:75-85

Prescott CE (2002) The influence of the forest canopy on nutrient cycling. Tree Physiology 22:1193-1200

Reddy SRC, Price C (1999) Carbon sequestration and conservation of tropical forests under uncertainty. Journal of Agricultural Economics 50:17-35

Rhoades CC (1997) Single-tree influences on soil properties in agroforestry: lessons from natural and savanna ecosystems. Agroforestry Systems 35:71-94

Senbeta F, Teketay D, Naslund BA (2002) Native woody species regeneration in exotic tree plantations at Munessa-Shashemene Forest, southern Ethiopia. New Forests 24:131-145

Silvanova (1996) Enterprise formations of the Munessa-Shashemene State Forestry Project. Oromia Bureau of Agriculture Development, Addis Ababa, Ethiopia

Solomon D, Lehmann J, Tekalign M, Fritzsche F, Zech W (2001) Sulfur fractions in particle-size separates of the sub-humid Ethiopian highlands as influenced by land use changes. Geoderma 102:41-59

Solomon D, Fritzsche F, Lehmann J, Tekalign M, Zech W (2002a) Soil organic matter dynamics in the subhumid agroecosystems of the Ethiopian Highlands: evidence from natural ^{13}C abundance and particle-size fractionation. Soil Science Society of America Journal 66:969-978

Solomon D, Fritzsche F, Tekalign M, Lehmann J, Zech W (2002b) Soil organic matter composition in the subhumid Ethiopian highlands as influenced by deforestation and agricultural management. Soil Science Society of America Journal 66:68-82

Solomon D, Lehmann J, Mamo T, Fritzsche F, Zech W (2002c) Phosphorus forms and dynamics as influenced by land use changes in the sub-humid Ethiopian highlands. Geoderma 105:21-48

Solomon D, Lehmann J, Martinez CE (2003) Sulfur K-edge XANES spectroscopy as a tool for understanding sulfur dynamics in soil organic matter. Soil Science Society of America Journal 67:1721-1731

Solomon D, Lehmann J, Kinyangi J, Liang BQ, Schafer T (2005) Carbon K-edge NEXAFS and FTIR-ATR spectroscopic investigation of organic carbon speciation in soils. Soil Science Society of America Journal 69:107-119

Teketay D, Granstrom A (1995) Soil seed banks in dry Afromontane forests of Ethiopia. J Veg Sci 6:777-786

Teketay D (1997) The impact of clearing and conversion of dry Afromontane forests into arable land on the composition and density of soil seed banks. Acta Oecol 18:557-573

Teshome T, Petty JA (2000) Site index equation for *Cupressus lusitanica* stands in Munessa Forest, Ethiopia. Forest Ecol Manag 126:339-347

Whitehead D, Beadle CL (2004) Physiological regulation of productivity and water use in *Eucalyptus*: a review. Forest Ecol Manag 193:113-140

Wubet T, Weiss M, Kottke I, Oberwinkler F (2003) Morphology and molecular diversity of arbuscular mycorrhizal fungi in wild and cultivated yew (*Taxus baccata*). Canadian Journal of Botany-Revue Canadienne De Botanique 81:255-266

Wubet T, Weiss M, Kottke I, Teketay D, Oberwinkler F (2004) Molecular diversity of arbuscular mycorrhizal fungi in Prunus africana, an endangered medicinal tree species in dry Afromontane forests of Ethiopia. New Phytologist 161:517-528

Yirdaw E (2001) Diversity of naturally-regenerated native woody species in forest plantations in the Ethiopian highlands. New Forests 22:159-177

Yirdaw E, Leinonen K (2002) Seed germination responses of four afromontane tree species to red/far-red ratio and temperature. Forest Ecol Manag 168:53-61

Yirdaw E, Luukkanen O (2004) Photosynthetically active radiation transmittance of forest plantation canopies in the Ethiopian highlands. Forest Ecol Manag 188:17-24

Study 1:

Soils of the Main Ethiopian Rift Valley escarpment: a catenary study

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Abstract

The mountainous environment of the Ethiopian highlands has a great variety of ecotopes and thus demands great flexibility in land management. Different climatic conditions and landscape positions induce different soil forming processes, leading to various soil types with specific risks and potentials. The present study describes a soil sequence of the Main Ethiopian Rift Valley, from the downslopes of the eastern escarpment to the marginal volcano structures. Six profiles under natural vegetation are described for classification according to the USDA Soil Taxonomy and WRB classification systems, and special site characteristics are discussed. The *Acacia* savannah of the footslopes (1900 m asl) is characterized by Vertisols, with often pronounced effects of seasonal waterlogging. The other soils are well-drained and reflect the increase in rainfall towards higher altitudes, causing a decline in topsoil pH and a change from cation-rich clay soils of the *Podocarpus*-dominated forest (2300 m asl) to strongly-leached Cambisols of the *Hagenia*-dominated forest around 2600 m asl. Soils of the highland savannah plain (2700 m asl) with a drier and cooler environment are less leached, but have a rather brownish colour. At 2900 m asl, Alisols are found in the *Hypericum* forest at the midslopes of the marginal volcanoes receiving high rainfall, whereas soil development is at a more initial state in the *Erica*-dominated forest at 3200 m asl. Clay mineral composition is kaolin-dominated for the upper five profiles, with a high poorly crystalline proportion in the upper savannah and the volcano upslopes. The lowermost profile probably had a polygenetic origin indicated by an abrupt change from a smectitic to a kaolinitic composition in the subsoil. Soil development on quite homogeneous bedrock appeared essentially controlled by relief and climate, making the area a suitable research site for further in-depth investigations on vegetation, human influence and land use.

Keywords:

Afromontane, carbon stocks, Munessa Forest, nitrogen, soil fertility, sulfur.

Introduction

Average elevation of Ethiopia is about 1250 m asl, with one third of the country exceeding 1500 m asl (calculated from SRTM-30 dataset). The country's highlands are dissected by tectonic structures and deeply incised rivers (Fig. 1-1), descending even to below sea level, and the ubiquitous neighbourhood of contrasting environments has determined ecosystem and land use evolution. Fertile volcanic soils prevail in wide areas of the highlands, and mean annual rainfall exceeds 800 mm (Ethiopian Mapping Authority 1988). Once covered by forest, the productive, temperate agro-climatic zone at 1500 - 3200 m asl, traditionally termed Woyna Dega and Dega, has undergone large-scale deforestation during the past 3000 years (Darbyshire et al. 2003; Nyssen et al. 2004), with sporadic forest recovery following climate-triggered depopulation (Darbyshire et al. 2003). Today, these highlands are densely populated, and nearly all arable land is used for cereal production. As a consequence, degradation of soil and water is common (Nyssen et al. 2004), and - despite their great socio-economic and ecological significance - even remnant forest patches have largely disappeared in wide regions (Teketay 1992). Planning for a sustainable land use in view of a growing population thus has to assess potentials and vulnerability of landscape and society, in order to harmonize food production and resource conservation, while counteracting wood shortage, erosion and landscape degradation.

This requires on the one hand land-use related analyses (Nyssen et al. 2000a; Nyssen et al. 2000b; Solomon et al. 2002a; Taddese et al. 2002; Bewket and Stroosnijder 2003; Billi and Dramis 2003; Sonneveld and Keyzer 2003; Brunner et al. 2004; Gindaba et al. 2004; Zeleke et al. 2004; Fritzsche et al. 2005; Lemenih et al. 2005). On the other hand, the relative importance of single aspects greatly depends on the landscape context (Nyssen et al. 2003; Carey et al. 2005; Porder et al. 2005), which was our motivation to investigate the poorly described spatial distribution of soils in central Ethiopia and to line out their special characteristics. We identified the escarpments of the Main Ethiopian Rift Valley (MER) as a suitable environment for this purpose.

Various studies have stressed the environmental change in the region due to human activities, above all deforestation. This comprises soil erosion (Billi and Dramis

2003), chemical soil degradation (Solomon et al. 2002a; Solomon et al. 2002c; Lemenih et al. 2005; Solomon et al. 2005) and the destabilization of the water and element budget in recent times (Legesse et al. 2002; Legesse et al. 2004), enhancing the risk of alkalinization of water resources in the Lakes Basin with an already problematic ion load (Chernet et al. 2001). However, only little work has been done on the soil geography of the MER, including a basic transect description by Lundgren (1971) and work on soil carbon by Lemenih and Itanna (2004). A systematic description of soil properties and a classification according to the current systems is still lacking. Such soil geographic work is facilitated by recently published, detailed studies on the younger geological history of the MER (Le Turdu et al. 1999; Benvenuti et al. 2002), up to the late Pleistocene and Holocene (Chalie and Gasse 2002) and historic times (Legesse et al. 2002).

In order to provide this basic information, we conducted the present investigation, characterizing six benchmark profiles of the representative landscape units of sub-humid Central Ethiopia in the context of climate, relief and geohistory, including their classification according to the WRB (FAO et al. 1998) and Soil Taxonomy systems (Soil Survey Staff 2003). Emphasis is put on forest soils, as they reflect natural conditions quite uniformly, while agriculture severely alters soil characteristics, such as bulk density, nutrient contents and soil organic matter (Solomon et al. 2001; Solomon et al. 2002b; Lemenih et al. 2005; Solomon et al. 2005), depending on the management practice. Our investigation on soil development is complemented by a grid-based spatial study on soils-vegetation interaction on 89 representative plots (Rückamp 2004, unpublished).

Materials and Methods

Study area and sampling sites

The soil catena of this study crosses the escarpment of the MER. This prominent large-scale structure with a NNE trend stretches from the Afar triple junction through central Ethiopia to join the Gregory Rift in the south, continuing through Kenya (Fig. 1-1b). The typical geomorphic setting is marked by gentle to moderate slopes with steep valleys incised by rivers that drain the highlands and the escarpment. Agriculture is practiced at all altitudes, but large natural forest remnants and plantation forests exist as well.

The samples for our transect study were collected around the town of Degaga in the larger Munessa-Shashemene Forest of central Ethiopia at 7°26'N 38°47'E to 7°24'N 38°58'E. This area is located in the Rift Valley Lakes Region at the eastern escarpment of the MER (Fig. 1-1). The Munessa-Shashemene Forest covers an area of about 23,000 ha and comprises natural forest remnants of different altitudinal belts as well as major plantations of exotic species, mainly *Cupressus lusitanica*, *Pinus patula* and *Eucalyptus* species. The region is subject to a pronounced ecological gradient from the semi-arid endorheic Ziway-Shalla basin at 1600 m asl, through the sub-humid escarpment to the drier Arsi highlands at about 2700 m asl, topped by shield volcano structures reaching more than 4000 m asl. The relief is the result of the Pliocene rifting process, involving intermediate volcanism in the highlands and acidic volcanism in the graben associated with the Wonji Fault Belt, which is seen as the actual axis of crustal extension (Le Turdu et al. 1999; Benvenuti et al. 2002). While the highest point of the catena, the trachytic Mt. Kubsa volcano, has not been active during the Quaternary, silicic activity of the Alutu caldera (2328 m asl) at the northern end of Lake Langano has continued until recently, which also deposited the Abernosa pumices in a last major explosive eruption 21 ka BP (Gasse and Vancampo 1994; Le Turdu et al. 1999). The geological substrate for soil development is quite homogeneous, intermediate volcanic rock of primarily Oligocene to Pliocene age with a more alkaline composition on the marginal volcanoes (Benvenuti et al. 2002). The studied profiles were all located in the volcanic complex above the Ziway-Shalla basin, made up of three units: the Rift floor, the plateau trapp series of the escarpment and the volcanoes of the Rift shoulder.

The investigated catena spans 6 profile pits over 20 km in length and 1300 m in elevation (Fig. 1-2). We sampled representative pedons of the typical vegetation and relief units. Small patches of remnant vegetation were selected on the savannah plains, as the degree of forest destruction was high (visible from the Landsat TM image superimposed in Fig. 1-1c). Excessive slope was avoided, except for the uppermost site in steep terrain. We monitored temperature and rainfall at 4 sites (1-2, 2, 3, 5) along the transect from 2001 to 2004, as climate data were only available from 2000 m asl (Degaga town) with 1075 mm and from 2700 m asl (nearby Munessa town) with 990 mm rainfall (Ethiopian Meteorological Service, 1995). The values cited in Fig. 1-2 show a general pattern, yet with considerable interannual fluctuations (Legesse et al. 2002; Schreck and Semazzi 2004). Soil temperature regime according to Soil Taxonomy was isothermic for the lower two profiles and isomesic for the upper four.

The following steps in different altitudinal belts were included, the vegetation of which has been described in detail by Abate and Rückamp (2004, unpublished):

1900 m: The footslope of the escarpment is resting in the Rift bottom series, composed of Quaternary rhyolites and tuffs. Its *Acacia* woodlands receive about 800 mm of annual rainfall at a mean annual temperature around 19 °C. The terrain is rather level, waterlogging is common. Most areas are used for agriculture or grazing.

2240 m: Closed high forest dominated by the conifer *Podocarpus falcatus* and deciduous *Croton macrostachys* covers the midslopes of the escarpment, which consists of intermediate lava series. Drainage is favourable, as soils are well-aggregated and slope is moderate. Rainfall is about 1500 mm, average temperature is 15 °C.

2580 m: The natural forest of the upslopes of the escarpment is dominated by *Hagenia abyssinica* and rich in the bamboo *Arundinaria alpina*. Slope is moderate, rainfall amounts to 1200 mm with mean annual temperature around 14 °C.

2670 m: The Arsi highlands are an undulating plain, dissected by small rivers. Nearly all terrain is used for agriculture or as pasture land. Only very small patches of natural vegetation remain, comprising the evergreen trees *Hagenia abyssinica*, *Prunus africana* and *Hypericum revolutum*. This highland savannah is markedly drier, rainfall hardly exceeds 1000 mm.

2860 m: The moderately steep (> 20 %) midslopes of the volcano structures of the Rift shoulder are cooler (13 °C) and receive considerable rainfall of 1600 mm per year. Natural vegetation is preserved, but degraded mainly due to grazing. *Hypericum revolutum* and *Rapanea simensis* are the dominant trees.

3200 m: The upslopes of the marginal volcanoes are steep (ca. 30°) and covered by stands of *Erica arborea* and *Hypericum revolutum*. The environment is cool and moist, frequently covered in clouds.

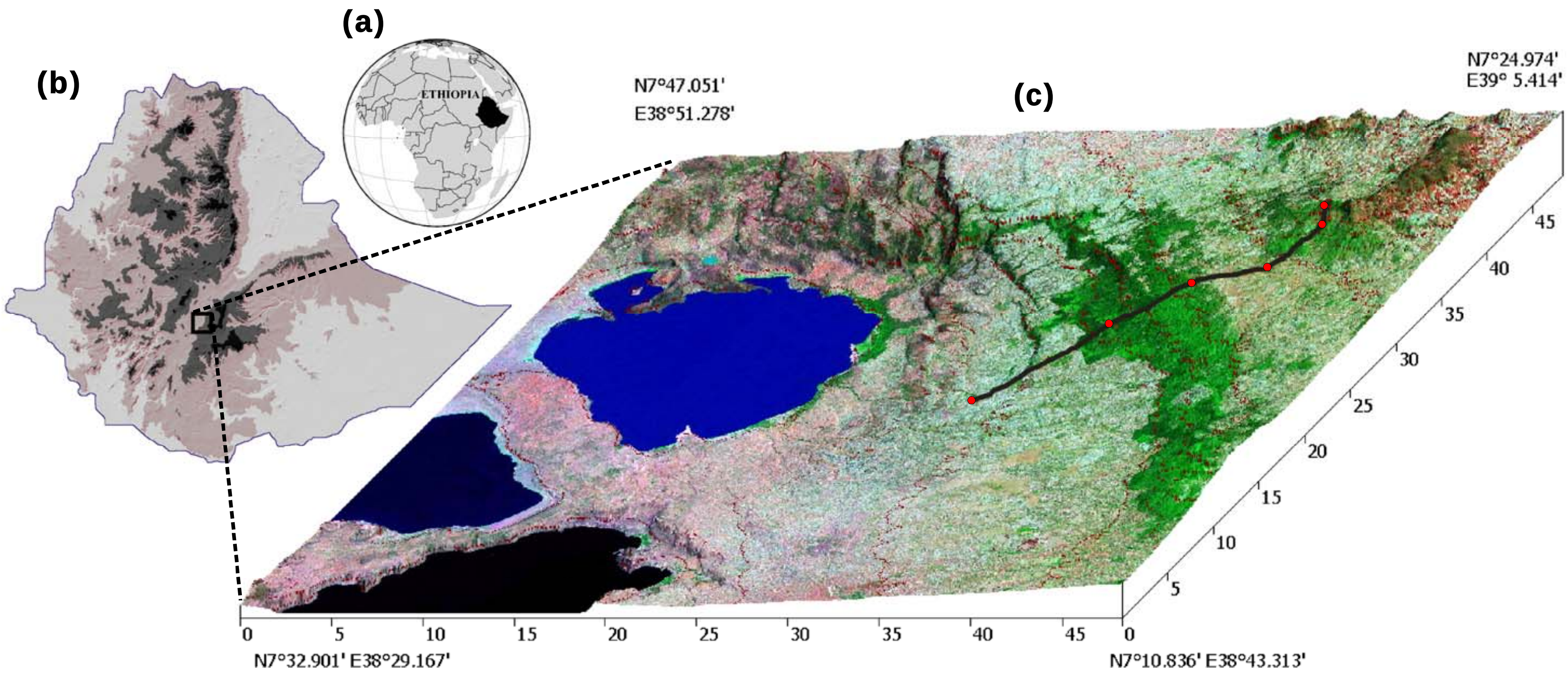
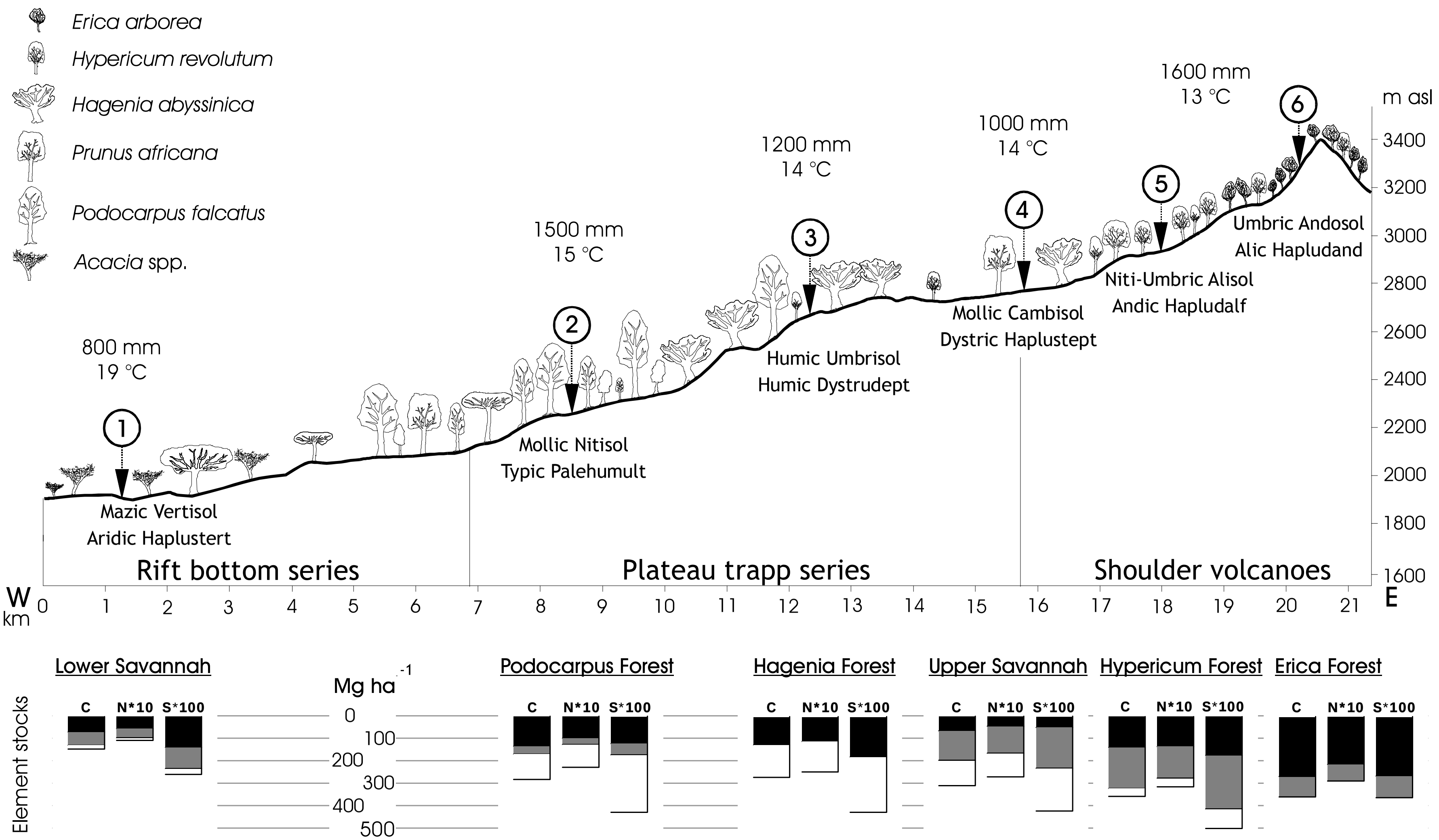


Fig. 1-1: Situation of the study area: (a) global position, (b) Ethiopia (relief steps by increasing intensity of shading: < 1000 m, 1000 m, 2000 m and 3000 m asl), (c) location of the transect ascending east of Lake Langano (contour lines every 200 m, sampled sites marked as red circles). Compiled from SRTM-3 dataset and Landsat-7 TM imagery dating from 2000, vertical exaggeration of two.



Profile calculated from SRTM-3 dataset, 4-fold vertical exaggeration

Fig. 1-2: Geo-ecological transect through the study area with the profiles designated, their classification in WRB and Soil Taxonomy systems, geological units and vegetation types underlain. Histograms display C, N and S stocks in mineral soil (0 - 100 cm depth) by horizons: black - topsoil, white - subsoil, grey - transition).

Sampling and analyses

Profile pits were opened to a depth of 150 cm in March 2000, except for the sites 1 (260 cm) and 6, where bedrock was reached at 115 cm. Horizons were identified, and profiles described thoroughly. Composite samples of soil (ca. 200 g) were taken from each horizon from three walls of the pits for chemical analysis. Additionally, 3 cores (100 cm^3) were taken for determination of bulk density. All samples were air dried at 55 °C, samples for chemical analysis were ground with a ball mill.

The following soil physical and chemical parameters were measured for each horizon: bulk density; texture according to ISSS (2000, 200, 20, 2 µm) by wet sieving and pipette method; soil colour by Munsell Soil Color Charts; total C, N and S by automated dry combustion (Elementar vario EL); pH in distilled water and 1 M KCl (1 : 2.5 w/v) by potentiometry; potential cation exchange capacity at pH 7 (CEC) and exchangeable basic cations (Avery and Bascomb 1974; Sumner and Miller 1996); Fe, Al, Mn from pedogenic oxides by dithionite-citrate-bicarbonate (Fe_d, Al_d, Mn_d) and oxalate (Fe_o, Al_o, Mn_o) extraction (Mehra and Jackson 1960; Blume and Schwertmann 1969). Metal cations were determined by atomic absorption spectrometry (Varian SpectrAA 400), CEC by flow injection analysis (Skalar San^{Plus} System). X-ray diffractometry (XRD) was used to identify dominant clay minerals and important accessory minerals (by Siemens D 5000 with Cu $K\alpha$ radiation).

Statistical calculations were performed using the Statistica 5.1 for Windows (StatSoft Inc.) and SPSS 10.0 (SPSS Inc.) software packages. For processing of relief data, the software MicroDEM 8.0 (Guth 1995) was used.

Results and Discussion

Figure 2 gives an geo-ecological overview of the studied transect, outlining relief, climate, vegetation, location of the sampled profiles, their classification and geological landscape units; additionally included are stocks of C, N and S by horizon. Analytical data of the soil profiles are given in Table 1-1. The organic layer was shallow (2 – 4 cm) at all sites and widely disturbed by humans and livestock. As the thickness of the organic layers was not sufficient to influence classification, only properties of the mineral soils are discussed in this study. A detailed investigation on forest floor was performed by Rückamp (2004, unpublished).

Table 1-1: Basic analytical characteristics of six soil profiles: Profile code, horizon, lower horizon boundary (lhb), bulk density (BD), coarse sand (CSa, 2000 – 200 µm), fine sand (FSa, 200 – 20 µm), silt (20 – 2 µm), clay (< 2 µm), Munsell colour (moist), pH (KCl), concentrations of C, N, S, C/N ratio, potential CEC, base saturation, exchangeable basic cations, extractable Fe and Al.

Site	horizon	lhb	BD	CSa	FSa	Silt	Clay	Colour	pH	C	N	S	C/N	CEC	K	Mg	Ca	BS	Fe_d	Fe_o	Al_o
		cm	g cm^{-3}	g kg^{-1}					(KCl)	g kg^{-1}				cmol$_c$ kg^{-1}				%	g kg^{-1}		
6	A1	13	0.61	179	124	382	314	9YR 2/1	4.2	151	11.1	1.4	13.6	53.8	0.56	2.38	9.14	22	22	11	13
	A2	35	0.76	142	136	413	310	7.5YR 2/1	4.2	90	7.6	1.0	11.8	37.7	0.21	0.71	3.32	11	27	14	18
	AB	55	0.82	66	167	531	236	7.5YR 2/2	4.4	56	4.6	0.6	12.3	24.9	0.12	0.62	2.61	14	32	15	19
	B/R	115		186	190	431	193	9YR 3/3	4.3	15	1.3	0.3	11.5	16.6	0.29	1.22	5.20	41	27	10	11
5	A	22	0.87	92	115	336	457	5YR 2.5/1.5	4.3	72	7.1	1.0	10.2	31.3	1.15	2.36	9.94	43	34	13	6
	AB	70	0.82	48	123	348	482	10YR 2/2	3.9	47	3.6	0.6	13.0	26.9	0.49	0.33	1.02	7	44	13	9
	Bt	100	1.04	18	68	249	665	5YR 3/4	3.8	12	1.2	0.3	9.5	18.3	0.85	0.71	2.93	25	76	9	5
	Btss	150+	1.19	40	117	302	541	6YR 4/4	4.2	5	0.8	0.2	5.6	14.4	0.34	1.95	6.19	60	64	12	5
4	A	9	0.52	99	105	352	444	10YR 2/1	5.3	140	9.8	1.1	14.2	46.3	1.14	8.75	35.94	99	26	11	3
	AB	39	1.13	116	108	328	448	7YR 3/3	4.8	39	3.5	0.5	11.0	18.3	4.03	3.59	10.68	100	38	14	5
	B1	76	1.14	70	94	346	490	5YR 3/3	4.0	21	1.8	0.3	12.1	19.9	1.48	2.21	2.69	32	44	11	6
	B2	113	1.41	76	108	333	483	5YR 3/3	3.9	7	1.0	0.2	7.3	12.4	2.08	1.02	2.64	46	46	8	3
	B3	160+	1.27	77	102	354	468	5YR 3/4	3.9	5	0.8	0.2	6.1	6.3	1.00	1.62	4.18	100	47	9	3
3	A1	12	1.08	87	99	341	473	9YR 2/2	5.3	69	6.0	0.9	11.5	30.8	2.26	4.01	17.84	78	40	13	3
	A2	22	1.07	80	101	338	482	5YR 3/3	4.2	37	3.3	0.6	11.3	14.9	1.09	2.23	4.71	54	46	12	5
	B1	42	0.98	91	95	322	492	5YR 3/3	3.7	28	2.5	0.5	11.0	19.4	0.63	0.65	1.52	15	47	12	5
	B2	75	1.02	63	92	329	516	5YR 3/3	3.6	19	1.6	0.3	12.0	27.4	0.70	0.36	1.87	11	51	11	4
	Bc1	115	1.22	84	106	329	481	4YR 3/4	3.7	8	1.1	0.2	7.9	23.0	0.42	0.83	3.40	20	58	9	3
	B3	150+	1.44	81	83	307	529	6YR 4/4	4.0	5	0.8	0.2	5.8	14.2	0.16	1.81	4.30	44	69	6	2
2	A	15	0.73	106	91	304	500	9YR 2/2	6.3	122	9.0	1.1	13.5	54.1	1.20	7.27	59.99	100	27	6	2
	AB	29	0.97	145	83	232	540	5YR 3/3	6.1	26	2.1	0.4	12.3	26.0	1.37	3.18	17.90	87	43	8	2
	Btss1	68	1.15	32	53	180	735	3YR 3/4	5.6	16	1.4	0.3	11.8	22.4	0.89	4.66	10.08	70	59	6	3
	Btss2	108	1.11	27	53	183	737	3YR 3/3	4.0	11	1.1	0.4	10.2	23.8	1.47	3.52	1.81	29	56	6	4
	Btss3	150+	1.01	25	41	166	768	2.5YR 3/5	3.7	5	0.9	0.2	5.6	16.9	0.82	1.47	1.23	22	57	4	3
1	A	19	1.51	251	155	220	373	10YR 3/2	5.5	17	1.3	0.3	13.2	21.9	0.67	3.58	17.63	100	17	6	1
	EAg	41	1.51	172	165	243	420	9YR 4/1	5.2	6	0.5	0.1	11.3	20.7	0.43	3.69	16.02	100	14	2	1
	BAgkss	82	1.58	88	85	169	659	10YR 3/2	6.0	9	0.6	0.1	14.4	33.3	0.95	6.96	28.74	100	12	2	1
	Btgkss	136	1.42	110	84	186	621	6YR 4/2	6.5	7	0.4	0.1	16.5	33.5	0.98	7.20	33.80	100	11	2	1
	2Btk	176	1.44	130	92	167	610	6YR 4/4	5.7	3	0.4	0.1	7.8	27.2	0.93	5.70	19.31	100	20	2	1
	2Bt	200	1.41	134	84	184	598	4YR 3/4	5.4	2	0.5	0.1	5.1	19.4	0.74	5.08	18.58	100	24	2	1
	2Bt/Ct	227		180	103	216	501	7YR 3/3	5.3	3	0.5	0.1	6.7	23.0	0.92	6.22	22.15	100	15	2	1
	2Ct	260+		159	123	240	478	6YR 3/4	5.1	3	0.5	0.1	6.5	21.6	0.92	6.49	22.71	100	16	2	1

General description and horizon classification

All soils were fine-textured with clay for the lower 5 profiles and loams for profile 6 (Table 1-1). Material > 2 mm was only found as rock fragments in profile 6 (up to 5.6 % in AB horizon, sharply increasing below) and as secondary nodules in profile 1 (< 5.5 %). Soil colour was brownish (Munsell Hue YR) and got more reddish with decreasing elevation. The diagnostic property "strongly humic" (WRB) applied to all profiles except the lowermost.

The categorization of the topsoils clearly reflected the influence of rainfall on SOM accumulation and base depletion. Topsoils were classified as mollic for profiles 2 and 4, while insufficient thickness at site 3 led to the description as umbric, together with the humid profiles 5 and 6. In the lower savannah, an ochric horizon / epipedon overlaid an albic horizon. The lower topsoil of profile 6 qualified for an andic horizon (WRB) and andic soil properties (Soil Taxonomy). Argic / argillic horizons were found in profiles 1, 2, 5, with the WRB diagnostic properties nitic at site 2 and alic at site 5, respectively. Cambic horizons were present in profiles 3, 4 and 6, the latter only according to Soil Taxonomy. The profile classification (Fig. 1-2) shows the increasing influence of the parent material with increasing elevation at a decreasing influence of temperature.

The classification of pedons and horizons is reflected in the hierarchical cluster analysis of the physical and chemical soil data (Fig. 1-3). The dendrogram shows the Vertisol (profile 1) as a distinct cluster, a grouping of the mollic horizons, and another cluster comprising the B horizons of the highly weathered, deep soils from the high-rainfall positions. The subsoil of profile 4 (cambic) showed the highest similarity with the cambic horizon of profile 3. Similarity between the high-rainfall AB horizons was also high. The A1 horizon of the uppermost profile was distinct from the other horizons, while its underlying horizons were linked at a low distance, ending up in a cluster with the medium-weathered subsoils.

Soil water

With exception of the lowermost pedon, all profiles were well drained. Nevertheless, low hydraulic conductivity of the clay soils and high wet-season precipitation led to hydromorphic features (mottling) present in all deep profiles.

Hydromorphosis in the studied soils was always diffuse through a wide zone and not affected by young tephra, as reported for soils from Kilimanjaro with placic horizons hampering the percolation of water (Schrumpf 2004). The shallow and coarser uppermost profile with big rock fragments reaching up to 45 cm depth showed no mottling. The relation of hydromorphic features to rainfall is visualized in Fig. 1-4. Mottling occurred only below 1 m in the drier upper savannah and in profile 2, which had a well developed soil structure, visible from the low bulk density (Table 1-1). Level terrain made profile 1 prone to waterlogging, leading to bleaching and mottling, and masking effects of the drier climate.

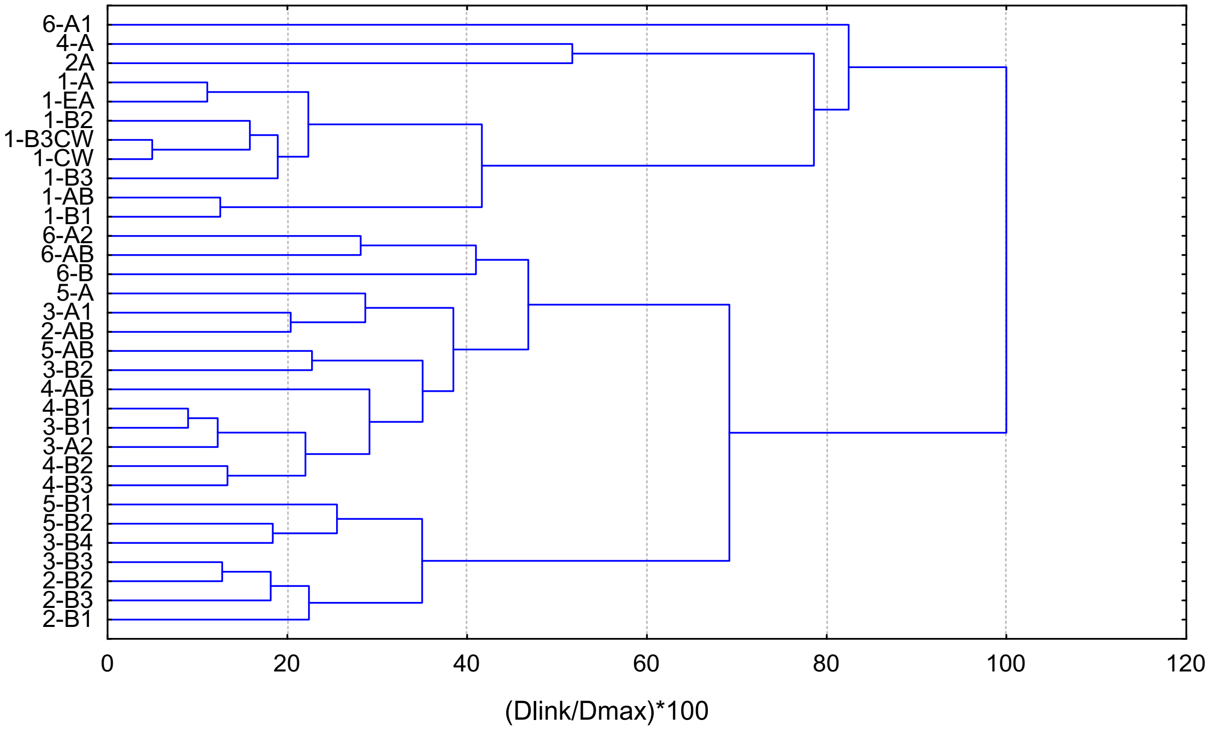


Fig. 1-3: Hierarchical clusters of the different horizons along the catena (Euclidean distances, hierarchy by weighted pair-group average).

Organic nutrients

Besides the importance of soil C for the global C cycle, soil organic matter is an important agent for nutrient retention and substrate for soil life. Nitrogen (N) and sulfur (S) are largely associated with organic matter, giving information about its quality. Trees in Munessa Forest had low tissue contents of N and S, indicating growth limitation by these macro-nutrients (Abate 2004).

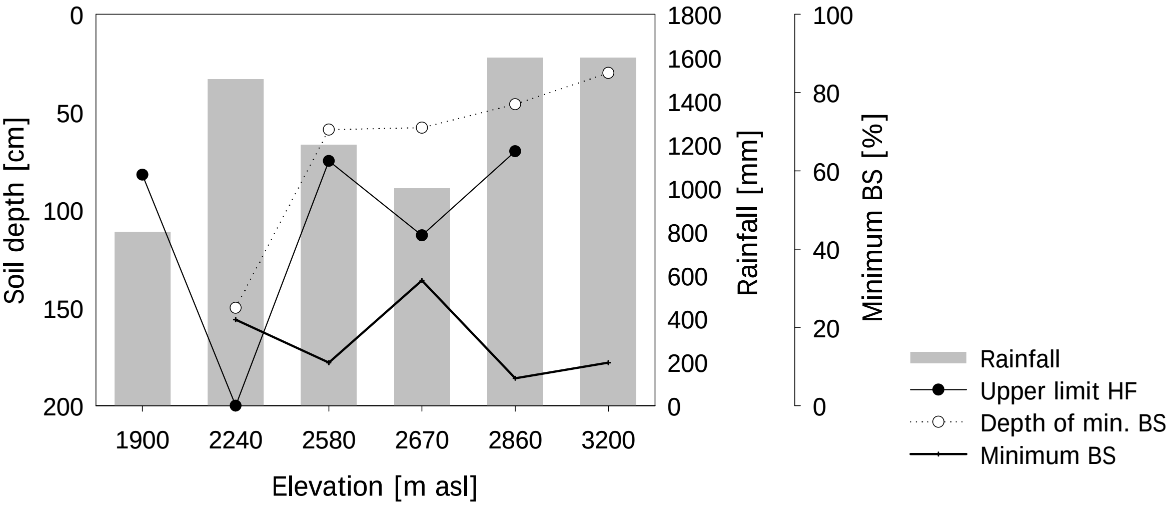


Fig. 1-4: Altitudinal pattern of annual rainfall, upper limit of hydromorphic features, depth of minimum base saturation (BS) and minimum BS.

As frequently observed, C stocks increased with elevation and got allocated closer to the surface (Fig. 1-2). The same pattern was observed for the N contents, with C/N ratios integrated to 1 m depth showing a minor variation of 11.0 to 13.6. The increase in C stocks can be ascribed to high rainfall, which has been shown to decrease oxygen availability and thereby decomposition (Schuur et al. 2001). Yet in our study, the effect of temperature on decomposition (Alexander and Pichott 1979; Kirschbaum 1995) yielded a better explanation, as visible from the dryer profile 4 exhibiting rather an increase of C, N and S. Changing mineralogical properties might also contribute to the stabilization of organic matter in organo-mineral complexes at higher elevations (Dubroeucq et al. 2002a), as visible from the increasing amounts of oxalate-extractable oxide-forming elements (Table 1-1).

C/N ratios ranged from 5.6 in the subsoil to 14.2 in the topsoil of the well-drained profiles (Table 1-1), with a slightly wider range in profile 1 due to beginning accumulation of secondary carbonates. Differences along the transect were only minor without a clear pattern. The possible control of climate on C/N ratios was only indicated by a higher C/N ratio for the highest profile with temperature being too low for proper mineralization.

Soil S stocks reflected the geological setting: Values up to 5 Mg ha^{-1} occurred on the volcanoes of the Rift shoulder, around 4 Mg ha^{-1} in the trapp complex, and below 3 Mg ha^{-1} at the Rift bottom. As the altitudinal increase of C stocks was more pronounced, C/S ratios of the stocks widened along the catena from 56 to 99. On profile level, C/S ratios narrowed with depth in profiles 1 through 5, presumably due to specific retention of sulfate on oxide surfaces, which had not yet accumulated in profile 6.

The absolute C concentrations in topsoil were at least twice as high as the figures reported for agricultural soils south of the study area at a comparable elevation (Zeleke et al. 2004). Corresponding topsoil C concentration of a *P. falcatus* dominated forest at 2100 m some 30 km south of the study site were about one third lower, yet at similar N concentration, resulting in a narrower C/N ratio of 9 - 10 (Lemenih et al. 2005). As bulk density was also similar to that at our sites, this resulted in considerably lower C and N stocks in the upper 20 cm. A nearby transect sampled by Lemenih and Itanna (2004) yielded largely comparable topsoil C concentrations for the upper 60 cm, also exhibiting a similar pattern of C/N ratios. Only a site at the Rift shoulder showed a distinct maximum of more than 230 Mg ha^{-1} (Lemenih and Itanna 2004). This might be attributed to specific site conditions, however, as the profiles above were in good agreement again, fitting into the gradual increase displayed in Fig. 1-2. The C/N ratios of the soil stocks of our study and their small altitudinal variation are in line with results by Eshetu et al. (2004) from a similar Ethiopian montane forest. The discrepancy of C/N ratios being about 10 % narrower in the study of Lemenih and Itanna (2004) might be ascribed to the different methods of wet vs. dry combustion, especially the correction factor required for the Walkley-Black method and blank correction for air-derived N in dry combustion. The element stocks of C, N and S were in the range reported by Schrumpf (2004) from Kilimanjaro, but tended to be smaller on average than the values from this more humid environment with tephric soils. Consistently narrower C/N ratios indicated better conditions for decay in Munessa-Shashemene Forest than at Kilimanjaro.

Weathering and soil reaction

The soil catena through Munessa-Shashemene Forest generally comprises soils of a rather advanced stage of pedogenesis on volcanic substrate, as can be seen from clay illuvation in the second-highest profile 5 (Sedov et al. 2003). The soils are much more developed than described from other regions of the East African Rift Valley with a high influence of Holocene tephra (Pyle 1999; Schrumpf 2004). The transect of our study is located on mainly effusive bedrock, and activity of the Alutu caldera has been low for the past 21 ka (Le Turdu et al. 1999). Recently deposited tephra from minor events, the last one dated 0.23 ka BP (Le Turdu et al. 1999), and distant sources is thus only of subordinate importance and might be intensively reworked on the slopes.

A progressing degree of mineral weathering is visible from various chemical parameters and becomes morphologically manifested as well. For the well-drained soils, colour is gradually changing from intense red at 2300 m to brownish at 3100 m (correlation of elevation and Munsell Hue YR in subsoil: $R = 0.92$, $P < 0.001$), which is due to accumulation of sesqui-oxides (Table 1-1). This pattern is typical of volcanic-derived toposequences and has been described for humid Cameroon (Tematio et al. 2004), humid Tanzania (Schrumpf 2004), sub-humid Northern California (Alexander et al. 1993) and semi-arid Mexico (Dubroeucq et al. 1998). Profile 6 and 1 can be seen as the starting and end members of soil evolution, but both are poor in pedogenic oxides, attributable to rejuvenation through erosion and a consequent lack of time in the first one, and to the low relief energy in the latter case.

Consistently lower pH values in KCl (Fig. 1-5) than in water point towards a low anion exchange capacity throughout the transect, indicative of an overall moderate degree of weathering. Considering the volcanic inputs in the Pleistocene, this is in line with findings from Hawaii (2500 mm mean annual rainfall), where soils younger than 20 ka still had high rates of weathering sufficient to stabilise primary minerals and recharge base cations (Stewart et al. 2001; Chadwick et al. 2003).

Along the altitudinal gradient, the well-drained profiles 2 – 6 exhibited a significant, negative linear correlation of topsoil pH and elevation ($R = -0.77$ for H_2O and $R = -0.80$ for KCl; $P < 0.01$), displayed in Fig. 1-5. While the two lowermost profiles did not fit into a linear relationship for subsoil pH values, the other profiles showed an opposite trend towards an increase in pH with elevation, which was stronger expressed for the reaction in pure H_2O ($R = 0.84$ vs. pH(KCl) with $R = 0.80$; $P < 0.01$). The pH(KCl) value hardly changed with elevation, but the pH(H_2O) showed a steep increase ($R = 0.78$ for the difference of both values, ΔpH, vs. elevation, $P < 0.01$). This increase in exchangeable acidity reflects differences in the exchange complex, above all the larger proportion of amorphous components with a higher variable charge (Chadwick et al. 2003). The trends of pH were clear in our study, and the observed topsoil pattern was also reflected in a catena study from Hawaii (Chadwick et al. 2003). However, studies from volcanic environments with no clear rainfall gradient found no such relationship (Meijer and Buurman 2003; Eshetu et al. 2004; Schrumpf 2004), thereby demonstrating the relation to rainfall.

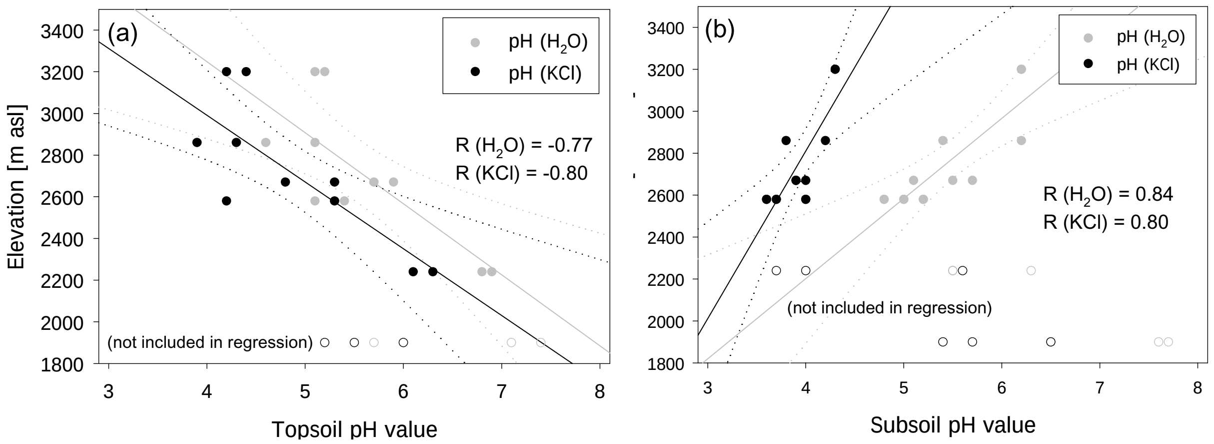


Fig. 1-5: Relationship of elevation pH (in H_2O and 1 M KCl) value for (a) topsoil and (b) subsoil (Pearson correlation for the profiles included in regression, dotted lines show 95 % confidence limits).

Exchange complex and metal cations

The (potential) CEC was high throughout the catena. No clear altitudinal pattern could be observed, but it has to be borne in mind that the altitudinal pH decrease reduces the effective CEC by loss of variable charge, which is particularly high in volcanic soils (Chorover et al. 2004). In order to identify controls on CEC, we employed multiple regression analysis, entering the parameters BD, % C, % N, clay content, Fe_d, Al_d, Mn_d, Fe_o, Al_o, Mn_o, Hue (Munsell), Value, Chroma. The results of different models (stepwise forward method) for the topsoil and subsoil CEC are given in Table 1-2.

Topsoil C content was a fair predictor for topsoil CEC (R^2 = 0.75), inclusion of Fe_o raised multiple R^2 to 0.91 ($P < 0.01$). The Munsell Value was significant in the next step, but increased multiple R^2 by only 0.05. Other parameters like clay content and other sesqui oxides were redundant in the model. This shows the dominance of SOC on topsoil CEC (Eshetu et al. 2004), while Fe_o and Value served to attenuate this influence in the horizons with less C, particularly transitional A horizons.

Subsoil CEC appeared dependent on a wider range of characteristics. The significance of pairwise correlations was lower, showing the strongest, negative correlations for the parameters Munsell Chroma and Fe_o, related to sesqui oxides and thereby weathering. The inclusion of clay content in the regression model starting with Chroma as a starting point increased multiple R^2 to 0.44 ($F = 5.6$). Explanatory value was better for Fe_o together with C concentration ($R^2 = 0.48$, $F = 6.5$). Inclusion of other parameters in the models did not yield significant improvement. The similar level of explanation for the two models using contrasting parameters indicates a multifaceted exchange complex in the subsoils.

Table 1-2: Multiple regression analysis for predicting CEC, separately for topsoils (1 model) and subsoils (two models): model, variable, standardized regression coefficients β, adjusted regression coefficients B, partial correlations r, multiple R^2 in stepwise model, probability of error.

Top/Sub	**Variable**	**β**	**B**	**r**	**stepwise R²**	**P**
top	%C	0.743	1.958	0.93	0.75	< 0.001
top	Feo	-0.605	-1.712	-0.92	0.91	< 0.001
top	Value	-0.439	-8.320	-0.78	0.96	0.003
top	Intercept		57.145			< 0.001
sub(a)	Chroma	-0.640	-5.737	-0.63	0.21	0.009
sub(a)	Clay	0.520	24.640	0.54	0.44	0.028
sub(a)	Intercept		26.473			0.002
sub(b)	Feo	-0.876	-1.504	-0.69	0.19	0.003
sub(b)	%C	0.702	6.062	0.60	0.48	0.013
sub(b)	Intercept		24.339			< 0.001

For topsoil model: $n = 14$, $df = 3/10$, $F = 86.1$, $P < 0.001$.
For subsoil models: $n = 17$, $df = 2/14$, $F(a) = 5.6$, $P(a) < 0.05$, $F(b) = 6.5$, $P(b) < 0.05$.

Calcium was the dominant basic cation in all profiles contributing more than 40 % (by charge) of the base cations, in line with data from central Ethiopia by Eshetu et al. (2004). The subsoil of profile 2 formed an exception by the dominance of Mg. The share of K was highest at medium soil depth in the profiles around the upper savannah (3, 4, 5). Only the poorly drained profile 1 had significant amounts of exchangeable Na (1.35 $cmol_c$/kg soil). Base cations depletion progressed continually with increasing rainfall (Fig. 1-4), while the depth of minimum BS got smaller with increasing elevation, reaching lowest BS values at moist soil conditions. Minimum BS was lower in the soils with superficial hydromorphic features, which might in fact be a sign of base depletion (Fig. 1-4).

Chadwick et al. (2003) identified a rainfall amount of 1400 mm per year as a kind of threshold for nutrient leaching in a catenary study from Hawaii, with sufficient replenishment of base cations through weathering at dryer sites. The higher base saturation in the upper savannah plain suggests this transition rather around 1000 mm in the colder climate of Munessa-Shashemene Forest.

Soil minerals, geohistory and pedogenesis

The qualitative mineralogical characterization by powder XRD revealed clear differences in the B horizons along the catena (Table 1-3). A distinct change in the mineralogical composition within a profile, however, was only observed at site 1 from dominance of smectites in the upper profile to kaolin minerals below the Btgkss horizon. In the well-drained upper 5 profiles, kaolinite was the dominant clay mineral, while profile 1 showed a strong smectite signal. Signal intensity of the phyllo-silicate region was only minor in the spectra from site 4, indicating a high amount of poorly crystalline constituents, coinciding with higher Fe_o/Fe_d ratios (Table 1-3). Besides kaolinite, halloysite appeared to be of major importance at this site. The most distinct peak of mica-like minerals was found at site 5.

XRD peaks of lower intensity indicated the presence of micas and mica-like clay minerals in profiles 3 – 6, as well as an increase in the residual oxides down to the highly-weathered profiles 3 and 2. Feldspars were only detected in the less weathered profile 6 and under the alkaline conditions of profile 1. Chlorites occurred only at the low pH values of profile 3 with impeded drainage. Residual quartz was identified in all profiles, and palygorskite in profiles 4 and 6.

This mineral makeup generally corresponds with the study by Eshetu et al. (2004) from the Ethiopian highlands. As stated above, the volcanic substrate of the region has much less effects on soil mineralogy than in studies of regions with young tephra layers (e. g. Dubroeucq et al. 2002b). The altitudinal patterns revealed systematic influence of climate and weathering and showed trends similar to the Hawaiian transect by Chadwick et al. (2003) with smectites at high water saturation owing to high rainfall, and halloysite under dryer conditions.

Table 1-3: Mineralogical characteristics of the uppermost B horizon along the soil catena through Munessa Forest from powder XRD, and Fe_o/Fe_d ratios integrated for the whole profiles.

Profile	dominant clay mineral	other important minerals	Fe_o/Fe_d
6	kaolinite	palygorskite, feldspars, micas, quartz	0.47
5	kaolinite, mica-like	quartz	0.20
4	amorphous, kaolinite, halloysite	mica-like, palygorskite, quartz	0.22
3	kaolinite	chlorite, hematite, mica-like, quartz	0.14
2	kaolinite	hematite, quartz	0.10
1	smectite	feldspars, quartz	0.13

Profile 2 appears the most advanced soil in the well-drained series; it has the strongest signal of kaolinite, a significant amount of hematite and in the AB horizon also brookite (TiO_2), residual oxides typical of highly weathered soils. No signs of a reset of pedogenesis by erosion were found morphologically, and ^{14}C age of charcoal from 60 cm depth of 3731 ± 80 a BP points to the same direction. Nevertheless, climate history established from sediment cores places this date the end of an arid phase (Gasse and Vancampo 1994; Chalie and Gasse 2002; Legesse et al. 2002), which underlines that some profile characteristics might be inherited from earlier periods with higher temperature and less rainfall.

Unlike the upper profiles, the lowermost profile shows signs of such a polygenetic origin. The smectitic clay of the Btgkss horizon, which extends into the topsoil, is the thermodynamically controlled end product for imperfectly drained tropical landscapes on volcanic soils (Ziegler et al. 2003). Nevertheless, smectite is a metastable phase in soils, that can be transformed into kaolin minerals under dry conditions and improved drainage (Ziegler et al. 2003). The abrupt mineralogical change at 82 cm depth to kaolinite probably indicates a climate change from such dryer conditions. The separation of the B1 and AB horizon from the rest of the profile in the cluster analysis by chemical parameters (Fig. 1-3) supports the notion of a changing environment. ^{14}C dating of the 2Btk horizon yielded an age of 10 ka. Thus, smectite formation must have taken place during the moist period from 12 – 5.4 ka BP (Chalie and Gasse 2002). Considering the rejuvenation of soil carbon taking place in non-fossilized soils, the buried, kaolinitic soil is likely to show the imprint of a prolonged dry spell climaxing in the Younger Dryas (Street 1979; Street-Perrott et al. 1985). Sedimentation on this paleosol might have been facilitated by strong ashfall in the region around 10 ka BP, as concluded from extreme sediment yields in cores from nearby Lake Abiyata (Le Turdu et al. 1999).

Such Holocene ashfall may also have contributed to base replenishment of profile 2, showing a high base saturation in the upper 70 cm, which seems to be beyond the capacity of vegetation to pump up nutrients under the present high-rainfall conditions. Small volcanic events of Alutu volcano in the graben with pumice and obsidian flows have been recorded until 2 ka BP (Le Turdu et al. 1999).

The mineral composition of profile 4 bears signs of volcaniclastic deposits as well. The apparently high proportion of amorphous material and the higher Fe_o/Fe_d ratios make a major volcanic contribution likely. This is supported by the dominance of kaolin minerals (kaolinite and halloysite) that are the kinetically controlled product of allophane weathering at more arid conditions with rapid wetting and drying cycles and low silica leaching (Ndayiragije and Delvaux 2003; Ziegler et al. 2003). Amorphous constituents might on the other hand be stabilized by the relatively high contents of organic matter (Parfitt and Wilson 1985; Chadwick et al. 2003). We suppose that wet conditions and intense weathering with higher leaching of silica result in stronger expression of pedogenesis and the formation of kaolinite in the other profiles (Ziegler et al. 2003), which might be the reason for the more striking weathering gradient in the Fe_o/Fe_d ratios and accessory minerals (Table 1-3).

Conclusions

Soil development along the studied catena emerged as essentially a weathering sequence, controlled almost solely by relief and climate. Besides weathering, erosion and accumulation influenced all profiles, but their recent effects appeared only minor under the natural vegetation. As all soils involved in our study were fine-textured, the pattern of chemical properties and taxonomic units were largely attributable to water regime, with pronounced leaching at the steeper sections. Pedogenic history and minor differences in parent material were not recognized to affect soil properties to an extent relevant for plant growth on the escarpment.

Yet in the graben, accumulation of soluble salts and the formation of smectites during moist phases of the Holocene influence site conditions significantly. The altitudinal decomposition gradient in the Rift Valley escarpment is moderate, and C/N ratios do not point to much worse litter quality with elevation. As nutrients appeared largely associated to the organic matter (directly and through CEC) and conserved by the high internal cycling in the natural forests, the ongoing forest destruction might lead to a significant decline in soil fertility and off-site damages to the water resources of the semi-arid basin. The altitudinal range covered by our study and the intermediate volcanic substrate are typical of much of the Ethiopian highlands. The studied region can thus serve as a model for soil formation in the Ethiopian highlands and suits well for in-depth studies on ecological gradients and ecosystem processes.

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References

Abate A (2004) Biomass and nutrient studies of selected tree species of natural and plantation forests: Implications for a sustainable management of the Munessa-Shashemene Forest, Ethiopia. PhD dissertation. Faculty of Biology, Chemistry and Geosciences. University of Bayreuth, Bayreuth, Germany, 163 p

Alexander EB, Pichott JH (1979) Soil organic matter in relation to altitude in equatorial Colombia. Turrialba 29:183-188

Alexander EB, Mallory JI, Colwell WL (1993) Soil-Elevation Relationships on a Volcanic Plateau in the Southern Cascade Range, Northern California, USA. Catena 20:113-128

Avery BW, Bascomb CL (eds) (1974) Soil survey laboratory methods., Harpenden

Benvenuti M, Carnicelli S, Belluomini G, Dainelli N, Di Grazia S, Ferrari GA, Iasio C, Sagri M, Ventra D, Atnafu B, Kebede S (2002) The Ziway-Shala lake basin (main Ethiopian rift, Ethiopia): a revision of basin evolution with special reference to the Late Quaternary. Journal of African Earth Sciences 35:247-269

Bewket W, Stroosnijder L (2003) Effects of agroecological land use succession on soil properties in Chemoga watershed, Blue Nile basin, Ethiopia. Geoderma 111:85-98

Billi P, Dramis F (2003) Geomorphological investigation on gully erosion in the Rift Valley and the northern highlands of Ethiopia. Catena 50:353-368

Blume H-P, Schwertmann U (1969) Genetic evaluation of profile distribution of aluminium, iron and manganese oxides. Soil Science Society of America Journal 33:438-444

Brunner AC, Park SJ, Ruecker GR, Dikau R, Vlek PLG (2004) Catenary soil development influencing erosion susceptibility along a hillslope in Uganda. Catena 58:1-22

Carey AE, Lyons WB, Owen JS (2005) Significance of landscape age, uplift, and weathering rates to ecosystem development. Aquat Geochem 11:215-239

Chadwick OA, Gavenda RT, Kelly EF, Ziegler K, Olson CG, Elliott WC, Hendricks DM (2003) The impact of climate on the biogeochemical functioning of volcanic soils. Chemical Geology 202:195-223

Chalie F, Gasse F (2002) Late Glacial-Holocene diatom record of water chemistry and lake level change from the tropical East African Rift Lake Abiyata (Ethiopia). Palaeogeogr Palaeocl 187:259-283

Chernet T, Travi Y, Valles V (2001) Mechanism of degradation of the quality of natural water in the Lakes Region of the Ethiopian rift valley. Water Res 35:2819-2832

Chorover J, Amistadi MK, Chadwick OA (2004) Surface charge evolution of mineral-organic complexes during pedogenesis in Hawaiian basalt. Geochimica Et Cosmochimica Acta 68:4859-4876

Darbyshire I, Lamb H, Umer M (2003) Forest clearance and regrowth in northern Ethiopia during the last 3000 years. Holocene 13:537-546

Dubroeucq D, Geissert D, Quantin P (1998) Weathering and soil forming processes under semi-arid conditions in two Mexican volcanic ash soils. Geoderma 86:99-122

Dubroeucq D, Geissert D, Barois I, Ledru MP (2002a) Biological and mineralogical features of Andisols in the Mexican volcanic higlands. Catena 49:183-202

Dubroeucq D, Geissert D, Barois I, Ledru M-P (2002b) Biological and mineralogical features of Andisols in the Mexican volcanic highlands. Catena 49:183-202

Eshetu Z, Giesler R, Högberg P (2004) Historical land use pattern affects the chemistry of forest soils in the Ethiopian highlands. Geoderma 118:149-165

Ethiopian Mapping Authority (1988) National Atlas of Ethiopia. EMA, Addis Abeba

FAO, ISRIC, ISSS (1998) World reference base for soil resources. Food and Agriculture Organization of the United Nations, Rome, Italy

Fritzsche F, Abate A, Fetene M, Beck E, Weise S, Guggenberger G (2005) Soil-plant hydrology of indigenous and exotic trees in an Ethiopian montane forest. Tree Physiology:(submitted)

Gasse F, Vancampo E (1994) Abrupt postglacial climate events in West Asia and North-Africa monsoon domains. Earth and Planetary Science Letters 126:435-456

Gindaba J, Olsson M, Itanna F (2004) Nutrient composition and short-term release from *Croton macrostachyus* Del. and *Millettia ferruginea* (Hochst.) Baker leaves. Biology and Fertility of Soils 40:393-397

Guth PL (1995) Slope and aspect calculations on gridded elevation models: examples from a geomorphometric toolbox for personal computers. Zeitschrift für Geomorphologie 101:31-52

Kirschbaum MUF (1995) The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic matter storage. Soil Biology and Biochemistry 27:753-760

Le Turdu C, Tiercelin JJ, Gibert E, Travi Y, Lezzar KE, Richert JP, Massault M, Gasse F, Bonnefille R, Decobert M, Gensous B, Jeudy V, Tamrat E, Mohammed MU, Martens K, Atnafu B, Chernet T, Williamson D, Taieb M (1999) The Ziway-Shala lake basin system, Main Ethiopian Rift: influence of volcanism, tectonics, and climatic forcing on basin formation and sedimentation. Palaeogeogr Palaeocl 150:135-177

Legesse D, Gasse F, Radakovitch O, Vallet-Coulomb C, Bonnefille R, Verschuren D, Gibert E, Barker P (2002) Environmental changes in a tropical lake (Lake Abiyata, Ethiopia) during recent centuries. Palaeogeogr Palaeocl 187:233-258

Legesse D, Vallet-Coulomb C, Gasse F (2004) Analysis of the hydrological response of a tropical terminal lake, Lake Abiyata (Main Ethiopian Rift Valley) to changes in climate and human activities. Hydrol Process 18:487-504

Lemenih M, Itanna F (2004) Soil carbon stocks and turnovers in various vegetation types and arable lands along an elevation gradient in southern Ethiopia. Geoderma 123:177-188

Lemenih M, Karltun E, Olsson M (2005) Assessing soil chemical and physical property responses to deforestation and subsequent cultivation in smallholders farming system in Ethiopia. Agriculture, Ecosystems and Environment 105:373-386

Lundgren B (1971) Soil studies in a montane forest in Ethiopia. In. Royal College of Forestry, Department of Forest Ecology and Forest Soils, Research Notes No.11, Stockholm

Mehra OP, Jackson ML (1960) Iron oxide removal from soils and clays by dithionite-citrate systems buffered with sodium bicarbonate. Clays and Clay Mineralogy 7:317-327

Meijer EL, Buurman P (2003) Chemical trends in a perhumid soil catena on the Turrialba volcano (Costa Rica). Geoderma 117:185-201

Ndayiragije S, Delvaux B (2003) Coexistence of allophane, gibbsite, kaolinite and hydroxy-Al-interlayered 2:1 clay minerals in a perudic Andosol. Geoderma 117:203-214

Nyssen J, Haile M, Moeyersons J, Poesen J, Deckers J (2000a) Soil and water conservation in Tigray (northern Ethiopia): the traditional daget technique and its integration with introduced techniques. Land Degrad Dev 11:199-208

Nyssen J, Poesen J, Haile M, Moeyersons J, Deckers J (2000b) Tillage erosion on slopes with soil conservation structures in the Ethiopian highlands. Soil Till Res 57:115-127

Nyssen J, Moeyersons J, Poesen J, Deckers J, Haile M (2003) The environmental significance of the remobilisation of ancient mass movements in the Atbara-Tekeze headwaters, Northern Ethiopia. Geomorphology 49:303-322

Nyssen J, Poesen J, Moeyersons J, Deckers J, Haile M, Lang A (2004) Human impact on the environment in the Ethiopian and Eritrean highlands - a state of the art. Earth-Sci Rev 64:273-320

Parfitt RL, Wilson AD (1985) Estimation of allophane and halloysite in three sequences of volcanic soils, New Zealand. In: Caldas EF, Yaalon DH (eds) Volcanic soils. Catena, Cremlingen-Destedt, pp 3-8

Porder S, Paytan A, Vitousek PM (2005) Erosion and landscape development affect plant nutrient status in the Hawaiian Islands. Oecologia 142:440-449

Pyle DM (1999) Widely dispersed Quaternary tephra in Africa. Global and Planetary Change 21:95-112

Schreck CJI, Semazzi FHM (2004) Variability of the recent climate of Eastern Africa. International Journal of Climatology 24:681-701

Schrumpf M (2004) Biogeochemical investigations in old growth and disturbed forest sites at Mount Kilimanjaro. PhD dissertation. University of Bayreuth, Bayreuth

Schuur EAG, Chadwick OA, Matson PA (2001) Carbon cycling and soil carbon storage in mesic to wet Hawaiian montane forests. Ecology 82:3182-3196

Sedov SN, Solleiro-Rebolledo E, Gama-Castro JE (2003) Andosol to Luvisol evolution in Central Mexico: timing, mechanisms and environmental setting. Catena 54:495-513

Soil Survey Staff (2003) Keys to Soil Taxonomy, Ninth edn. United States Department of Agriculture, Natural Resources Service, Washington, USA

Solomon D, Lehmann J, Tekalign M, Fritzsche F, Zech W (2001) Sulfur fractions in particle-size separates of the sub-humid Ethiopian highlands as influenced by land use changes. Geoderma 102:41-59

Solomon D, Fritzsche F, Lehmann J, Tekalign M, Zech W (2002a) Soil organic matter dynamics in the subhumid agroecosystems of the Ethiopian Highlands: evidence from natural ^{13}C abundance and particle-size fractionation. Soil Science Society of America Journal 66:969-978

Solomon D, Fritzsche F, Tekalign M, Lehmann J, Zech W (2002b) Soil organic matter composition in the subhumid Ethiopian highlands as influenced by deforestation and agricultural management. Soil Science Society of America Journal 66:68-82

Solomon D, Lehmann J, Mamo T, Fritzsche F, Zech W (2002c) Phosphorus forms and dynamics as influenced by land use changes in the sub-humid Ethiopian highlands. Geoderma 105:21-48

Solomon D, Lehmann J, Kinyangi J, Liang BQ, Schafer T (2005) Carbon K-edge NEXAFS and FTIR-ATR spectroscopic investigation of organic carbon speciation in soils. Soil Science Society of America Journal 69:107-119

Sonneveld BGJS, Keyzer MA (2003) Land under pressure: soil conservation concerns and opportunities for Ethiopia. Land Degrad Dev 14:5-23

Stewart BW, Capo RC, Chadwick OA (2001) Effects of rainfall on weathering rate, base cation provenance, and Sr isotope composition of Hawaiian soils. Geochimica et Cosmochimica Acta 65:1087-1099

Street FA (1979) Late Quaternary precipitation estimates for the Ziway-Shala basin, Ethiopia. Palaeoecology of Africa 1:99-110

Street-Perrott FA, Roberts N, Metcalfe S (1985) Geomorphic implications of late Quaternary hydrological and climatic changes in the Northern Hemisphere tropics. In: Douglas I, Spencer T (eds) Environmental Change and Tropical geomorphology. Allen & Unwin, London, pp 165-184

Sumner ME, Miller WP (1996) Cation exchange capacity and exchange coefficients. In: Sparks DL et al. (eds) Methods of Soil Analysis, Part 3: Chemical Methods. Soil Science Society of America, Madison, USA, pp 1201-1229

Taddese G, Saleem MAM, Abyie A, Wagnew A (2002) Impact of grazing on plant species richness, plant biomass, plant attribute, and soil physical and hydrological properties of vertisols in East African highlands. Environ Manage 29:279-289

Teketay D (1992) Human impact on a natural montane forest in southeastern Ethiopia. Mt Res Dev 12:393-400

Tematio P, Kengni L, Bitom D, Hodson M, Fopoussi JC, Leumbe O, Mpakam HG, Tsozue D (2004) Soils and their distribution on Bambouto volcanic mountain, west Cameroon highland, central Africa. Journal of African Earth Sciences 39:447-457

Zeleke TB, Grevers MCJ, Si BC, Mermut AR, Beyene S (2004) Effect of residue incorporation on physical properties of the surface soil in the South Central Rift Valley of Ethiopia. Soil Till Res 77:35-46

Ziegler K, Hsieh JCC, Chadwick OA, Kelly EF, Hendricks DM, Savin SM (2003) Halloysite as a kinetically controlled end product of arid-zone basalt weathering. Chemical Geology 202:461-478

Study 2:

Signal improvement in elemental analyzer-continuous flow isotope ratio mass spectrometry for samples with low sulfur contents by on-line concentration adjustment

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Abstract

Elemental analyzer-continuous flow isotope ratio mass spectrometry has become a standard procedure for the determination of δ^{34}S values in recent years. Yet common procedures are frequently dissatisfactory for organic as well as mineral samples with very low concentrations of sulfur. We present a method employing cold trapping of SO_2 to adjust gas concentration for the subsequent determination of its isotope signature. Analytical accuracy is comparable to the common on-line measurement after elemental analysis (CF-EA-IRMS) without trapping, showing a maximum standard deviation of ± 0.4 ‰ δ^{34}S. The absence of memory effects is demonstrated by subsequent analysis of samples with a large difference in δ^{34}S and by prolonged freezing of the carrier gas, yielding virtually no S concentration peak. The method was tested using less than 15 % (6 µg) of the sulfur required for a conventional isotope analysis at comparable signal intensity, but even smaller samples can be analyzed precisely. This facilitates the on-line δ^{34}S determination in small biologic and mineral samples virtually regardless of the matrix, as measurements of sandstone, soil and plant samples have shown.

Keywords:

Cold trapping, IRMS, low concentration, organic samples, sulfur isotope analysis.

Introduction

While studied for a long time in geochemistry, sulfur isotopic composition has moved only recently into the focus of a wider range of ecological applications (e.g. Awonaike et al. 1993; Mayer and Krouse 1996; Monaghan et al. 1999; Norman et al. 2002; Lott et al. 2003; Tea et al. 2003; Fox et al. 2004). This might on the one hand be ascribed to the fact that sulfur in ecosystems has occupied a far less prominent position due to its low concentration and common availability in industrialized countries, on the other hand analytical procedures have posed obstacles to processing large sample sets fast and precisely.

Rather precise off-line methods (Yanagisawa and Sakai 1983) involve plenty of disadvantages for routine analyses, such as large sample mass and high time requirement for preparation, as well as memory effects due to SO_2 adsorption in the analytical line (Han et al. 2002). Thus, continuous-flow (CF) analysis currently constitutes the only viable method to analyze large numbers of samples with high differences in δ^{34}S.

The methodological improvements presented in this contribution proved necessary, as conventional analysis did not allow us to reliably determine isotope signatures from samples obtained in a ^{34}S field labelling study on sustainable forestry in Ethiopia. This was to be ascribed to the low S concentration of these plant and tropical soil samples, sometimes amounting to less than 300 mg kg^{-1}, at very wide C:S ratio of up to 200. This would have required high sample mass implying incomplete combustion. More important, the high carbon content led to excessive generation of CO_2 – and thereby dilution of the SO_2 peak. Open-split dilution was suitable to spare the ion source – but it was of no use to avoid SO_2 peak broadening leading to low signal intensity.

Different strategies have been pursued to tackle these problems. Giesemann et al. (1994) applied pure chemicals obtained through off-line conversion of natural samples. Most recent work has focused on methods optimizing combustion of natural samples and GC separation of SO_2 (Grassineau et al. 2001; Kester et al. 2001; Studley et al. 2002; Yun et al. 2004). Although these techniques have helped to push the analytical limit, success is largely dependent on sample matrix. In this contribution, we describe a different approach that makes the δ^{34}S analysis virtually independent of the sample matrix, i.e. achieving higher detector signal intensities by pre-concentrating SO_2 in a cold trap.

Materials and Methods

The measurement of the $\delta^{34}S$ isotope ratios was performed at the Freiberg Isotope Laboratory of the Institute of Mineralogy using a Carlo Erba EA1110 elemental analyzer coupled to a Thermo Finnigan Delta^{plus} (Thermo Finnigan, Bremen, Germany) isotope ratio mass spectrometer (IRMS). Different standards (6.5 - 10 µg S) with a known isotopic composition (Table 2-1) and grinded sandstone, soil and plant samples (4 – 10 µg S) were packed in 3.3 x 5 mm (7.5 mg) tin capsules with V_2O_5 added to enhance combustion. A sketch draw of the continuous-flow analytical system (He as a carrier at 90 ml_n min^{-1}) is represented in Fig. 2-1.

The samples were combusted in an oxygen atmosphere at 1020 °C in a quartz reactor tube filled with quartz wool, WO_3 and Cu wire. Due to the additional heating by the combustion of the tin, complete conversion of S compounds to SO_2 can be assumed (Barrie and Prosser 1996). As - even with properly dried organic samples - water condensation can appear in the device right after leaving the combustion furnace, stainless steel tubing constantly heated to 110 °C was used to directly connect a water trap filled with P_2O_5 to the furnace outlet. Subsequent GC separation of the sample gas was performed using a Poropak QS Teflon column at 85 °C.

Table 2-1: Known isotope ratios ($\delta^{34}S$ VCDT) of standard substances, measured values, linearly corrected values, sample numbers and standard deviations.

Identifier	compound	known# $\delta^{34}S$	measured $\delta^{34}S$ (‰ VCDT)	corrected $\delta^{34}S$	n	SD
Ag_2S*	Ag_2S	1.0	1.19	0.91	7	0.16
S-1	Ag_2S	-0.3	-0.15	-0.46	7	0.35
S-3	Ag_2S	-32.3	-27.66	-32.33	9	0.42
SO-6	$BaSO_4$	-34.1	-28.83	-33.88	4	0.36
NBS127	$BaSO_4$	20.3	18.15	20.44	9	0.20

#Data from IAEA (2004), except for identifier „Ag_2S"
*laboratory-internal standard

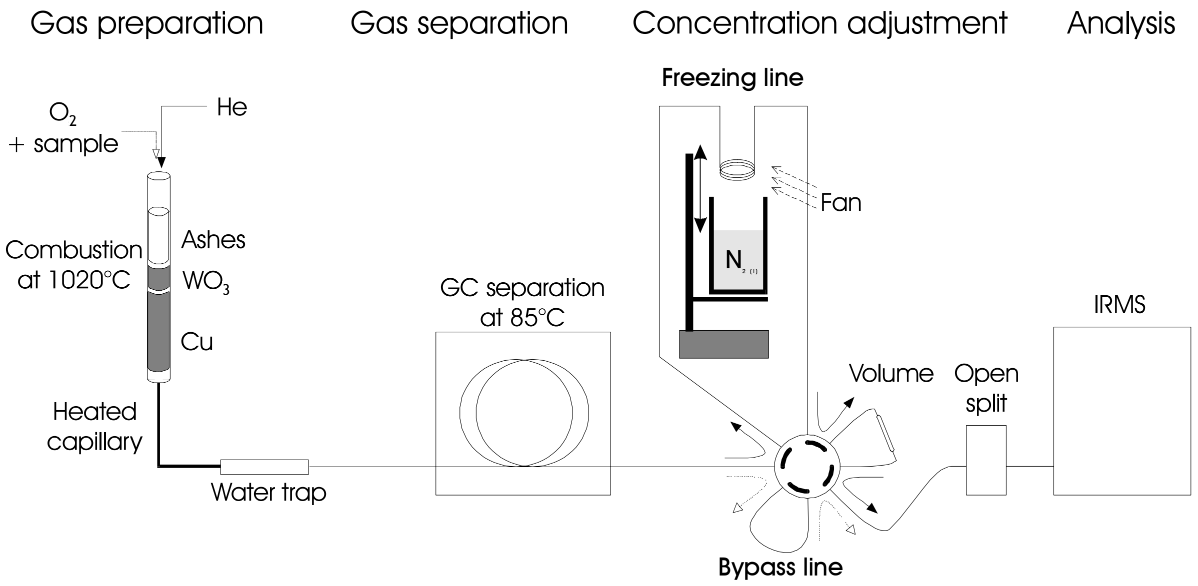

Fig. 2-1: Sketch draw of the technical configuration of the analytical system.

Separation of CO_2 and SO_2 by cold-trapping requires proper combustion and GC separation, as the freezing points of CO_2 and SO_2 are almost the same (-76 °C and -79 °C at atmospheric pressure, respectively). The outlet capillary of the GC system was connected to a Valco 8-port valve (VICI AG, Schenkon, Switzerland) to switch the flow between a freezing capillary for concentrating the SO_2 peak and a bypass line, controlled by an electronic unit to automatically implement a time program. The 8-port configuration enabled us to manipulate gas flow characteristics in order to modify signal peak shape. The sample gas was directed from the valve outlet into a ConFlo II open split interface (Thermo Finnigan, Bremen, Germany) connected to the IRMS.

Concentration adjustment of the SO_2 was done as follows: Peaks of N_2 and CO_2 from the elemental analyzer were directed through the bypass line and diluted with He by the open-split interface in order to keep the ion flux in the IRMS low. Sample gas (SO_2) flow was then switched into windings 50 cm long of the freezing capillary (150 cm Hastelloy C®, 0.7 mm inner diameter, VICI AG, Schenkon, Switzerland) dipped into liquid nitrogen to trap the SO_2 peak. Hastelloy C® was chosen as a material with high resistance to corrosion and favourable thermal properties such as lower heat conductivity than stainless steel, avoiding too rapid release of the frozen solid SO_2. After a specified time, the nitrogen bath was removed, and the capillary was heated by a hot-air fan. A freezing duration of 170 s was identified as appropriate for trapping the complete SO_2 peak from all kind of samples. Although room temperature is sufficient to evaporate solid SO_2 completely (boiling point

-10 °C), a hot-air fan ensures more constant conditions and complete desorption of SO_2 or H_2SO_3 as well as traces of water from the tubing. The gasified SO_2 had to pass an additional volume before entering the open-split interface to broaden the peak finally detected in the IRMS.

Sample gas was measured referring to laboratory standard SO_2 gas from one of the dual inlet bellows, following 100 s after the thawed sample SO_2 peak. All measured values were reported in the $\delta^{34}S$ notation according to the VCDT scale after linear correction for exact amplification. Samples were corrected for amplification ratio and signal intensity by linear calibration (Grassineau et al. 2001). Background was monitored for every sample to ensure analytical precision, providing information on ageing of the combustion reactor as well.

Results and Discussion

Typical chromatograms are presented for the conventional method without pre-concentration (Fig. 2-2a) and employing concentration adjustment (Fig. 2-2b), obtained by combustion of an equivalent of 43.7 µg S and 6.2 µg S, respectively. While peak height is the same in both cases, the peak area reflecting the amount required for one analysis is only 15 % in Fig. 2-2b. Two standard gas peaks were measured in both cases to check the stability of the signal. It is essential to collect SO_2 in the freezing capillary until well beyond the retention time of the main SO_2 peak, as the complete peak has to be trapped until the true background level is reached, in order to avoid chromatographic isotope effects.

The analytical results from standard samples of known isotopic composition over a wide range of $\delta^{34}S$ values are displayed in Table 2-1. Accuracy of the isotope determination was ± 0.4 ‰ $\delta^{34}S$ (1 σ) or better for both pure chemicals (Table 2-1), organic and rock samples (Table 2-2). This concurs with the value for isotope measurements without concentration adjustment using the same instrumental setup. Isotope ratio determination was linear within the tested range of more than 50 ‰. Correlation of the measured values with their expected isotopic composition (Fig. 2-3) was 1 for the median and mean values, and slightly smaller for all individual values ($r^2 = 0.9997$). Fig. 2-4 shows the corrected measured values of the samples maintaining the analysis order to check for memory effects. Samples with even a large difference in $\delta^{34}S$ appeared unaffected by the previous samples. This concurs with the results by Yun et al. (2004). Inter-sample contamination due to incomplete combustion and SO_2 retention in the sample line was tested by running the trapping apparatus for several cycles of the elemental analyzer with empty samples and heating the tubing. This procedure is more sensitive than running blanks in the standard procedure as applied by Grassineau et al. (2001). Still, subsequent rapid thawing led to SO_2 peaks at background level.

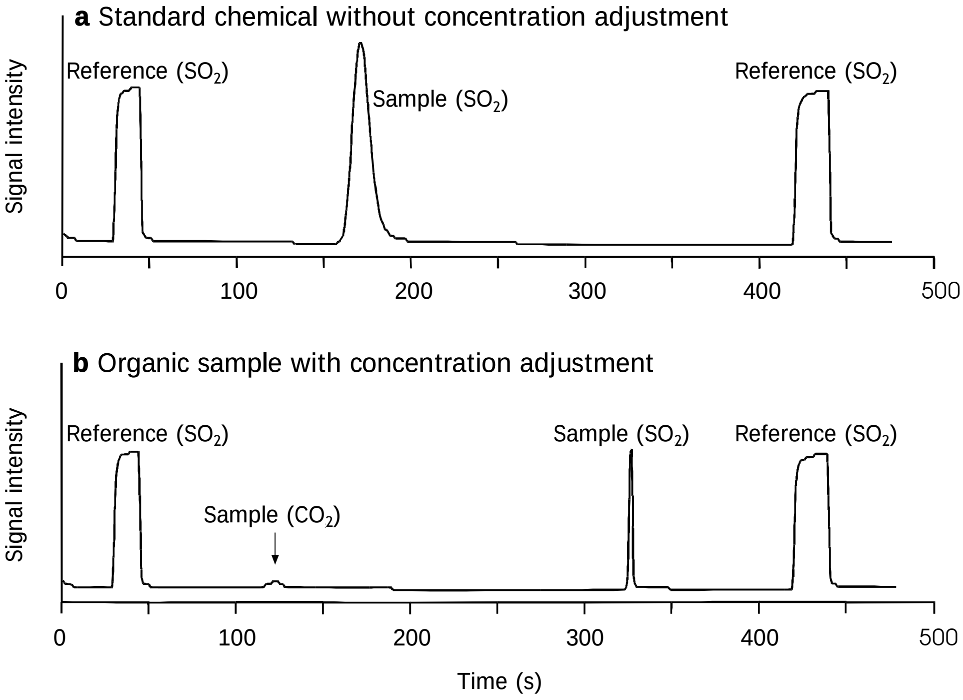

Fig. 2-2: Ion current of the IRMS detector (a) with standard procedure (43.7 µg S as Ag_2S, with buffer volume) and (b) employing concentration adjustment (6.2 µg S).

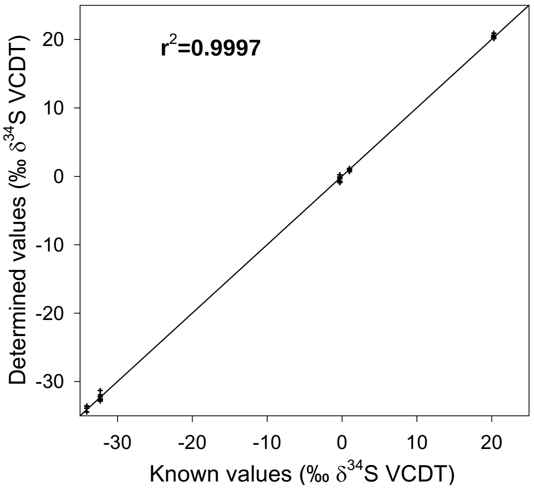

Fig. 2-3: Correlation of known $\delta^{34}S$ values and isotopic values determined employing concentration adjustment for five standards (6.7 – 10.0 µg S content).

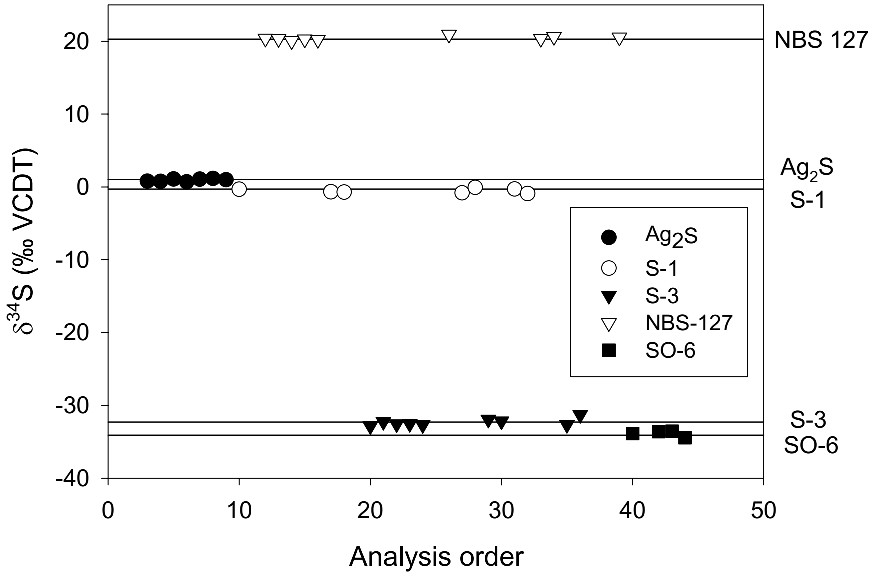

Fig. 2-4: Measured values of standard samples in analysis order (mean values are represented as reference lines).

First measurements of two sandstone samples of very low sulfur content (Table 2-2), which could not be measured with the standard configuration, yielded analytical precision comparable to pure chemicals (± 0.3 ‰ $\delta^{34}S$). They were slightly more positive than the values obtained from water and soda extracts, presumably due to more complete conversion and less contamination for the direct-combustion method. Analysis of plant and soil samples yielded standard deviations below 0.3 ‰ (n = 4). The method was extensively applied on more than one thousand soil and plant samples as well as soil extracts from Ethiopia (Fritzsche et al. 2005).

Table 2-2: Sulfur content and replicate corrected measurements of isotope ratios ($\delta^{34}S$ values) of sandstone samples from Germany and soil and plant samples from Ethiopia (individual replicates, means and standard deviations for measurements).

	S content	**1**	**2**	**3**	**4**	**Mean**	**SD**
Sample type	mg S kg^{-1}	$\delta^{34}S$ (‰ VCDT)					
Sandstone 1	1415	7.03	6.69	6.64	6.85	**6.81**	0.18
Sandstone 2	202	-29.27	-29.81	-29.51	-29.84	**-29.61**	0.27
Topsoil	766	10.53	10.44	10.59	10.08	**10.41**	0.23
Leaves	1200	9.36	9.88	9.54	9.74	**9.63**	0.23

Conclusions

The presented procedure provides a means to automatically analyze samples containing very little sulfur, extending the measuring range by up to one magnitude. It is suitable to analyze large sample sets, as one analysis requires only about 500 seconds. Still, technical adjustments to guarantee a clean gas line and close monitoring of the whole analytical system are inevitable to obtain reliable results. Cold trapping proved an accuracy-maintaining method to enhance signal intensity without the disadvantage of excessive sample size, applicable to samples with different matrices. The integration of an 8-port valve in the concentration-adjustment unit implies several advantages: 1) Immediate response to the freezing procedure ensures exact trapping of closely succeeding peaks. 2) Micro-amounts of sulfur can be measured after thawing in a closed system minimizing isotope fractionation. 3) Modification of the buffering volume in combination with the speed of thawing gives wide-ranging flexibility to the analyst to react to different sample properties. Integrating a mass flow detector before the concentration adjustment unit would allow to automatically control multiple trapping lines for multiple gas analysis, extendable even to GC-C-IRMS procedures. An optimization of the presented system might improve analytical performance to determine δ^{34}S of samples containing less then 10 % of the amount of sulfur required without concentrating.

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References

Awonaike KO, Danso SKA, Zapata F (1993) The use of double isotope (^{15}N and ^{34}S) labelling technique to assess the suitability of various reference crops for estimating nitrogen fixation in *Gliricidia sepium* and *Leucaena leucocephala*. Plant and Soil 155/156:325-328

Barrie A, Prosser J (1996) Automated analysis of light-element stable isotopes by isotope ratio mass spectrometry. In: Boutton TW, Yamasaki SI (eds) Mass Spectrometry of Soils. Dekker, New York, pp 1-46

Fox MA, Zhao FJ, McGrath SP (2004) A new method for the determination of the $^{34}S/^{32}S$ ratio of water-soluble sulphur in soil. International Journal of Environmental Analytical Chemistry 84:323-329

Fritzsche F, Solomon D, Tichomirowa M, Guggenberger G (2005) Sulfur cycling in natural forest versus plantations: a ^{34}S litter-labelling experiment in a South-Ethiopian montane forest. Oecologia:(submitted)

Giesemann A, Jäger HJ, Norman AL, Krouse HR, Brand WA (1994) On-line sulfur-isotope determination using an elemental analyzer coupled to a mass spectrometer. Analytical Chemistry 66:2816-2819

Grassineau NV, Mattey DP, Lowry D (2001) Sulfur isotope analysis of sulfide and sulfate minerals by continuous flow-isotope ratio mass spectrometry. Analytical Chemistry 73:220-225

Han L, Tanweer A, Szaran J, Halas S (2002) A modified technique for the preparation of SO_2 from sulphates and sulphides for sulphur isotope analysis. Isotopes in Environmental Health Studies 38:177-183

Kester CL, Rye RO, Johnson CA, Schwartz C, Holmes C (2001) On-line sulfur isotope analysis of organic material by direct combustion: preliminary results and potential applications. Isot Environ Healt S 37:53-65

Lott CA, Meehan TD, Heath JA (2003) Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base. Oecologia 134:505-510

Mayer B, Krouse HR (1996) Prospects and limitations of an isotope tracer technique for understanding sulfur cycling in forested and agro-ecosystems. Isot Environ Healt S 32:191-201

Monaghan JM, Scrimgeour CM, Stein WM, Zhao FJ, Evans EJ (1999) Sulphur accumulation and redistribution in wheat (*Triticum aestivum*): A study using stable sulphur isotope ratios as a tracer system. Plant, Cell and Environment 22:831-839

Norman AL, Giesemann A, Krouse HR, Jäger HJ (2002) Sulphur isotope fractionation during sulphur mineralization: results of an incubation-extraction experiment with a Black Forest soil. Soil Biology and Biochemistry 34:1425-1438

Studley SA, Ripley EM, Elswick ER, Dorais MJ, Fong J, Finkelstein D, Pratt LM (2002) Analysis of sulfides in whole rock matrices by elemental analyzer-continuous flow isotope ratio mass spectrometry. Chemical Geology 192:141-148

Tea I, Genter T, Naulet N, Morvan E, Kleiber D (2003) Isotopic study of post-anthesis foliar incorporation of sulphur and nitrogen in wheat. Isot Environ Healt S 39:289-300

Yanagisawa F, Sakai H (1983) Thermal decomposition of barium-sulfate vanadium pentaoxide silica glass mixtures for preparation of sulfur-dioxide in sulfur isotope ratio measurements. Analytical Chemistry 55:985-987

Yun M, Wadleigh MA, Pye A (2004) Direct measurement of sulphur isotopic composition in lichens by continuous flow-isotope ratio mass spectrometry. Chemical Geology 204:369-376

Study 3:

Soil-plant hydrology of indigenous and exotic trees in an Ethiopian montane forest

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Abstract

Fast-growing trees are widely planted in the tropics to counteract deforestation. However, their specific strategies in water use are potentially detrimental to productivity and ecosystem water budget. In a comparative field study on seasonal soil-plant water dynamics of two exotics (*Cupressus lusitanica* and *Eucalyptus globulus*) and indigenous *Podocarpus falcatus* in South Ethiopia, we combined a 2.5-years record for climate and soil water availability, natural-abundance $\delta^{18}O$ profiles of soil and xylem water, destructive root sampling and transpiration measurements. Soil was driest under *C. lusitanica* with its dense canopy and shallow root system. This was most striking following a deficient wet season, with the wettest soil under *E. globulus*. Wet season transpiration of *C. lusitanica* was half of the other species. With dry soil, *P. falcatus* and *C. lusitanica* reduced transpiration by a factor of six and two, respectively, whereas *E. globulus* showed a five-fold increase. A shift of water uptake to deeper layers with the progressing dry season by all species was mirrored for *C. lusitanica* and *P. falcatus* by the relocation of live fine root biomass (LFR) to deeper layers. Under *P. falcatus*, variability of matric potential, narrow $\delta^{18}O$ depth gradients and high LFR indicated fast water redistribution. Subsoil water uptake was only important for *E. globulus*, having low topsoil LFR and tap roots exploiting deep water. *Podocarpus falcatus* emerged best adapted to varying soil moisture; however, both conifers might decrease growth in dry phases substantially. *Eucalyptus globulus* appeared largely independent of topsoil water, but might reduce groundwater recharge.

Keywords:

Cupressus lusitanica, delta-18O, *Eucalyptus globulus*, *Podocarpus falcatus*, root distribution, sap flow, seasonality, tensiometry.

Introduction

Scarcity of wood is a mounting problem in many parts of the tropics. This can be ascribed to the fact that a growing rural population is heavily dependent on fuel wood and timber for construction; at the same time, forest resources have been over-utilized and destroyed for a long time. Demand for wood by the urban centres aggravates forest exploitation. As a countermeasure, plantations have been established in many countries, mainly of fast-growing exotic tree species to ensure high production (FAO 2003). Although indigenous tree species appear favourable from the conservationist point of view as well as concerning their adaptation to their natural environment, they have been widely neglected (Negash 2003). This holds also true for Ethiopia, where deforestation has led to a decline in forest cover from about 20 % around 1900 to less than 3 % at present (de Vletter 1991). Starting from 1900, *Eucalyptus* as well as *Cupressus* and *Pinus* species have been promoted for forestry. But the performance of different trees greatly varies with climatic conditions, unsuitable species might lead to ecosystem degradation, and large plantations might influence particularly dry-season river discharge, which is valuable for irrigation (Pohjonen and Pukkala 1990; McJannet et al. 2000).

As exotic trees already play a fundamental role in commercial forests, sustainable forestry requires a sound scientific knowledge base about both indigenous and exotic tree species under a given environment. This was the motivation for an interdisciplinary study on sustainable forest utilization in South-Central Ethiopia, aiming at recommendations to secure the various beneficial functions of forests. A mosaic of natural forest remnants and systematically managed plantations of different exotics in the Munessa-Shashemene Forest with homogeneous site conditions facilitates direct comparison of different species at minimal variation of external factors (Abate 2004; Fritzsche et al. 2005).

In this contribution, we focus on soil hydrology and the response to changes in water availability of two popular, yet contrasting exotic (*Cupressus lusitanica* Mill. and *Eucalyptus globulus* Labill.) and one highly-valued indigenous tree species (*Podocarpus falcatus* (Thunb.) Mirb.) in this sub-humid environment. We hypothesized that (a) indigenous trees are well adapted to the soil moisture regime, while exotic trees show an inappropriate response, which can result in drought stress. This is attributable to (b) species-specific physiological strategies of transpiration regulation, or to (c) differences in the exploited soil volume due to the different root architecture and fine root activity. In order to test these hypotheses, soil as well as plants have to be included in a hydrological study.

Soil-atmosphere water transfer in forest ecosystems can hardly be studied by a single technique, as it is mainly mediated through vegetation (Unsworth et al. 2004), involving a variety of plant species and individuals growing in a complex structure. Various approaches have been pursued to get a comprehensive view on the mutual influence of soil moisture and vegetation. These include integrating soil water availability and root distribution (Yanagisawa and Fujita 1999); soil water content, water stable isotopes and δ^{13}C measurements to establish long-term water use efficiency (Ohte et al. 2003); water isotopic composition, soil water content and root profiles (Le Roux et al. 1995); sap flow, soil water content and water stable isotopes (Smith et al. 1998); and soil water content, sap flow and eddy fluxes (Unsworth et al. 2004).

In the present study, we are augmenting a 2.5-year time series of soil matric potential and a 2-month δ^{18}O time series with seasonally-resolved complementary approaches: Rooting systems of the respective trees species were characterized for their macroscopic architecture and their live fine root biomass (LFR) distribution; total transpiration of the respective tree species and their specific response to seasonal conditions were quantified by the sap flow.

While the matric potential at different depths gives information about the direction and extent of net water movement, the δ^{18}O approach allows to determine the source of water transferred through the pore system and plant roots. This is made possible by the fact that differences in rain water (Weltzin and McPherson 1997) and evaporation (Allison 1982) lead to isotope profiles of soil water (Melayah et al. 1996), whereas plant water uptake involves virtually no isotope fractionation (Bariac et al. 1994). By comparing the water isotope ratio of oxygen or hydrogen in the plant tissue with the isotope ratio in the soil water, an apparent depth of water uptake by a plant can be identified, as can be hydraulic redistribution through plant roots (Meinzer et al. 2001a). Such hydraulic redistribution was recognized to play an important role in maintaining ecosystem functioning by boosting biological activity in soil habitats that might otherwise be subject to water stress (e. g. Richards and Caldwell 1987; Moreira et al. 2003; Querejeta et al. 2003). Roots are the main instrument of plant water uptake and redistribution, and in turn they influence the soil pore system development. Root architecture and LFR are therefore essential parameters in soil hydrology. Measurements of water flux in the stem to the sites of transpiration as well as photosynthetic parameters inform about net root performance (Fetene and Beck 2004). Sap flow measurements give quite reliable estimates for canopy transpiration, while porometric measurements of stomatal conductance are primarily useful to identify physiological reactions, with various constraints in up-scaling.

By employing these different methodological approaches to study soil-plant water dynamics, we finally aim at the identification of environmentally sound silvicultural management systems.

Materials and Methods

Study area

This study was conducted at the eastern escarpment of the southern Main Ethiopian Rift Valley in the Munessa-Shashemene Forest (7°26’N 38°52’E), which is occupying an area of about 23000 ha (Silvanova 1996). The escarpment extends from the Rift Valley Lakes Basin at about 1600 m asl, covered by lacustrine sediments and pyroclastics from the Pliocene, to more than 3500 m asl at the marginal volcano structures composed of Pliocene trachytes (Benvenuti et al. 2002). Closed high forest spreads between 2000 m asl and 2800 m asl. The study site is located at an elevation of 2280 m asl with slopes of 5 - 15 % and has a sub-humid climate. Annual rainfall is about 1500 mm, mean annual temperature is 15 °C, ranging from 8 °C to 24 °C on the daily average. Although there is some rain throughout the year, rainfall shows a bimodal distribution with a rather unreliable small rainy season from March to May and a big rainy season from July to September. Relative humidity of the air ranges from 35 - 70 % in the dry season to well above 90 % during the rainy season.

The vegetation of the natural forest, as described by Abate (2004), is dominated by canopy species such as *Podocarpus falcatus* (Thunb.) Mirb., *Croton macrostachys* Hochst. ex Del., *Olea europaea* ssp. *cuspidata* (Wall. Ex. DE) Cifferri, *Schefflera abyssinica* Harms, and *Allophyllus abyssinica* (Hochst.) Radlkofer. The plantation forests were planted as monocultures of *Cupressus lusitanica* Mill. and *Eucalyptus globulus* Labill.

Soils are rich in clay and show a clear altitudinal zonation (Fritzsche et al. 2005), as the parent material of intermediate volcanites is quite homogenous throughout the area. Soils of the plots under investigation were classified as Mollic Nitisols according to the WRB system (FAO et al. 1998) and Typic Palehumults according to US Soil Taxonomy (Soil Survey Staff 2003). Table 3-1 gives an overview about chemical and physical properties of the studied soils. Site conditions were homogeneous, with the transport-related parameters texture and bulk density showing no significant differences between the three forest types under study (Y. Ashagrie, unpublished data). The analytical data concur with other studies in the same forest some 25 km to the south (Lemenih et al. 2004b).

Table 3-1: Basic characteristics of the soils under the studied trees.

Species	**Horizon**	**Depth**	**C_{org}**	**N**	**pH(KCl)**	**BD**	**Sand**	**Silt**	**Clay**
		cm	$g\ kg^{-1}$			$g\ cm^{-3}$	$g\ kg^{-1}$		
C. lusitanica	Ah	25	55.6	5.54	5.6	0.91	90	270	640
	AB	41	20.7	2.08	5.1	1.00	140	360	500
	B1	81	17.0	1.77	4.8	1.11	60	170	770
	B2	105	16.1	1.70	4.6	1.12	60	310	630
P. falcatus	Ah	15	122.3	9.04	6.3	0.73	196	304	500
	AB	29	25.7	2.09	6.1	0.97	228	232	540
	B1	68	16.4	1.39	5.6	1.15	85	180	735
	B2	108	11.3	1.10	4.0	1.11	80	183	737
	B3	150	5.3	0.95	3.7	1.01	66	166	768
E. globulus	Ah	10	59.3	6.30	5.3	0.91	140	370	490
	AB	27	45.7	4.93	5.1	0.94	140	300	560
	B1	69	20.0	2.24	4.8	1.07	100	240	660
	B2	106	13.0	1.51	4.7	1.12	100	170	730

Notes: "Depth" means the lower boundary; C_{org}: Organic carbon; N: Total nitrogen; BD: Bulk density.

All experiments of this study were conducted within a distance of less than 1 km at the same elevation, in a degraded *Podocarpus falcatus* (Thunb.) Mirb. dominated natural forest stand, in a *Cupressus lusitanica* Mill. plantation with an average of 610 trees ha^{-1} established in 1982 and in a *Eucalyptus globulus* Labill. stand planted in 1981 with 595 trees ha^{-1} counted on the average.

Methodology

Climate

Climate parameters were recorded every 15 min. by two µMetos automatic meteorological stations (Pessl Instruments, Weiz, Austria), one placed on an open area between the plots and another one in the canopy of the natural forest. The parameters most relevant for soil water budget were rainfall, wind speed and temperature, as well as daylight vapour pressure deficit (VPD) and solar radiation (400 – 900 nm) as the main driving forces of vegetation-mediated atmospheric water transfer. Potential evapotranspiration was estimated according to the Penman-Monteith equation from the open-area data.

Soil water matric potential

Single-tree-centred plots were set up in triplicate in the respective forest stands within a distance of 160 m from each other. Trees with a diameter at breast height (DBH) of about 20 - 30 cm and with undamaged crowns of typical shape were selected. Clusters of ceramic cup tensiometers reaching 20, 50 and 100 cm below the mineral soil surface were installed in April 2001 at a distance of about 1.5 m from the boles of the sample trees with three to four tensiometers per depth layer. The experimental plots were fenced and permanently guarded to avoid encroachment of animals. As soil water appeared to be still very dynamic at 100 cm, additional tensiometers were installed at 200 cm soil depth in October 2001. From May 2001 until October 2003, soil water potential (represented by the tensiometric potential) was recorded from tensiometers using a needle manometer, on a biweekly basis during dry periods and weekly during the rainy seasons.

Stable isotope signature of water

Out of the nine instrumented trees, six individuals were selected for the stable water isotope ($\delta^{18}O$) study, two *P. falcatus*, two *E. globulus* and two *C. lusitanica*. From October 2002 to December 2002, plant samples were collected from each tree in three replicates by cutting non-green woody twigs from the outer sun crown to obtain plant water not affected by ^{18}O enrichment due to atmospheric water transfer from leaves (Pate and Dawson 1999; Barbour et al. 2004). Corresponding soil samples were taken using a Pürckhauer-type auger from the respective depths (25, 50, 100, 200 cm), since soil water yields from suction cups were insufficient during the study period. Augering was done at a distance of about 3 m from the respective trees, not to disturb the sampling plots. Soil samples were cleaned from allochthonous material and cut out of the auger tip for every depth to get original samples. All samples were immediately transferred into gas-tight Exetainer® vials (Labco Ltd., High Wycombe, United Kingdom) and the vial atmosphere was exchanged by 1 % CO_2 in Helium (Linde AG, Unterschleissheim, Germany) as a gas for direct equilibration (Scrimgeour 1995). With the advantage of very modest requirements of sample size, this method has been shown to yield good results particularly for clay-rich media (Kelln et al. 2001). All samples were kept deep-frozen until measurement. Determination of the stable isotope ratios ($\delta^{18}O$ value) of the water in the samples was performed at the Centre for Environmental Research (UFZ) Halle-Leipzig using a Thermo Finnigan Delta S (Thermo Finnigan, Bremen, Germany) isotope ratio mass spectrometer (IRMS) coupled to a modified Gas Bench II application (Thermo Finnigan, Bremen, Germany), which had been improved by a cooling device to ensure constant conditions for equilibration and to avoid water condensation in the analytical circuit. Gas from the headspace of the vials was dried by gas diffusion and introduced into the IRMS from a sample loop after passing a chromatography column to purify CO_2 from other gases. Measurements were performed in triplicate after 24 h of equilibration at 19.5 °C. The isotope ratios were calculated with reference to laboratory standard CO_2 gas calibrated on international standards; samples of known isotopic composition were included in each analysis to guarantee correct results. The isotope ratio of ^{18}O and ^{16}O was reported in the delta notation to express small differences in isotope abundance by relating the measured isotope ratios R_{sample} to the ratio R_{st} of the standard VSMOW:

$$\delta^{18}O = \frac{R_{sample} - R_{st}}{R_{st}} \cdot 1000‰ \qquad \text{with} \quad R = \frac{at\%^{18}O}{at\%^{16}O}$$

Reproducibility determined by repeated measurements of test samples was 0.4 ‰ δ^{18}O (1 SD), similar to the value reported by Hsieh et al. (1998). In order to obtain characteristic δ^{18}O values for the plant samples as well as the soil water, median values are displayed of six (plant samples) and four (soil samples) replicates, respectively.

Root system

Root architecture of the respective tree species was studied by excavating one adult individual of comparable size (13 cm DBH) from the tree species according to Böhm (1979). The knowledge about root organization is essential for understanding fine root function and dynamics. Live fine root biomass was estimated by augering soil cores (8 cm diameter) around trees of comparable DBH from different depths (0 - 10 cm, 10 - 35 cm, 35 - 60 cm, 60 - 85 cm, 85 - 100 cm) and subsequent washing, identification and quantification of the live fine roots. Three lines were sampled at distances of 1 m, 2 m and 3 m from the bole of the same trees for the two seasons, as roots of different species have been shown to react differently to changing soil moisture availability (Reynolds et al. 1999). Sampling was done for dry season LFR in April 2002, and for wet season LFR in August 2002. These methods to study the root distribution were validated by profile wall mapping (Abate 2004).

Transpiration

Sap flow was measured on 5 individual trees from each species using the constant heat dissipation method (Granier 1987) on several days of the wet and dry seasons. Sap flow calculated from the gradient in temperature was scaled to whole-plant transpiration by multiplying the flux density with the sapwood area. These values were multiplied with the tree density to estimate canopy transpiration. Sap flow measurements have been shown not to represent the complete canopy water flux of a forest ecosystem (Wilson et al. 2001; Unsworth et al. 2004). Yet, the cited studies were not conducted in even-aged monocultures with a simple structure. Moreover, a complete water balance is not essential for the present study, as it primarily aims at identifying differences, which can be expected to have a different extent in other environments.

Statistical analysis

To obtain the soil matric potential at given depth for one date, the arithmetic mean over all tensiometers from the three plots of each tree species was calculated.

Water tension during soil drying was compared between the respective tree species by a Student's t test, treating the readings of each date as paired samples by subtracting the arithmetic mean of one species to correct for trends. It was assumed that preconditions like independence and normal distribution of the individual values as well as homogeneous variances for the dates of the sampling period were met.

The annual course of the variability of matric potential within the respective ecosystems was determined after smoothening the curve of the mean matric potentials for each date (Ψ) by their weighted neighbouring values according to the formula:

$$\Psi_i^* = \frac{3}{8} \cdot \left(\Psi_i + \frac{1}{2}\Psi_{i+1} + \frac{1}{2}\Psi_{i-1} + \frac{1}{3}\Psi_{i+2} + \frac{1}{3}\Psi_{i-2} \right) \quad \text{for all sampling dates } i$$

Variances for each date were calculated from the original individual replicates referring to these smoothened values Ψ^*. Finally, these variances were smoothened employing the same algorithm in order to get clearer information and erase artefacts at steep sections of the curves. These values constitute a combined variance of spatial and temporal variability, helping to identify mechanisms of water transport. This method is valid at least for the comparison of the curves for the respective species.

Results

Climate

Rainfall, temperature, as well as daylight VPD and solar radiation (Fig. 3-1) showed a clear seasonality, although there were considerable oscillations throughout the year on a weekly scale. The rainy season of 2002 yielded very little rainfall with only 75 % of the preceding and following "normal" years, causing a serious drought situation in the region. Temperature was quite balanced for the whole period of investigation with seasonal variations of about 3 °C, peaking in the small rainy season preceding the main rains. Vapour pressure deficit ran parallel to solar radiation and was mainly influenced by cloud cover; it was usually less than 0.5 kPa in the main rainy seasons, reaching up to 2.1 kPa at a high variability in the dry season and the small rainy seasons.

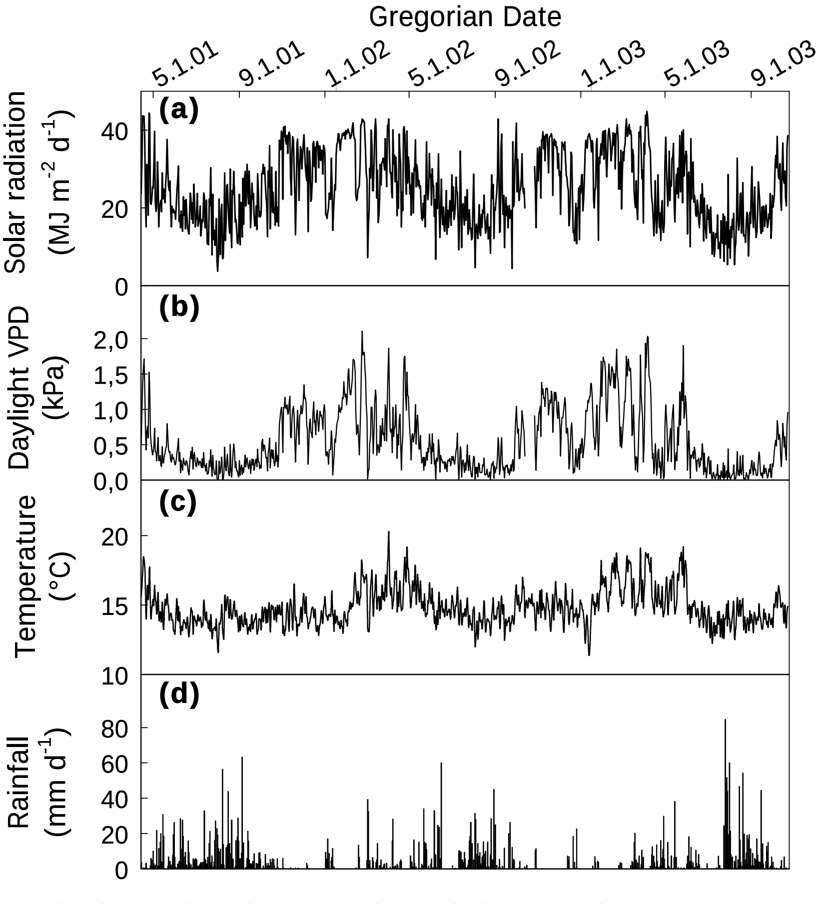

Fig. 3-1: Water-budget related meteorological data for the period of investigation on a daily basis: (a) Solar radiation, (b) Average of water vapour pressure deficit for daylight hours, (c) Temperature, (d) Rainfall.

Soil water transport and availability by matric potential

In principle, tensiometry provides a means to study changes in soil water budget and availability by monitoring the water potential directly (Dünisch et al. 2003). However, the calculation of water fluxes requires comprehensive information on the relationship of water potential, water content and hydraulic conductivity have to be known - which is particularly complicated for a clay soil with changes in the pore system due to swelling and shrinking, as they are typical for the sub-humid tropics. A further obstacle is posed by preferential flow, especially in the given clay soils with very low matric hydraulic conductivity. The pronounced dry season of the study site is complicating an exact determination of matric potential, as the equilibration of the water potential in the tensiometers after refilling with the surrounding soil is slower under dry conditions due to low unsaturated hydraulic conductivity. Notwithstanding these limitations, tensiometry gives valid information about changes in moisture, the direction of water movement and the water availability, which is physiologically more important than water content. Thus, we restrict ourselves to the comparison of the soil matric potential at sites with uniform soil conditions that should directly reflect species-dependent differences. The fine texture and the short distance between the plots justified to assume uniform pore systems for the soil matric; structural differences in aggregation are mainly relevant at high water potentials.

The mean soil water matric potential for the study period from May 2001 to October 2003 is represented in Fig. 3-2. The difference of cumulative rainfall and estimated evaporation termed "water balance" is given as a reference to relate the graphs to atmospheric water fluxes; surface runoff was negligible on the plots. No measurements were identified as outliers distorting the dataset, as mean and standard deviation corresponded well with median and inter-quartile range. Topsoil water availability showed a clear seasonality following the line of the "water balance" with only a minor lag. The year 2002 was much drier than 2001 and 2003, visible from the excess of evapotranspiration and markedly reduced soil moisture. Still, soil moisture was not yet reaching critical levels, since matric potential did not exceed values of -80 kPa during the investigation period.

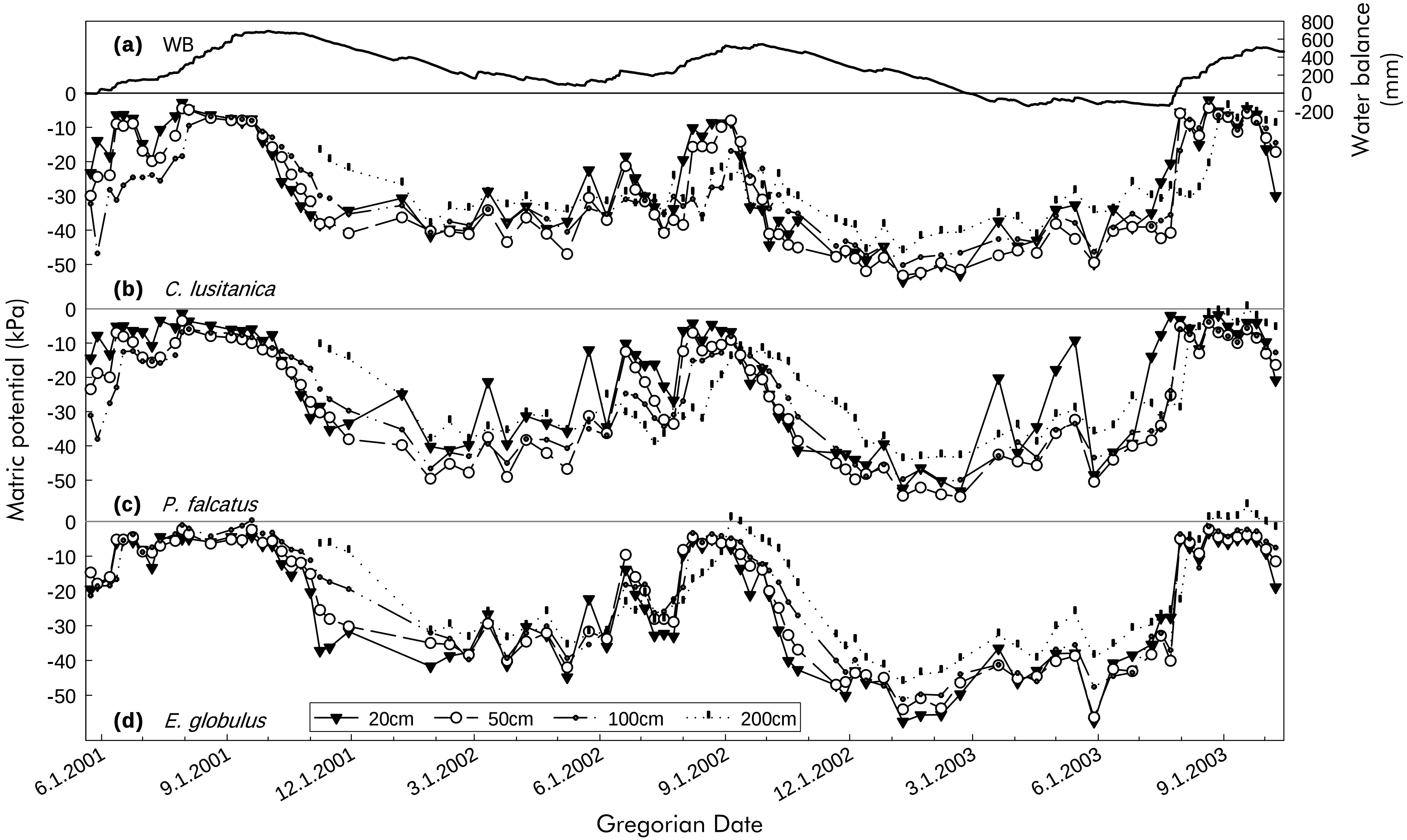

Fig. 3-2: Time series of "atmospheric water balance" and soil matric potential (from tensiometers at 20, 50, 100, 200 cm soil depth) for 2.5 years: (a) Water balance, (b) *Cupressus lusitanica,* (c) *Podocarpus falcatus,* (d) *Eucalyptus globulus.*

The soil under *C. lusitanica* exhibited the lowest mean matric potential, proving this to be the driest treatment. The range of matric potential was also lowest. Gradients at the onset of the dry season were steeper than for the other species, which means faster depletion of available soil water. This was much more pronounced for the topsoil than for the subsoil. Under *E. globulus*, soil water was highly dynamic over a wide range in all depth layers for all years. The replenishment of the profiles with water during the large rainy season took place at different speed. While *E. globulus* exhibited hardly a lag between the different soil layers reaching even saturation, *C. lusitanica* took longer than the duration of the rainy season to balance soil water budget. Saturation was not achieved, in 2002 very little infiltration reached below 50 cm. Water infiltration under *P. falcatus* showed a clear lag of about one month to reach equilibrium with the lowermost layers. Dry season rainfall had the strongest effect on topsoil under *P. falcatus*.

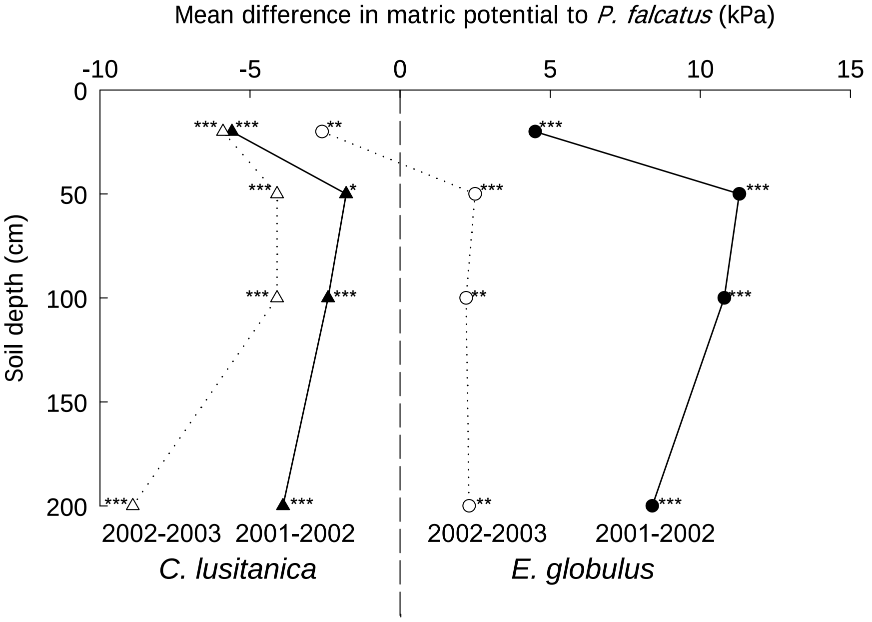

Fig. 3-3: Difference in soil matric potential relative to *Podocarpus falcatus* during the dry season of 2002 (10-01 to 2-02) and 2003 (9-02 to 2-03), respectively (t-test significance level for differences from 0; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

Differences in the matric potential of the respective depths of the three tree species during the dry season from October 2001 to February 2002 and from September 2002 to February 2003 (Fig. 3-3) were significant in all cases at $P < 0.001$ for the pair *C. lusitanica* - *E. globulus*, reaching up to 18 kPa. In the wetter year 2001, matric potential under *P. falcatus* was more similar to *E.*

globulus than to *C. lusitanica*. Maximum differences were always observed for *C. lusitanica* and *E. globulus*, except for the topsoil in the dry year 2001 when *P. falcatus* had the highest topsoil moisture. Water availability relative to the underlying soil was best in the topsoil of *P. falcatus*. In years with little rainfall (2002), relative gradients with soil depth were steepest under *C. lusitanica*, showing insufficient infiltration. As the difference was minor in dry years, soil under *E. globulus* was far wetter following the good rainy season.

Variability of soil matric potential

The variability of the matric potential can also provide information about water transport in soil. A high variability indicates fast redistribution of soil water in the profile, which can be the effect of preferential flow or hydraulic redistribution by plant roots. Moreover, a physiological feedback reaction of the trees such as an enhancement of root water uptake and transpiration can quickly absorb inhomogeneous distribution of soil water. Preferential flow in the heavy clay soils of the study sites might primarily result from cracks and – at a smaller scale - aggregation. In the field, large cracks were only observed on open profile walls, while fresh profile walls showed clear infiltration fronts.

Fig. 3-4 displays the smoothened time series of the variances relative to the smoothened mean matric potential for the respective depth of the three tree species, giving a combined information on both spatial and temporal variability. Rainfall is included as a reference, as variability might be particularly sensitive to rainfall in dry periods. Rainy season variability was minimal for all species in good rainy seasons. In 2002, the picture was very different. Variability under *C. lusitanica* did not reach values well below the mean. At 200 cm, only *E. globulus* achieved quite uniform (saturated) conditions. Dry season variability at 100 and 200 cm was minimal under *C. lusitanica*, which indicates matric flow at a low rate. In contrast, *P. falcatus* soil had the highest variability in soil water below 20 cm during dry periods with sporadic rainfall and during the small rainy season, indicating inhomogeneous water redistribution due to soil structure or active roots. Under *E. globulus*, variability at 200 cm reacted quite quickly to rainy seasons indicating fast and heterogeneous infiltration.

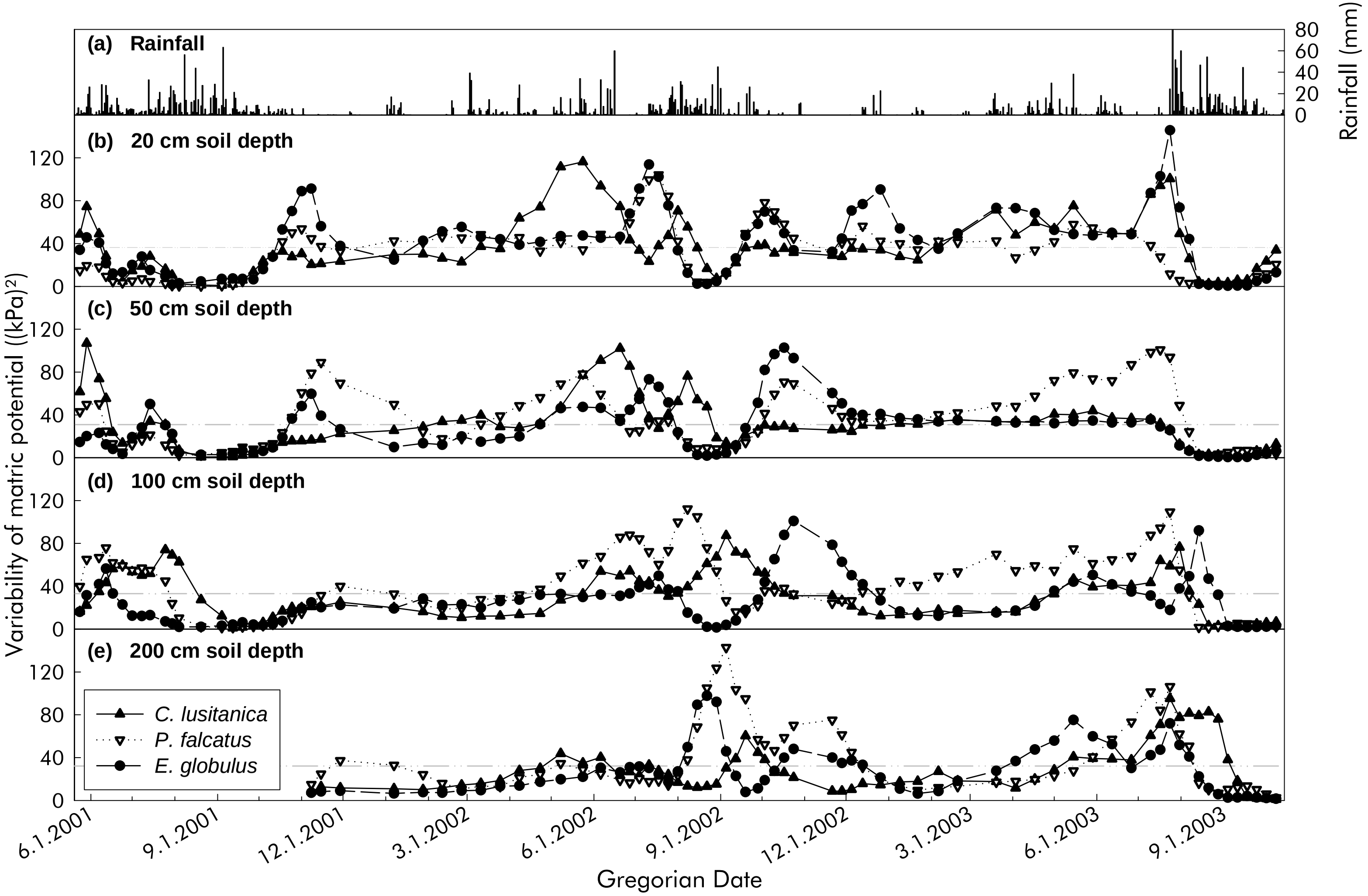

Fig. 3-4: Time series of spatial-temporal variances of matric suction for the respective depths of all treatments: (a) Rainfall, (b) 20 cm soil depth, (c) 50 cm soil depth, (d) 100 cm soil depth (e) 200 cm soil depth. Shaded grey lines represent the mean variability for all treatments of the respective depths.

δ^{18}O values

After the rainy season of 2002, natural isotopic composition of soil and plant water oxygen (δ^{18}O) was measured for two months with only very few rainfall events. The median values of the δ^{18}O values as well as their span within the profile of one species at one date are given in Table 3-2. The δ^{18}O values of deeper layers reflected the isotope signature of rain water from the main rainy season around -1 ‰ δ^{18}O, concurring with the values reported by Hailemichael et al. (2002) for a dataset covering several locations of the Ethiopian highlands and the Main Ethiopian Rift Valley. The range of δ^{18}O within the upper meter is well in line with studies from other regions (e.g. Drake and Franks 2003). Rainfall with light isotopic composition right before the sampling on 18 Oct. decreased the δ^{18}O values down to a considerable depth.

Table 3-2: Oxygen isotope ratios (δ^{18}O VSMOW) after the main rainy season of 2003 by tree species: Xylem water (median, *n* = 6), soil water (median, *n* = 4) at 20, 50, 100, 200 cm depth, and vertical span (in italics). Values higher or equivalent to the xylem water are represented as bold numbers.

		04 Oct.	11 Oct.	18 Oct.	25 Oct.	06 Nov.	20 Nov.	05 Dec.
C. lusitanica	Xylem	**2.3**	**1.5**	**0.6**	**1.4**	**0.7**	**0.4**	**0.4**
	20	2.0	1.2	**1.3**	**1.4**	**1.8**	**2.2**	**1.4**
	50	1.4	0.9	**0.7**	0.5	0.4	0.3	-0.2
	100	1.6	0.4	**0.8**	0.5	0.1	-0.1	-1.0
	200	0.4	0.1	-0.2	0.3	-0.4	-0.2	-0.9
	span	*1.9*	*1.5*	*1.5*	*1.1*	*2.1*	*2.4*	*2.4*
P. falcatus	Xylem	**2.1**	**1.6**	**0.1**	**1.7**	**1.3**	**1.2**	**1.3**
	20	2.0	1.2	**1.1**	1.6	1.1	0.6	0.7
	50	1.4	0.9	**0.8**	1.0	0.4	0.3	-0.2
	100	1.7	1.0	**0.8**	1.0	0.5	0.1	0.1
	200	0.7	0.5	0.0	0.1	-0.2	-0.3	-0.3
	span	*1.3*	*1.1*	*1.1*	*1.5*	*1.5*	*1.5*	*1.6*
E. globulus	Xylem	**1.2**	**0.8**	**0.4**	**1.5**	**1.2**	**0.1**	**0.1**
	20	**1.3**	**1.2**	**1.0**	**1.5**	**1.5**	**1.2**	**0.7**
	50	1.1	0.4	0.2	0.8	0.0	-0.3	-0.5
	100	0.5	-0.3	-0.3	-0.4	-0.6	-0.8	-1.1
	200	-0.1	-0.6	-0.9	-0.5	-0.7	-1.2	-1.3
	span	*1.4*	*1.9*	*1.9*	*2.0*	*2.2*	*2.5*	*2.0*

Root distribution

Pictures of excavated trees from the respective species visualize the different rooting systems (Fig. 3-5). *C. lusitanica* had a rather inhomogeneous flat root system hardly extending below 1 m with a high density at low distance. *P. falcatus* developed strong, expansive roots including tap roots reaching below 1.5 m. *E. globulus* seemed to pursue a very expansive strategy by extending low-biomass roots to far distances (> 3.5 m), including strong tap roots to more than 2 m depth. Live fine root biomass down to 100 cm soil depth as a quantitative measure is displayed in Fig. 3-6. *P. falcatus* had the largest LFR by far (open bubbles in Fig. 3-6). *C. lusitanica* reached two thirds of this value, whereas *E. globulus* had only 20 % of the LFR of *P. falcatus* in the upper 100 cm. Resolving this general picture in more detail (bar and dot chart of Fig. 3-6) reveals differences in depth distribution as well as seasonal shifts. Live fine roots of *C. lusitanica* showed a pronounced decrease with depth during the wet season. For the dry season, LFR was always higher with a higher proportion of LFR allocated to a depth below 35 cm. For *P. falcatus*, the LFR was much higher for the dry season than for the wet season, except for the upper 10 cm at 2 m distance from the bole. Rooting systems of *P. falcatus* and *C. lusitanica* became less homogenous during the dry season. Both species extended their roots during the dry season to extract a larger soil volume by increasing the roots horizontally, stepping up total LFR, and allocating more resources to deeper layer that still stored more moisture. *E. globulus* on the other hand kept its root biomass more or less constant in the dry season, both horizontally and vertically. A minor shift from the upper 10 cm to the lower topsoil (10 - 35 cm) was observed, as well as a trend to increasing LFR at 100 cm.

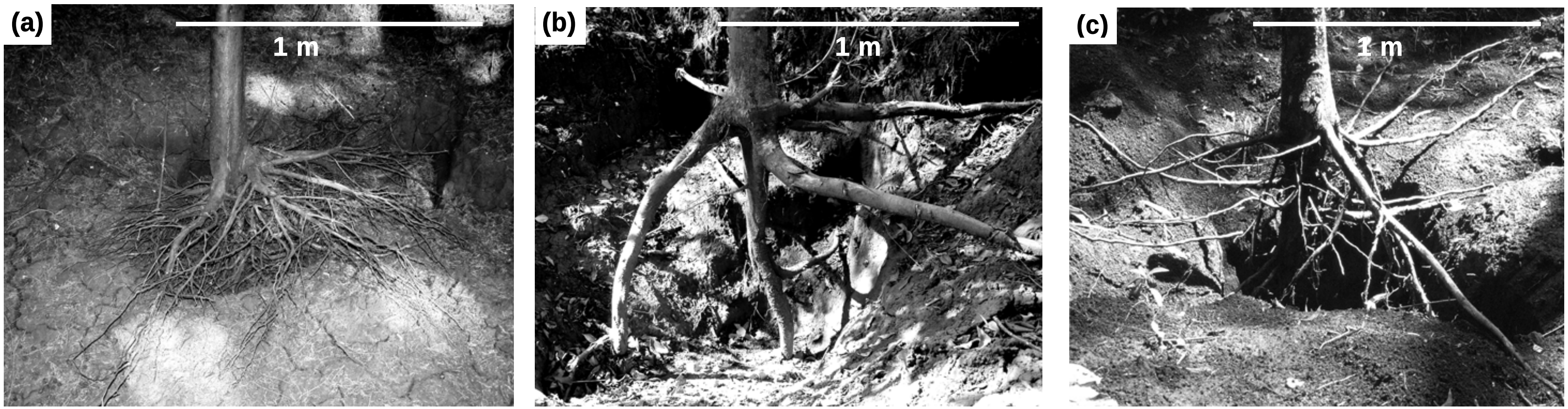

Fig. 3-5: Root architecture by excavation method of (a) *Cupressus lusitanica*, (b) *Podocarpus fa*lcatus, (c) *Eucalyptus globulus*.

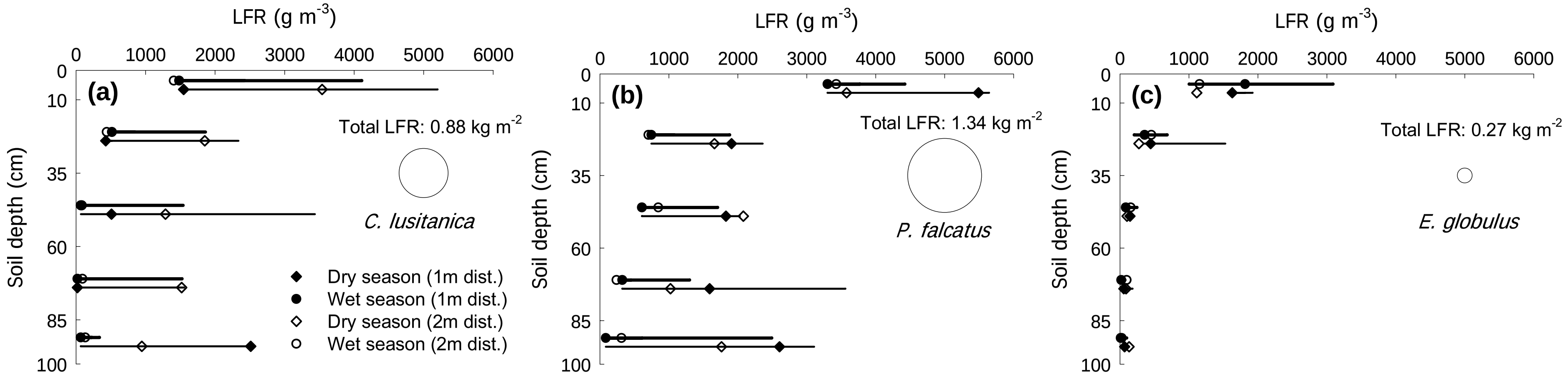

Fig. 3-6: Total live fine root biomass (LFR, bubbles) down to 100 cm (n = 90) and its spatial distribution for the dry and wet season of 2002 for (a) *Cupressus lusitanica*, (b) *Podocarpus falcatus*, (c) *Eucalyptus globulus* (Median and range for 1 m distance from the bole, means for 2 m distance; n = 3).

Transpiration by heat dissipation

Sap flow measurements (Table 3-3) yielded similar wet season transpiration values for *P. falcatus* and *E. globulus* trees of around 8.0 to 10.3 mm d^{-1} at 20 cm DBH. The values for *C. lusitanica* were approximately double at 17.7 mm d^{-1}. Under dry conditions, the species under investigation exhibited a quite different behaviour: As *E. globulus* enhanced transpiration by a factor of five to 38.2 mm d^{-1} during the dry season, *P. falcatus* reduced transpiration by a comparable magnitude to 1.7 mm d^{-1}. *C. lusitanica* also reduced sap flow, but only to a minor extent of about 50 %.

Table 3-3: Average daily transpiration values for several individuals of *Cupressus lusitanica*, *Podocarpus falcatus* and *Eucalyptus globulus* as measured in wet and dry period in Munessa-Shashemene Forest (c. 20 cm diameter at breast height; *n* = 5, mean ± 1 SD).

	Average total daily transpiration			
	Wet period	Dry period	Wet period	Dry period
	kg H_2O d^{-1}		mm H_2O d^{-1}	
Cupressus lusitanica	17.66 ± 2.51	9.00 ± 1.73	2.34 ± 0.33	1.19 ± 0.23
*Podocarpus falcatus**	10.26 ± 1.12	1.66 ± 0.28	*0.91 ± 0.10*	*0.15 ± 0.02*
Eucalyptus globulus	8.00 ± 1.73	38.33 ± 1.52	0.67 ± 0.14	3.21 ± 0.13

*Estimates of canopy transpiration of *P. falcatus* in mm H_2O d^{-1} (*in italics*) are subject to major scaling errors, as the stand is no uniform monoculture. A similar stand structure with 600 trees ha^{-1} was assumed.

The transpiration values of the plantations were directly comparable, as these were homogeneous stands of the same age and tree density. Upscaling should be possible by multiplication of the planting density for the uniform stands (Hatton et al. 1995). Scaling of the values is problematic for *P. falcatus* in the natural forest with its heterogeneous stand structure including very high trees.

Discussion

All individual methods showed clear differences between the three species under investigation. We interpret this as species effects, as soil and weather conditions can be considered uniform, and age and planting density of the plantations were virtually identical. The latter is essential, as variation in canopy structure can be expected to have a great influence on physiological behaviour (Hunt and Beadle 1998; McJannet and Vertessy 2001). For the *P. falcatus*-dominated natural forest, not all of these criteria of similarity could be met. Still the study trees grew in a closed canopy not too close to very large old trees. Comparison of all three treatments should therefore be appropriate. From the application aspect of sustainable forestry, *P. falcatus* primarily served as a reference representing long-term site adaptation, while it is currently no direct competitor to the fast-growing exotics for timber production in large-scale plantations. Little work has been undertaken so far on the soil-plant hydrology of *C. lusitanica* and *P. falcatus*. But the inclusion of *E. globulus* in the present study allows us to relate our results to a large number of scientific studies (Whitehead and Beadle 2004), while the integration of *P. falcatus* gives us a reference to the long-term natural equilibrium. The scarcity of published data accents the necessity to amalgamate the different aspects from the same site.

The findings of our experiments in Munessa Forest appear internally consistent about the different tree species. The isotopic composition of soil and plant water showed the same trend in seasonality of water uptake as the LFR allocation, i.e. a shift to water uptake from deeper layers in the dry season. Isotopic evidence and soil matric potential indicated the same processes of water redistribution, i.e. faster transport under *P. falcatus* both upward and downward, and matric flux under *E. globulus* with displacement of soil water from upper layers after rain. The most intense positive response of transpiration to water availability identified in the sap flow measurements for *P. falcatus* was in line with the variability of the tensiometers. The different strategies of the species in water acquisition were also reflected in their root architecture as seen on excavated individuals.

The specific behaviour of *E. globulus* appears primarily related to its root system, which is generally accepted for *Eucalyptus* species (Stone and Kalisz 1991). It was investigated in detail for *Eucalyptus* hybrids in sub-humid Congo by Laclau et al. (2001), who found roots reaching down to a depth of 9 m, and highest soil water depletion in the ambience of the tap roots. The dimorphic root system of *E. globulus* with lateral roots and tap roots helps to maintain high rates of transpiration and photosynthesis during dry conditions by switching to tap roots for water uptake (Dawson and Pate 1996). Other *Eucalyptus* species have also been shown to rely to a major proportion on groundwater, being highly flexible in turning towards the water resources of highest availability (Thorburn et al. 1993; Thorburn and Walker 1994). Dawson and Pate (1996) stressed the importance of this behaviour to sustain major lateral roots in dry soil during the dry season, which permits a quick response to wetter conditions in the nutrient-rich topsoil. This is supported by a ^{15}N labelling experiment on our study sites, indicating faster tracer uptake after the dry season by *E. globulus* (Fischer et al. 2005).

Root density of *E. globulus* was in the range established in other studies (Jones et al. 1999; Moroni et al. 2003). The estimate of LFR of deeper layers has to be seen critically, as the trees had not been totally excavated, leaving tap roots unaccounted for. Low LFR might lead to an overestimation of the water status under *E. globulus*, as it causes a less-structured soil with a lower water capacity, which is supported by our personal field observation of distinctly sharper edges of soil peds in the B horizon. A further indicator for a degrading structure reducing aeration were young hydromorphic features on aggregate faces of the subsoil. The water-acquisition strategy of *E. globulus* explains the minimal seasonality of its LFR in the Munessa-Shashemene Forest, as the small amount of topsoil fine roots can be supported by hydraulically lifted water. As supposed by White et al. (2002), the resulting reduced competition for water should be one reason for the lush understory vegetation, besides a favourable light climate (Lemenih et al. 2004a; Yirdaw and Luukkanen 2004).

Sap flow measurements for *Eucalyptus* spp. are available from various regions. Sap flow under drying *E. globulus* in Portugal was in good agreement with Penman evapotranspiration and showed a decrease in transpiration with the progressing dry season from 3.6 mm d^{-1} to 0.5 mm d^{-1} (David et al. 1997). The maximum rate was higher than in our investigation (2.3 mm d^{-1}), but this might be attributed to a younger age in Portugal (Roberts et al. 2001). The decline in transpiration in the dry season is a phenomenon commonly observed for trees, including *P. falcatus* and *C. lusitanica* in this study. But our study showed an increased transpiration of *E. globulus* under high-radiation, high-VPD conditions of the dry season. This different physiological behaviour is probably an effect of age. The Portuguese stand was just 8 years old with 1020 trees ha^{-1}, less than half the age of the *E. globulus* plantation of this study at nearly double tree density. However, the main reason for the reduction of transpiration in Portugal might have been the steady depletion of soil water in level terrain with coarse-textured soils. For sloping terrain of Southern Australia, enhanced transpiration of *Eucalyptus* spp. during dry periods has been described (McJannet and Vertessy 2001), where the trees were shown by their δ^2H isotope signature to access groundwater, as has been for sub-humid tropical Australia (O'Grady et al. 1999; Eamus et al. 2000). Still, only the results of O’Grady et al. (1999) showed a magnitude of seasonal variation and a range of daily transpiration comparable to our findings, covering roughly the same range of 0.5 to 1.9 mm d^{-1} (good rainy seasons showed lower transpiration). They attributed this to sufficient water availability to tap roots and a high VPD overcompensating the reduction in transpiration by effective stomatal control. Though on an aerial basis, they supposed an aseasonal pattern of transpiration due to changes in leaf area index of other species. The hypothesis of increased dry-season transpiration has been corroborated by well-watered pot experiments involving *E. globulus* conducted in the Mediterranean climate of Western Australia (Pate and Dawson 1999). While stomatal control derived from δ^{13}C values of leaves proved effective, it was not sufficient to compensate for higher water loss at high VPD. These studies imply a direct effect on canopy transpiration of monocultures – as long as understory vegetation only plays a minor role in water transfer. Such direct impact on canopy transpiration has been doubted by Cook et al. (1998), who pursued a comprehensive approach on soil water and micro-meteorology for representative seasons in northern Australia. They suggested high understory fluxes, amounting to about 50 % of total evapotranspiration, to explain the difference of above-canopy eddy fluxes and scaled stem-flow transpiration. However, recent studies of Unsworth et al. (2004) and Wilson et al. (2001) demonstrated a scaling problem of sap flow measurements to canopy level.

At our plots in the Munessa-Shashemene Forest, a sufficient water reservoir should have been available to deep-rooting trees, as a constant slope stretches over more than 500 m in elevation. Thus, reduced groundwater recharge can be supposed for the *E. globulus* plantation despite high topsoil moisture. This characteristic of *E. globulus* is commonly utilized in slope drainage management in Australia (McJannet et al. 2000).

For *C. lusitanica*, the only comparable data available are sap flow measurements on *Cupressus sempervirens* L. var. *horizontalis* by Schiller et al. (2004) planted in rows in Israel. In this semi-arid environment, a decline of transpiration in dry periods to less than 15 % of wet season sap flow was observed, covering a range of c. 0.2 to 1.6 mm d^{-1}. This is a wider range than in the present study with 0.6 to 1.2 mm d^{-1}. However, the canopy investigated by Schiller et al. (2004) consisted of younger (15 a) trees with only 70 % of the DBH at a higher density of 1000 trees ha^{-1}. The resulting higher sap flux density, as well as the greater proportion of sapwood area per tree and per ground area explain the range and maximum values (Meinzer et al. 2001b; Fetene and Beck 2004). The minimum values might be a consequence of the dry climate in Southern Israel, receiving only about one third of the rainfall in Munessa, and the sandy soil texture with soil moisture depleted faster.

Our data show the soil under *C. lusitanica* to be driest, with LFR quite high and dynamic. Soil water recharge was hampered by the high interception of the canopy. The shallow root architecture did not allow the plants to rely on groundwater, as was reflected in the marked increase in dry season LFR allocated to deeper layers, also visible from the apparent depth of water uptake by $\delta^{18}O$. Topsoil was efficiently exploited by the roots, a probable reason for denser understory at relief positions with higher soil moisture, such as steepening slopes. The shallow root system makes *C. lusitanica* more vulnerable to drought stress and wind damage. Isotope labelling studies with ^{15}N also indicated higher nutrient losses because of minimal recovery from deeper layers (Fischer et al. 2005). While under *P. falcatus* and *E. globulus* water was transferred to the atmosphere mainly through the canopy and understory vegetation, direct evaporation appeared to play an important role in the bare *C. lusitanica* plantations, leading to steeper topsoil $\delta^{18}O$ gradients. *C. lusitanica* had the strongest reduction in LFR at 2 m distance from the bole during the wet season (open symbols in Fig. 3-6). This contracted wet-season root pattern despite enhanced physiological activity indicates that the primary mission of the more expensive distal roots is water uptake. The seasonality in LFR of *C. lusitanica* is likely to be emphasized by its fine root architecture showing a high proportion of first-order fine roots (personal observations), and by a shorter fine root lifespan (Pregitzer et al. 2002).

A strong response of transpiration to water availability in combination with a shallow apparent depth of water uptake from $\delta^{18}O$ indicates lower water consumption of *P. falcatus*. Tight stomatal regulation probably contributes to the quick relaxation of soil matric potential after occasional wetting. This assumption concurs with data by Lüttge et al. (2003), whose $\delta^{13}C$ measurements of leaves from the sites of this study revealed a higher water use efficiency of *P. falcatus* compared to *E. globulus*. Measurements on leaf-scale dependency of transpiration on VPD at the study sites also point towards this direction (Fetene and Beck 2004). However, specific whole-tree transpiration of *P. falcatus* is likely to be greater in a homogeneous canopy, as the studied trees were growing in a stand including much higher trees, largely decoupling atmospheric fluxes from the internal boundary layer and inducing heterogeneity of radiation and thus transpiration (Hunt and Beadle 1998). *P. falcatus* develops tap roots (Fig. 3-5), but they appear less effective than the ones of *E. globulus*. However, their performance could be masked by water redistribution through roots at night, directing a considerable proportion of water lifted by the tap roots to the dense fine root system and the topsoil with a lower water potential. Such hydraulic redistribution is facilitated by low soil hydraulic conductivity and high rooting density (Ryel et al. 2002) – conditions given in the natural forest. Water redistributed passively by roots can amount to more than 30 % of the available soil water in upper layers and 60 % of water taken up by single species (Brooks et al. 2002), but an inverse moisture gradient can also lead to a downward flow through roots (Ryel et al. 2003). While rather inactive in water uptake, fine roots of the topsoil and their mycorrhizal associates can be supported this way during drought phases to extract nutrients (Caldwell et al. 1998; Jobbagy and Jackson 2001; Querejeta et al. 2003). A major extent of hydraulic redistribution has already been described for environments similar to our study site (Meinzer et al. 2004). Although it is beyond the capacity of tensiometry to directly assess this process, several indicators point towards the importance of hydraulic redistribution in soil-plant hydrology of *P. falcatus*: (a) the high variability of soil matric potential under *P. falcatus* at 50 and 100 cm depth, (b) the xylem water $\delta^{18}O$ resembling the topsoil for the whole sampling period and (c) the little gradient between topsoil and subsoil isotope signature. The lack of major tap roots in *C. lusitanica* and the low rooting density of *E. globulus* might make these species less effective in hydraulic redistribution (Brooks et al. 2002; Ryel et al. 2002). From the ecosystem perspective, the fast equilibration of soil water potential under *P. falcatus* and the resulting topsoil moisture regulation appears to be a substantial benefit from the indigenous species, promoting soil life and thus nutrient availability and root vitality itself. The assumption of more active nutrient cycling under *P. falcatus* is supported by data from ^{15}N labelling, showing faster tracer uptake from the topsoil of *P. falcatus* compared to the other species (Fischer et al. 2005). Yet, further investigations on differences in hydraulic conductivity of roots from the respective trees and root sap flow measurements identifying amount and direction of water transfer are required to finally elucidate the impact of root architecture on living conditions of the surrounding soil.

Conclusions

Combining the techniques of tensiometry, water stable-isotope analysis, rooting pattern and transpiration gives a comprehensive picture of the water utilization by the tree species under study. The natural forest appears as the most complex system with strong physiological feedback of the dominant *P. falcatus*. This includes (a) reduced transpiration during the dry season, (b) its influence on soil structure through its high LFR, and (c) hydraulic redistribution through its roots. These characteristics balance living conditions, thereby sustaining soil quality and ecosystem diversity.

The exotic trees popular in plantation forestry differ from indigenous *P. falcatus* in two directions: While transpiring more water, *E. globulus* taps deeper resources and seems therefore better adapted to drought. May this seem positive from the production point of view, there could be several drawbacks: Fine root biomass is much lower, which might be a reason for the degrading soil structure with all its adverse consequences for water, nutrient and gas transport; and the presumably high water consumption from groundwater can affect river discharge on a catchment scale and exacerbate shortage of water in the region. However, high topsoil moisture content allows indigenous species to regenerate (Feyera et al. 2002) and thus to increase floristic and structural diversity. In contrast, soil under the shallow-rooting species *C. lusitanica* is significantly drier than the other two species. This makes these trees susceptible to drought-related failure in years with reduced rainfall – and it is one major obstacle for natural regeneration, degrading the soil seed bank and forcing human action to change species composition. The presented evidence about indigenous and exotic species with contrasting strategies may also help to categorize site adaptation of other species considered for afforestation.

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References

Abate A (2004) Biomass and nutrient studies of selected tree species of natural and plantation forests: Implications for a sustainable management of the Munessa-Shashemene Forest, Ethiopia. PhD dissertation. Faculty of Biology, Chemistry and Geosciences. University of Bayreuth, Bayreuth, Germany, 163 p

Allison GB (1982) The relationship between ^{18}O and deuterium in water in sand columns undergoing evaporation. Journal of Hydrology 55:163-169

Barbour MM, Roden JS, Farquhar GD, Ehleringer JR (2004) Expressing leaf water and cellulose oxygen isotope ratios as enrichment above source water reveals evidence of a Péclet effect. Oecologia 138:426-435

Bariac T, Gonzalez-Dunia J, Katerji N, Bethenod O, Bertolini JM, Mariotti A (1994) Variabilité spatio-temporelle de la composition isotopique de l'eau (^{18}O, ^{2}H) dans le continuum sol-plant-atmosphère. 2. Approche en conditions naturelles (Spatial variation of the isotopic composition of water (^{18}O, ^{2}H) in the soil-plant-atmosphere system. 2. Assessment under field conditions). Chemical Geology 115:317-333

Benvenuti M, Carnicelli S, Belluomini G, Dainelli N, Di Grazia S, Ferrari GA, Iasio C, Sagri M, Ventra D, Atnafu B, Kebede S (2002) The Ziway-Shala lake basin (main Ethiopian rift, Ethiopia): a revision of basin evolution with special reference to the Late Quaternary. Journal of African Earth Sciences 35:247-269

Böhm W (1979) Methods of studying root systems. Springer, Berlin, Germany

Brooks JR, Meinzer FC, Coulombe R, Gregg J (2002) Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. Tree Physiology 22:1107-1117

Caldwell MM, Dawson TE, Richards JH (1998) Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113:151-161

Cook PG, Hatton TJ, Pidsley D, Herczeg AL, Held A, O'Grady A, Eamus D (1998) Water balance of a tropical woodland ecosystem, Northern Australia: a combination of micro-meteorological, soil physical and groundwater chemical approaches. Journal of Hydrology 210:161-177

David TS, Ferreira MI, David JS, Pereira JS (1997) Transpiration from a mature *Eucalyptus globulus* plantation in Portugal during a spring-summer period of progressively higher water deficit. Oecologia 110:153-159

Dawson TE, Pate JS (1996) Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. Oecologia 107:13-20

Drake PL, Franks PJ (2003) Water resource partitioning, stem xylem hydraulic properties, and plant water use strategies in a seasonally dry riparian tropical rainforest. Oecologia 137:321-329

Dünisch O, Erbreich M, Eilers T (2003) Water balance and water potentials of a monoculture and an enrichment plantation of *Carapa guianensis* Aubl. in the Central Amazon. Forest Ecol Manag 172:355-367

Eamus D, O'Grady AP, Hutley L (2000) Dry season conditions determine wet season water use in the wet-dry tropical savannas of northern Australia. Tree Physiology 20:1219-1226

FAO, ISRIC, ISSS (1998) World reference base for soil resources. Food and Agriculture Organization of the United Nations, Rome, Italy

FAO (2003) State of the world's forests, 2003. In. Food and Agriculture Organization of the United Nations, Rome

Fetene M, Beck EH (2004) Water relations of indigenous versus exotic tree species, growing at the same site in a tropical montane forest in southern Ethiopia. Trees - Structure and Function 18:428-435

Feyera S, Beck E, Lüttge U (2002) Exotic trees as nurse-trees for the regeneration of natural tropical forests. Trees - Structure and Function 16:245-249

Fischer H, Fritzsche F, Zech W, Guggenberger G (2005) Nitrogen dynamics in three forest types of the South-Ethiopian highlands. Plant and Soil:(submitted)

Fritzsche F, Zech W, Guggenberger G (2005) Soils of the Main Ethiopian Rift Valley: a catenary study. Catena:*(submitted)*

Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiology 3:309-320

Hailemichael M, Aronson JL, Savin S, Tevesz MJS, Carter JG (2002) $\delta^{18}O$ in mollusk shells from Pliocene Lake Hadar and modern Ethiopian lakes: implications for history of the Ethiopian monsoon. Palaeogeogr Palaeocl 186:81-99

Hatton TJ, Moore SJ, Reece PH (1995) Estimating stand transpiration in a *Eucalyptus-populnea* woodland with the heat pulse method - measurement errors and sampling strategies. Tree Physiology 15:219-227

Hsieh JCC, Savin SM, Kelly EF, Chadwick OA (1998) Measurement of soil-water $\delta^{18}O$ values by direct equilibration with CO_2. Geoderma 82:255-268

Hunt MA, Beadle CL (1998) Whole-tree transpiration and water-use partitioning between *Eucalyptus nitens* and *Acacia dealbata* weeds in a short-rotation plantation in northeastern Tasmania. Tree Physiology 18:557-563

Jobbagy EG, Jackson RB (2001) The distribution of soil nutrients with depth: global patterns and the imprint of plants. Biogeochemistry 53:51-77

Jones HE, Madeira M, Herraez L, Dighton J, Fabiao A, Gonzalez-Rio F, Marcos MF, Gomez C, Tome M, Feith H, Magalhaes MC, Howson G (1999) The effect of organic-matter management on the productivity of *Eucalyptus globulus* stands in Spain and Portugal: tree growth and harvest residue decomposition in relation to site and treatment. Forest Ecol Manag 122:73-86

Kelln CJ, Wassenaar LI, Hendry MJ (2001) Stable isotopes ($\delta^{18}O$, $\delta^{2}H$) of pore water in clay-rich aquitards: a comparison of measurement techniques. Ground Water Monitoring and Remediation 21:108-116

Laclau J-P, Arnaud M, Bouillet J-P, Ranger J (2001) Spatial distribution of *Eucalyptus* roots in a deep sandy soil in the Congo: relationships with the ability of the stand to take up water and nutrients. Tree Physiology 21:129-136

Le Roux X, Bariac T, Mariotti A (1995) Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. Oecologia 104:147-155

Lemenih M, Gidyelew T, Teketay D (2004a) Effects of canopy cover and understory environment of tree plantations on richness, density and size of colonizing woody species in southern Ethiopia. Forest Ecol Manag 194:1-10

Lemenih M, Olsson M, Karltun E (2004b) Comparison of soil attributes under *Cupressus lusitanica* and *Eucalyptus saligna* established on abandoned farmlands with continuously cropped farmlands and natural forest in Ethiopia. Forest Ecol Manag 195:57-67

Lüttge U, Berg A, Fetene M, Nauke P, Peter D, Beck E (2003) Comparative characterization of photosynthetic performance and water relations of native trees and exotic plantation trees in an Ethiopian forest. Trees - Structure and Function 17:40-50

McJannet D, Vertessy R (2001) Effects of thinning on wood production, leaf area index, transpiration and canopy interception of a plantation subject to drought. Tree Physiology 21:1001-1008

McJannet DL, Vertessy RA, Clifton CA (2000) Observations of evapotranspiration in a break of slope plantation susceptible to periodic drought stress. Tree Physiology 20:169-177

Meinzer FC, Clearwater MJ, Goldstein G (2001a) Water transport in trees: current perspectives, new insights and some controversies. Environmental and Experimental Botany 45:239-262

Meinzer FC, Goldstein G, Andrade JL (2001b) Regulation of water flux through tropical forest canopy trees: do universal rules apply? Tree Physiology 21:19-26

Meinzer FC, Brooks JR, Bucci S, Goldstein G, Scholz FG, Warren JM (2004) Converging patterns of uptake and hydraulic redistribution of soil water in contrasting woody vegetation types. Tree Physiology 24:919-928

Melayah A, Bruckler L, Bariac T (1996) Modeling the transport of water stable isotopes in unsaturated soils under natural conditions. Part1. Theory. Water Resources Research 32:2047-2054

Moreira MZ, Scholz FG, Bucci SJ, Sternberg LS, Goldstein G, Meinzer FC, Franco AC (2003) Hydraulic lift in a neotropical savanna. Functional Ecology 17:573-581

Moroni MT, Worledge D, Beadle CL (2003) Root distribution of *Eucalyptus nitens* and *E. globulus* in irrigated and droughted soil. Forest Ecol Manag 177:399-407

Negash L (2003) In situ fertility decline and provenance differences in the East African Yellow Wood (*Podocarpus falcatus*) measured through in vitro seed germination. Forest Ecol Manag 174:127-138

O'Grady AP, Eamus D, Hutley LB (1999) Transpiration increases during the dry season: patterns of tree water use in eucalypt open-forests of northern Australia. Tree Physiology 19:591-597

Ohte N, Koba K, Yoshikawa K, Sugimoto A, Matsuo N, Kabeya N, Wang LH (2003) Water utilization of natural and planted trees in the semiarid desert of Inner Mongolia, China. Ecol Appl 13:337-351

Pate JS, Dawson TE (1999) Assessing the performance of woody plants in uptake and utilisation of carbon, water and nutrients - implications for designing agricultural mimic systems. Agroforestry Systems 45:245-275

Pohjonen V, Pukkala T (1990) *Eucalyptus globulus* in Ethiopian forestry. Forest Ecol Manag 36:19-31

Pregitzer KS, de Forest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL (2002) Fine root architecture of nine North American trees. Ecol Monogr 72:293-309

Querejeta JI, Egerton-Warburton LM, Allen MF (2003) Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. Oecologia 134:55-64

Reynolds JF, Virginia RA, Kemp PR, de Soyza AG, Tremmel DC (1999) Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecol Monogr 69:69-106

Richards JH, Caldwell MM (1987) Hydraulic lift - substantial nocturnal water transport between soil layers by *Artemisia-tridentata* roots. Oecologia 73:486-489

Roberts S, Vertessy R, Grayson R (2001) Transpiration from *Eucalyptus sieberi* (L. Johnson) forests of different age. Forest Ecol Manag 143:153-161

Ryel RJ, Caldwell MM, Yoder CK, Or D, Leffler AJ (2002) Hydraulic redistribution in a stand of *Artemisia tridentata*: evaluation of benefits to transpiration assessed with a simulation model. Oecologia 130:173-184

Ryel RJ, Caldwell MM, Leffler AJ, Yoder CK (2003) Rapid soil moisture recharge to depth by roots in a stand of *Artemisia tridentata*. Ecology 84:757-764

Schiller G, Moshe Y, Ungar ED (2004) Transpiration of *Cupressus sempervirens* L. as influenced by canopy structure. Israel J Plant Sci 52:9-19

Scrimgeour CM (1995) Measurement of plant and soil water isotope composition by direct equilibration methods. Journal of Hydrology 172:261-274

Silvanova (1996) Enterprise formations of the Munessa-Shashemene State Forestry Project. In. Oromia Bureau of Agriculture Development, Addis Ababa, Ethiopia

Smith DM, Jarvis PG, Odongo JCW (1998) Management of windbreaks in the Sahel: the strategic implications of tree water use. Agroforestry Systems 40:83-96

Soil Survey Staff (2003) Keys to Soil Taxonomy, Ninth edn. United States Department of Agriculture, Natural Resources Service, Washington, USA

Stone EL, Kalisz PJ (1991) On the maximum extent of tree roots. Forest Ecol Manag 46:59-102

Thorburn PJ, Hatton TJ, Walker GR (1993) Combining measurements of transpiration and stable isotopes of water to determine groundwater discharge from forests. Journal of Hydrology 150:563-587

Thorburn PJ, Walker GR (1994) Variations in stream water uptake by *Eucalyptus camaldulensis* with differing access to stream water. Oecologia 100:293-301

Unsworth MH, Phillips N, Link T, Bond BJ, Falk M, Harmon ME, Hinckley TM, Marks D, U KTP (2004) Components and controls of water flux in an old-growth Douglas-fir-Western Hemlock ecosystem. Ecosystems 7:468-481

de Vletter J (1991) Forest genetic resources of Ethiopia. In: Engels JMM, Hawkes JG, Worede M (eds) Plant genetic resources of Ethiopia. Cambridge University Press, Cambridge, pp 82-100

Weltzin JF, McPherson GR (1997) Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. Oecologia 112:156-164

White DA, Dunin FX, Turner NC, Ward BH, Galbraith JH (2002) Water use by contour-planted belts of trees comprised of four *Eucalyptus* species. Agr Water Manage 53:133-152

Whitehead D, Beadle CL (2004) Physiological regulation of productivity and water use in *Eucalyptus*: a review. Forest Ecol Manag 193:113-140

Wilson KB, Hanson PJ, Mulholland PJ, Baldocchi DD, Wullschleger SD (2001) A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance. Agr Forest Meteorol 106:153-168

Yanagisawa N, Fujita N (1999) Different distribution patterns of woody species on a slope in relation to vertical root distribution and dynamics of soil moisture profiles. Ecological Research 14:165-177

Yirdaw E, Luukkanen O (2004) Photosynthetically active radiation transmittance of forest plantation canopies in the Ethiopian highlands. Forest Ecol Manag 188:17-24

Study 4:

Nitrogen dynamics in three forest types of the South-Ethiopian highlands

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Abstract

Plantation forestry can help retard the destruction of tropical forests. It mainly relies on few fast-growing species, with largely unclear effects on nutrient cycling, including nitrogen (N). Here, we conducted a comparative field study on a natural *Podocarpus falcatus*-dominated forest and plantations of *Cupressus lusitanica* and *Eucalyptus globulus* in South Ethiopia. Besides quantification of nutrient pools and natural-abundance $\delta^{15}N$ analysis, we employed ^{15}N soil labelling at 0 cm and 40 cm depth to trace N transfer in soil and vegetation during 13 months. The natural forest had the lowest N content, but the highest proportion of extractable N and similarly strong correlations in topsoil and subsoil between the bulk and extractable N species, indicating high turnover in both layers. Under *E. globulus*, bulk N contents and low topsoil extractability showed preferential N stabilization. Under *C. lusitanica*, an increase in the proportion of inorganic species in the subsoil showing no correlation with bulk N presumably resulted from topsoil leaching. Natural-abundance $\delta^{15}N$ in the *E. globulus* stand was higher by c. 3 ‰ than under *P. falcatus*. Constant differences to foliage pointed towards recent processes like leaching and denitrification. Initial uptake of the ^{15}N tracer was high in all forests, with pronounced recirculation to the soil being strongest effect with *C. lusitanica*. Shallow but rapid uptake of the ^{15}N label by *C. lusitanica* and preferential exploitation of deep resources by *E. globulus* with *P. falcatus* being active in both layers demonstrated the dependency on the root system. Tracer incorporation into understorey plants was more dynamic and reflected the active soil N pool. Nitrogen turnover emerged highest in the natural forest. Losses were largest under shallow-rooted *C. lusitanica*, while topsoil N cycling was comparable to natural vegetation under *E. globulus*. Understorey plants seem important in ecosystem N conservation through rapid retention and recirculation.

Keywords:

^{15}N labelling, *Cupressus lusitanica, Eucalyptus globulus,* forest plantation,
inorganic N, *Podocarpus falcatus*.

Introduction

Tropical montane forest are highly acknowledged for their role in protecting vulnerable environments, stabilizing watersheds and conserving biodiversity. But the demand for land, timber and fuelwood puts increasing pressure on this resource, leading to the fast degradation of remaining forest areas. As a countermeasure, plantations of fast-growing trees have been promoted for a long time. In the case of Ethiopia, deforestation has been particularly intense, depriving large regions of virtually any trees and leaving less then 10 % of the original forest area (Pohjonen and Pukkala 1990; FAO 2003). In order to supply its rural population of more than 80 % with timber and timber products, fast-growing species were introduced starting from 1894, primarily different *Eucalyptus* species.

However, plantations can be detrimental to their environment, which has been a particular matter of discussion for the genus *Eucalyptus* (e. g. Lisanework and Michelsen 1993; Binkley and Resh 1999). Yet comparative studies on nutrient cycling of plantations and natural forests have only been conducted on some aspects and for a few species (Cuevas and Lugo 1998). The sustainable management of forest plantations requires the selection of well-suited species for different sites, as well as an appropriate silviculture. Excessive nutrient losses have to be avoided, as they usually lead to a gradual decline in productivity and can make ecosystem conversion irreversible. While not necessarily limiting in tropical montane forests, nitrogen (N) is a macro-nutrient that reacts quite sensitively to changes in nutrient cycling (Bigelow et al. 2004). Its atmosphere-coupled nutrient cycle is comparably open, and it occurs in inorganic and organic compounds, neutral, cationic and anionic species, solid, soluble and gaseous forms. Its turnover in the soil-plant system is quite high (Davidson et al. 1992; Hart and Myrold 1996; Vervaet et al. 2004), and its net translocation in kaolinitic tropical soils is not significantly buffered by adsorption. It is thus a good proxy for ecosystem nutrient sustainability. Methods to study the dynamics of N include fertilization experiments, microcosm studies, incubations, direct monitoring of ecosystem pools and fluxes, stable-isotope investigations at natural abundance, and stable-isotope labelling. While the approaches of classical chemistry require a high experimental effort and input variables such as water fluxes to finally yield net rates (e. g.

Piirainen et al. 2002; Laclau et al. 2003), stable-isotope methods can help to elucidate processes while avoiding or minimizing the experimental influence on the ecosystem. Measurements of the N stable isotope composition ($\delta^{15}N$) at natural abundance and after labelling with a highly-enriched tracer are somehow complementary, as the first gives information about long-term conditions and shifts in ecosystem nutrient cycling including its tightness (Högberg 1990, 1997), while the latter approach allows to track a defined amount of atoms through the ecosystem, thereby elucidating processes of nutrient cycling in their temporal dependency (Garcia-Montiel and Binkley 1998; Zeller et al. 2001; Hangs et al. 2003a). Nitrogen uptake in tropical forests takes place from a small inorganic and low-molecular organic fraction mainly of the topsoil and forest floor. This highly active fraction reacts much more sensitively to a tracer application than the large slow-turnover pool and thus reflects current processes that are directly coupled with the vegetation. As the size of the inorganic fraction is largely kinetically determined under favourable tropical conditions, the extractable organic N pool may give a better information about the status of potentially available N (Zhong and Makeschin 2003), a major part of which can also directly contribute to plant nutrition (Lipson and Nasholm 2001; Yu et al. 2002). The phosphate-extractable fraction has been shown to comprise a defined, protein-like fraction correlating well with available N determined by soil incubation (Matsumoto et al. 2000).

In this study, we compare ecosystem N cycling in two monocultures of widely-planted exotic tree species (*Cupressus lusitanica* Mill. and *Eucalyptus globulus* Labill.) with a natural forest dominated by the highly valued indigenous tree *Podocarpus falcatus* (Thunb.) Mirb. in order to identify specific characteristics affecting sustainability. Our approach included quantitative monitoring of differently available N pools, natural-abundance $\delta^{15}N$ values of different pools, and a ^{15}N labelling experiment. Applying a ^{15}N tracer adds the possibility to monitor the speed of redistribution processes as well as the quantity of uptake by the vegetation. The application to two soil depths extends this information to root activity and vertical distribution of nutrient cycling, including interspecies relationships (Lehmann et al. 2001; Rowe et al. 2001). Tracing the ^{15}N label for more than one year enable us to elucidate aspects such as N reallocation within soil and plants and seasonality.

We wanted to test the following hypotheses:

(1) Forest conversion causes changes in N dynamics, affecting both pool sizes and rates of transfer between pools. This is due to specific

a) alteration in abiotic (convective and diffusive) transport of N
b) microbial transformations
c) plant activities (root and mycorrhizal uptake and rhizodeposition).

(2) Understorey vegetation plays a major part in N cycling

(3) Forest types with less biological activity are more prone to N losses.

Materials and Methods

Site description

The experiment was carried out in the Munessa-Shashemene Forest, South Ethiopia (7° 26’ N 38° 52’ E). This forest area of about 23000 ha (Silvanova 1996) is located on the eastern escarpment of the Main Ethiopian Rift Valley, which stretches from the Ziway-Shalla basin at 1600 m asl to about 3500 m asl. The whole escarpment is made up of intermediate Pliocene volcanites, mainly trachytes (Benvenuti et al. 2002) and covered by forest between 2000 m and 2800 m asl. The site of this study is situated on a gently inclined step (5 - 15 %) at 2280 m asl. The climate is sub-humid, with annual rainfall of about 1500 mm at the research site (Fritzsche et al. 2005c), falling in a rather unreliable small rainy season from March to May and a big rainy season from July to September (Seleshi and Zanke 2004). Rainfall for the period of this experiment amounted to 1330 mm. Mean annual temperature equals 15 °C, with an average daily range from 8 °C to 24 °C. Soils of the area are fertile, oxide-rich, kaolinitic red clays, classified as Typic Palehumults (Soil Survey Staff 2003) and Mollic Nitisols (FAO et al. 1998), respectively (Fritzsche et al. 2005c).

Natural vegetation is a semi-deciduous forest, dominant species are the evergreen conifer *Podocarpus falcatus* (Thunb.) Mirb. and deciduous *Croton macrostachys* Hochst. ex Del., followed by *Olea europaea* ssp. *cuspidata* (Wall. Ex. DE) Cifferri, *Schefflera abyssinica* Harms, and *Allophyllus abyssinica* (Hochst.) Radlkofer (Abate 2004). The degraded natural forest stand is embedded in a mosaic of plantations of exotic tree species. For this study, we included two plantations of *Cupressus lusitanica* Mill. (20 years old) and *Eucalyptus globulus* Labill. (21 years old) within

1 km distance of the degraded natural stand. Understorey was dense and diverse in the natural forest and the *E. globulus* plantation, while the stand of *C. lusitanica* was largely bare, only covered by some grass (*Oplismenus compositus* (L.) P. Beauv.). The structure of the investigated canopies was typical for a wide region (Yirdaw 2001; Yirdaw and Luukkanen 2003; Abate 2004). Physical properties like texture and bulk density did not differ significantly within the area of the plots (Ashagrie, unpublished thesis) and concur with other data some 25 km south (Lemenih et al. 2004).

Experimental setup, ^{15}N labelling and sampling

Three fenced experimental plots were established within 160 m at comparable relief positions of each of the three forest types around healthy adult trees of the respective dominant species. One plot was left unlabeled, and two were labelled with $^{15}NH_4Cl$ (98 % ^{15}N, Campro Scientific, Berlin, Germany) following the large 2002 rainy season. The tracer solution was injected beneath the litter layer (0 cm) and to 40 cm soil depth, respectively, at 120 points of an orthogonal grid (40 cm mesh width) around the central trees, covering a circular area of about 20 m^2. The resulting N input from the $^{15}NH_4Cl$ label was equivalent to 1.0 kg ^{15}N ha^{-1}.

Soil and plant samples were collected from all plots (unlabelled and labelled) in a time series of 13 months (Table 4-1). Soil samples from a distance of 1 m from the central trees were taken with an auger in four replicates from 0 – 30 cm soil depth and thereafter from 30 – 60 cm. As the plots needed to be conserved for other experiments, only 5 dates could be included. Leaves were sampled by collecting young mature, sun-exposed leaves from the crown of the central trees and neighbour trees growing on the labelled plots (from the dominant species, plus *Croton macrostachys* in the *E. globulus* stand, plus in the natural forest *Nuxia congesta* R. Br. ex Fresen. and *Maytenus arbutifolia* (Hochst. ex A. Rich.) R. Wilczek). The understorey vegetation was integrated into the sampling programme, with *Rubus steudneri* Schweinf. abundant on the *E. globulus* plots, as well as *Oplismenus compositus* (L.) P. Beauv. from all three forest types. All leaf samples were taken from a minimum of three different positions and combined. All samples were air-dried.

Table 4-1: Sampling programme for soil and vegetation samples. The sampling on day 0 took place preceding the ^{15}N labelling.

Date	Days after labelling	Soil	Central trees and understorey	Neighbour trees
10/01/02	0*	+	+	+
10/11/02	10	+	+	+
10/19/02	18	o	+	o
10/27/02	26	o	+	o
11/06/02	36	+	+	+
11/21/02	51	o	+	o
12/06/02	66	o	+	+
03/24/03	174	+	+	+
04/23/03	204	o	+	+
05/27/03	238	o	+	+
10/24/03	388	+	+	+

*Plots for ^{15}N labelling before tracer application

Analyses and statistical treatment

The analytical programme was identical for both labelled and unlabelled plots. After grinding of soil and plant samples, total N content was measured using a CN autoanalyzer Vario EL (Elementar, Hanau, Germany). Additionally, soil samples were extracted with a neutral 0.1 M KH_2PO_4 solution (3 g soil + 20 ml solution), and concentrations of nitrate, ammonia and soluble N (N_e) were measured by flow injection analysis (San^{plus}System, Skalar, Erkelenz, Germany). Extractable organic N (N_{eo}) was calculated as difference of N_e and N_{ei} (= NO_3^- + NH_4^+).

The isotopic composition ($\delta^{15}N$ value) of soil and leaf samples was determined with an elemental analyzer coupled to an isotope ratio mass spectrometer (Carlo Erba CN 2500 coupled with Delta^{plus} Isotope MS via Conflo II Interface, Thermo Finnigan, Bremen, Germany), with laboratory standards and the international standards IAEA-N-1, IAEA-N-2, USGS 26, USGS 32 (IAEA Analytical Quality Control Services 2004) included every five samples. The isotope signature of inorganic N was determined by the same procedure after transferring an aliquot from the soil extracts into filter discs by micro diffusion (Stark and Hart 1996), yielding a recovery > 80 %.

Statistical analyses were executed with SPSS 10.0 (ANOVA with post-hoc test Tamhane's T2). As tracer injection into soil involves several methodological problems (Di et al. 2000), the $\delta^{15}N$ datasets could not be assumed to be normal-distributed. We thus display median values and used Spearman's rank correlation coefficient (R_S). The relative root activity was calculated by relating the increment in ^{15}N tracer enrichment in the leaves from the two plots labelled in 0 cm and 40 cm, respectively (Lehmann and Muraoka 2001).

Results

Bulk C and N concentrations

Carbon concentration in both topsoil and subsoil as displayed in Table 4-2 was slightly higher in the natural forest than in the plantations, yet not significant. In contrast, topsoil N concentrations tended to be highest in the *E. globulus* plantations and lowest in the natural forest. Subsoil N concentrations did not differ among the forest types. Seasonality of both elements was pronounced, peaking after the large rainy season. C/N ratios showed little seasonal variation and were always highest for the topsoil of the natural forest (around 13) with lower values for its subsoil by 0.5. *C. lusitanica* had the second-highest C/N ratios of around 11.3 for both layers investigated. The highest N concentration under *E. globulus* resulted in topsoil C/N ratios of only 9.5, but widening to 10.3 in the subsoil.

Leaf dry-matter N concentrations increased in the order *Cupressus* (1.3 %) < *Eucalyptus* = *Podocarpus* (1.7 %) < *Rubus* (2.8 %) < *Oplismenus* (3.5 %) < *Croton* (5.0 %). Differences among the dominant tree species were not significant. Seasonal variation of these concentrations (data not shown) was about ± 10 % for the trees and slightly higher for the herbaceous species, showing a consistent pattern of decreasing concentrations in the dry season. Leaf C/N ratios were about 40 for *C. lusitanica*, 30 for *P. falcatus* and *E. globulus*, around 16 for *Croton macrostachys*, and typically ranging about 10 – 15 for the understorey vegetation.

Table 4-2: Contents of C, N, and the phosphate-extractable species NH_4^+, NO_3^-, and extractable organic N in three forest types and two depth layers (SE in parenthesis; n = 8 for day 0, n = 12 for later dates; median values are displayed in bold font).

		C. lusitanica **plantation**					*P. falcatus* **natural forest**					*E. globulus* **plantation**				
Days		**0**	**10**	**36**	**174**	**388**	**0**	**10**	**36**	**174**	**388**	**0**	**10**	**36**	**174**	**388**
C (g/kg)	0 - 30 cm	68.8 (6.8)	85.3 (5.6)	**53.0** (4.2)	51.5 (7.3)	34.9 (3.5)	**56.4** (2.8)	82.5 (6.4)	61.0 (2.8)	46.8 (7.3)	46.9 (3.1)	60.0 (5.5)	78.5 (3.1)	**56.9** (2.7)	34.6 (2.2)	41.9 (3.1)
	30 - 60 cm	**29.7** (2.3)	45.7 (1.7)	27.9 (3.1)	21.0 (1.2)	31.6 (4.2)	**33.1** (2.6)	53.7 (6.7)	36.1 (4.0)	26.8 (2.7)	26.7 (1.3)	**27.2** (2.9)	38.1 (2.8)	35.0 (4.5)	19.3 (1.6)	19.2 (1.1)
N (g/kg)	0 - 30 cm	5.8 (0.5)	7.0 (0.4)	**4.6** (0.3)	4.5 (0.5)	3.1 (0.3)	**4.3** (0.2)	6.1 (0.4)	4.6 (0.2)	3.6 (0.5)	3.6 (0.2)	6.2 (0.5)	7.9 (0.3)	**5.8** (0.3)	3.9 (0.2)	4.5 (0.3)
	30 - 60 cm	**2.6** (0.2)	3.7 (0.1)	2.4 (0.2)	2.1 (0.1)	2.8 (0.3)	**2.6** (0.1)	3.9 (0.4)	2.8 (0.3)	2.2 (0.1)	2.1 (0.1)	**2.6** (0.3)	3.7 (0.3)	3.3 (0.5)	1.9 (0.2)	1.8 (0.1)
NH_4^+ (mg/kg)	0 - 30 cm	40.6 (1.9)	26.5 (1.2)	21.8 (1.2)	**24.9** (1.2)	23.5 (2.2)	47.0 (3.6)	33.5 (1.6)	**31.4** (3.4)	28.0 (3.1)	31.1 (3.8)	56.1 (4.2)	33.0 (2.0)	**30.0** (1.6)	23.6 (1.1)	27.4 (2.2)
	30 - 60 cm	26.6 (2.4)	18.1 (0.5)	16.7 (0.5)	19.1 (1.9)	**18.3** (1.3)	38.6 (6.7)	**25.5** (1.2)	26.6 (2.6)	22.4 (1.1)	22.0 (1.8)	25.1 (1.2)	19.7 (1.7)	22.6 (2.1)	19.2 (1.0)	**21.3** (0.8)
NO_3^- (mg/kg)	0 - 30 cm	**32.8** (3.2)	43.7 (5.8)	27.2 (4.1)	49.7 (3.9)	31.0 (4.4)	30.4 (4.2)	67.3 (9.5)	**39.4** (3.8)	37.6 (5.4)	42.2 (2.6)	20.6 (5.3)	75.7 (7.2)	**41.0** (4.3)	47.5 (4.3)	31.9 (3.5)
	30 - 60 cm	20.2 (4.9)	**23.4** (3.2)	20.5 (4.3)	27.5 (3.8)	24.1 (3.3)	12.3 (2.3)	36.4 (3.6)	17.1 (2.4)	27.7 (2.8)	**18.7** (1.7)	4.2 (0.9)	33.7 (8.3)	**24.1** (4.3)	26.3 (4.5)	19.4 (1.5)
N_{eo} (mg/kg)	0 - 30 cm	273.9 (14.7)	200.7 (10.8)	156.2 (12.2)	171.0 (9.7)	**178.4** (15.0)	272.3 (18.3)	**219.3** (11.7)	241.3 (12.2)	175.1 (5.3)	211.5 (7.4)	284.8 (17.4)	229.7 (12.0)	**212.6** (11.7)	159.3 (5.2)	182.3 (4.9)
	30 - 60 cm	177.2 (13.4)	131.3 (5.2)	117.2 (7.6)	118.1 (10.4)	**126.9** (12.2)	204.6 (20.5)	189.2 (8.6)	**176.8** (10.8)	154.6 (8.1)	172.8 (6.0)	148.3 (7.9)	**136.2** (20.6)	126.4 (11.3)	107.4 (8.7)	138.0 (7.4)
C/N	0 - 30 cm	11.8 (0.2)	12.2 (0.4)	**11.3** (0.4)	11.1 (0.5)	11.1 (0.3)	**13.0** (0.3)	13.5 (0.3)	13.4 (0.3)	12.7 (0.3)	13.0 (0.2)	**9.5** (0.2)	10.0 (0.1)	9.8 (0.1)	8.8 (0.2)	9.3 (0.2)
	30 - 60 cm	11.6 (0.2)	12.4 (0.3)	**11.4** (0.4)	10.1 (0.2)	11.3 (0.2)	12.7 (0.4)	13.6 (0.3)	**12.6** (0.3)	12.1 (0.4)	12.4 (0.2	**10.3** (0.1)	10.3 (0.2)	10.6 (0.3)	10.0 (0.2)	10.5 (0.2)

N concentrations in soil extracts

Total phosphate-extractable N (N_e) was higher in the topsoil, with a less accentuated decline with soil depth in the natural forest (Table 4-2). The concentrations of extractable organic N (N_{eo}) were roughly four times as high as total extractable inorganic (N_{ei}). However, the proportion of N_{eo} was markedly lower in 30-60 cm depth of the plantations. A seasonal pattern was visible for all forest types, being more pronounced for the inorganic species. The amount of N_{eo} and NH_4^+ was largest at the end of the rainy season. The NO_3^- concentration peaked little after the rainy season, with an inverse trend of decreasing NH_4^+.

The extractable species contributed 5.4 to 9.0 % to bulk N showing highest values in the natural forest (Table 4-3) and intermediate values in the conifer plantation. This proportion increased with depth and was generally more pronounced for N_{eo}, except for *C. lusitanica*. *E. globulus* yielded the largest relative increase with soil depth of up to 41 %.

Table 4-3: Contribution of N_{eo} and N_{ei} (= NH_4^+ + NO_3^-), respectively, to bulk N of two soil layers, including the ratio of these layers (SE in parenthesis, n = 112 for *C. lusitanica*, n = 110 for *P. falcatus*, n = 111 for *E. globulus*, total n = 333).

	C. lusitanica		*P. falcatus*		*E. globulus*		**All forests**	
	%N_{eo}	%N_{ei}	%N_{eo}	%N_{ei}	%N_{eo}	%N_{ei}	%N_{eo}	%N_{ei}
0 - 30 cm	4.56^{ab*} (0.33)	1.48^{AB} (0.09)	5.34^{a} (0.23)	1.77^{A} (0.09)	3.93^{b} (0.15)	1.44^{B} (0.06)	4.60 (0.15)	1.46 (0.09)
30 - 60 cm	5.38^{b} (0.31)	1.76 (0.12)	7.09^{a} (0.29)	1.93 (0.09)	5.52^{b} (0.31)	1.79 (0.12)	6.00 (0.18)	1.75 (0.07)
layer ratio lower/upper	1.18 (0.09)	1.19 (0.09)	1.33 (0.06)	1.09 (0.07)	1.41 (0.07)	1.24 (0.08)	1.30 (0.04)	1.20 (0.07)

[*] Different superscripts in one row indicate significant differences ($P < 0.05$) between the forest types for one parameter.

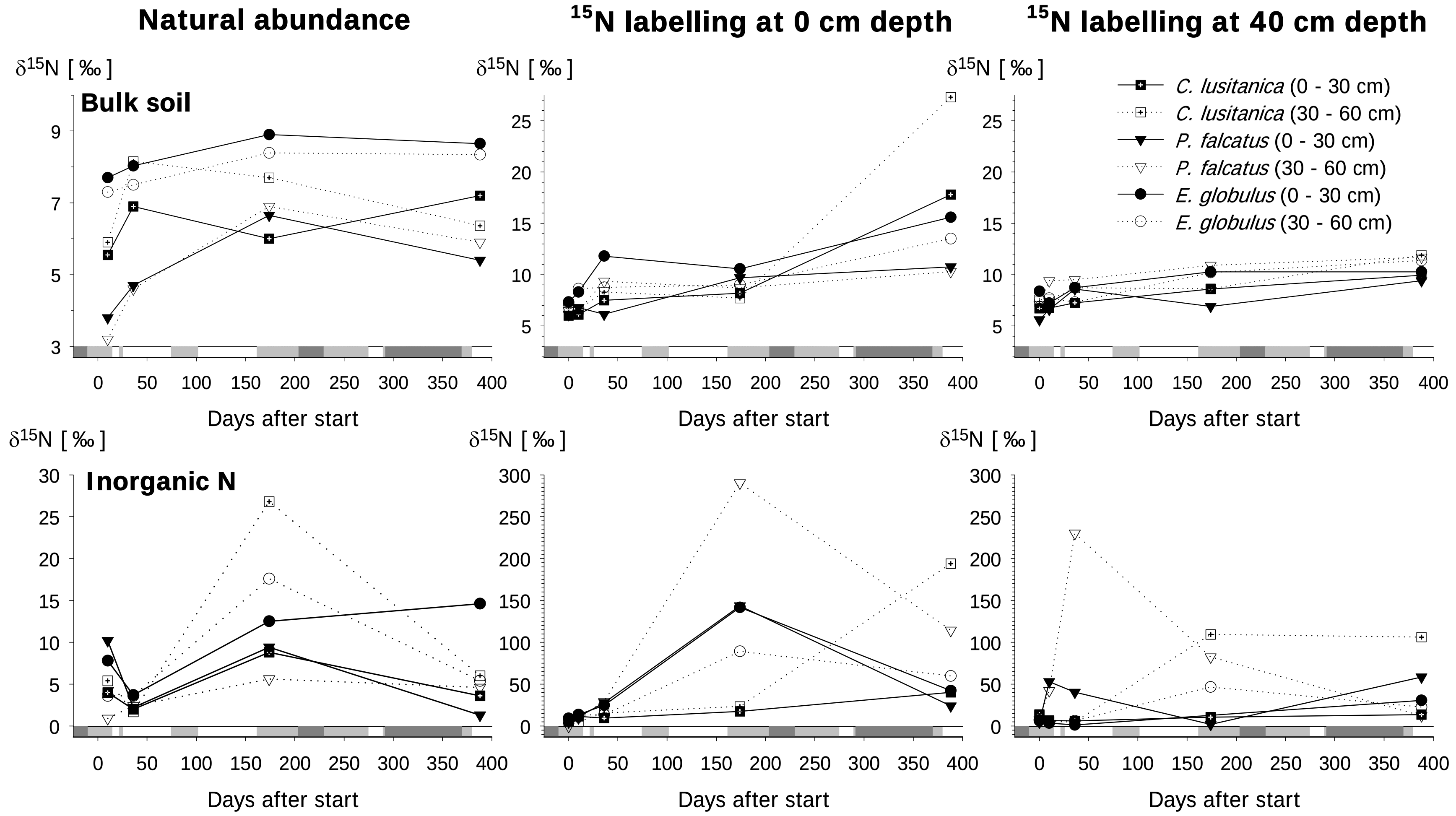

Fig. 4-1: Time series of δ^{15}N values of bulk soil (upper row) and extracted inorganic N (lower row) in two soil layers of three forest types: natural abundance (left column), after ^{15}N labelling beneath the organic layer (middle column) and after ^{15}N labelling at 40 cm soil depth (right column). Grey shading near the time axis indicates rain (dark grey for periods of heavy and continuous rain). Note the different scales used for bulk soil and extracts after labelling.

$\delta^{15}N$ values at natural abundance

The isotopic composition of bulk soil N ranged from about 3 ‰ to 9 ‰ $\delta^{15}N$ (Fig. 4-1). Highest values were found in the topsoil of the *E. globulus* plantation, slightly decreasing in 30 – 60 cm depth. The natural forest soil showed identical values for topsoil and subsoil, lower by an average 3 ‰. The softwood plantation was intermediate, but subsoil $\delta^{15}N$ values were generally higher than in the topsoil. Minimum bulk $\delta^{15}N$ values occurred at the rainy season and, except for *C. lusitanica*, steadily increased during the dry season. The inorganic species covered a wider range than bulk N and also exhibited a much greater dry-season increase. Seasonality was most strongly expressed for the subsoil of the plantations, and lightest isotopic composition was found after the end of the rainy season at declining soil moisture.

Leaves of the dominant tree species had all values around 0 % $\delta^{15}N$, with those of the plantation trees being enriched by around 2.5 ‰ to the natural forest during the dry season (not shown). This difference in $\delta^{15}N$ values between the forest types was better visible during the whole sampling period in the grass *Oplismenus compositus*, ranging around –2.0 ‰ in the natural forest, and being higher by c. 3.5 ‰ under *C. lusitanica* and 5.2 ‰ under *E. globulus*, respectively.

Soil $\delta^{15}N$ values after labelling

Soil labelling with ^{15}N resulted in an increase in bulk $\delta^{15}N$ of up to 23 ‰ (Fig. 4-1). This peak, however, was only found at the end of the sampling period, as ^{15}N enrichment increased with time. Labelling at 0 cm depth mainly affected the uppermost layer of the *E. globulus* stand. For the other species, the effect at 30 – 60 cm was similar or even larger. Labelling at 40 cm depth resulted in a low $\delta^{15}N$ increases of up to 5 ‰ for both layers. The tracer effect in the deeper layer was larger in the natural forest, equal in the *C. lusitanica* stand and smaller in the *E. globulus* plantation.

Extractable inorganic N was more affected, with a tracer signal on the average three times as high as for bulk N. Superficial labelling was hardly reflected in the topsoil of the softwood plantation, but increased to high peaks in the other forest types after the rainy season. As for the bulk soil, maximum values occurred in both layers of the *C. lusitanica* plantation at the end of the sampling period. Tracer injection to 40 cm depth yielded a quite different pattern for N_{ei}. In the natural forest it decreased after a peak in the dry season and reached a new peak only in the upper layer. In the plantations, the tracer effect was much less. The topsoil values gradually increased, and the subsoil peak after the dry season hardly decreased in the following rainy season. Subsoil enrichment was higher under *C. lusitanica*.

Plant uptake

^{15}N labelling induced highly elevated $\delta^{15}N$ values in the vegetation, reaching up to 10,000 ‰ in the understorey (Fig. 4-2). The response was strongest for *Oplismenus compositus* (open circles) following the superficial labelling, decreasing from the *C. lusitanica* to the natural forest. In the *C. lusitanica* stand, the 0 cm tracer signal of the central tree declined in the dry season and increased again in the next rainy season. As expected, neighbouring trees took up a lesser amount while showing the same pattern. The dry-season decline was less distinct following the deep labelling. Final ^{15}N enrichment tended to be higher for the 40 cm treatment. *P. falcatus* took up more ^{15}N from the subsoil label and exhibited a long dry-season decline only for the superficial labelling. Neighbouring *P. falcatus* trees had lower enrichments, which held also true for most other woody plants. Only the pioneer species *Croton macrostachys* (0 cm depth) showed the same pattern as the central tree.

The isotope signal in leaves of *E. globulus* trees steadily increased, reaching higher values in the 40 cm treatment, yet at greater fluctuation. $\delta^{15}N$ values of *Rubus steudneri* leaves in the understorey of this stand rose quickly after superficial tracer application, to drop again sharply after a longer wet period. Uptake from 40 cm depth appeared even higher and $\delta^{15}N$ values remained at a high level. *Croton macrostachys* also accumulated the tracer quickly, with a slight preference for the upper layer and only a minor decrease of the $\delta^{15}N$ values with time.

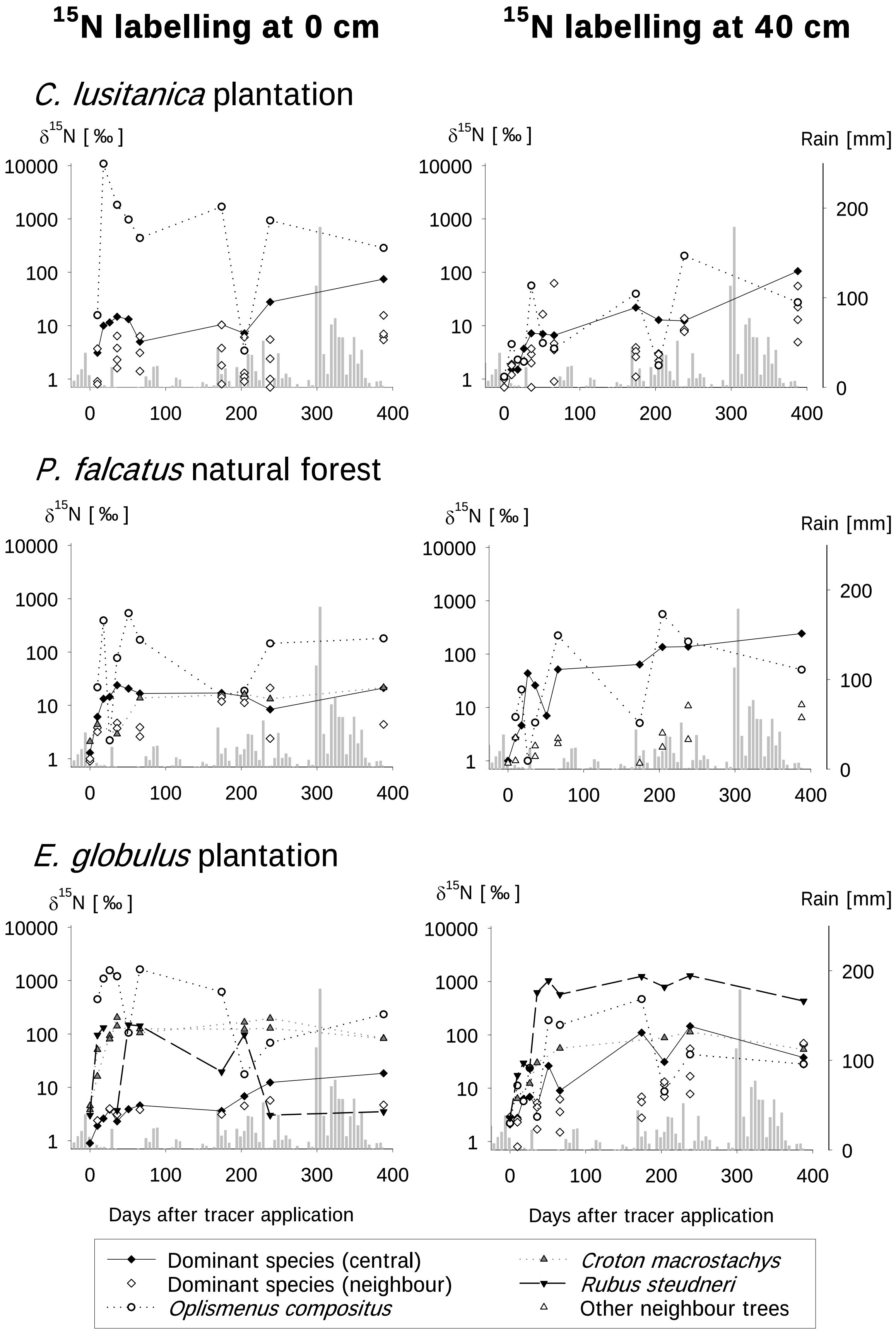

Fig. 4-2: Time series of δ^{15}N values of central trees, neighbouring trees and understorey vegetation in three forest types after ^{15}N tracer injection to 0 cm and 40 cm soil depth. Rainfall is included, note the logarithmic scaling.

Tracer recovery

Tracer recovery in the soil from superficial labelling finally reached 80 % for *C. lusitanica*, about 50 % for *E. globulus* and roughly 35 % for the natural forest. The deep label largely disappeared from the soil. It soon reached a maximum of 20 % in the natural forest, but only gradually increased to 10 – 20 % in the plantations. While being subject to high uncertainties due to intra-plant distribution and reallocation (Proe et al. 2000; Evans 2001), figures of recovery in the aboveground biomass of the vegetation (typically 5 – 10 %) were in the range of other studies (Mead and Preston 1994; Zeller et al. 2001), with a trend towards the highest values in the natural forest after deep labelling. Despite the higher values in foliage, recovery of the deep label on ecosystem level did not exceed 35 %.

Discussion

Bulk nutrient concentrations

Equal N concentrations in the 30 – 60 cm layer of the investigated plots give evidence of the suitability of the research plots for the study undertaken. The soil characteristics of the present study are in line with published data for C and N contents from adjacent soil profiles (Ashagrie et al. 2005), but contradict some studies from other regions of Ethiopia. Lemenih and Itanna (2004) found lower C/N ratios at smaller subsoil N contents in *P. falcatus* dominated natural forest, and a nutrient decline was frequently observed under plantations (Michelsen et al. 1996; Lemenih et al. 2004). Besides differences in site conditions, influences of plantation establishment and management were proposed by these authors as the cause for their nutrient stocks. The site of our study, however, was distant from settlements and thus less affected than most other Ethiopian forests by human activities comprising litter export as fuel and agriculture after clear-cutting of the natural forest.

The higher topsoil N concentrations of the plantations, particular that of *E. globulus*, at lower C/N ratios point towards an accumulation of N after forest conversion. This accumulation appears to affect mainly the topsoil, inverting the

C/N gradient towards lower values in the subsoil. While a certain stabilised N pool might be inherited from the establishment phase with initial burning and high mineralization (Prieto-Fernandez et al. 2004; Knicker et al. 2005), specific processes might have caused differences between the plantations. High N immobilization in recalcitrant fractions is a common phenomenon for *E. globulus* (Aggangan et al. 1999; Rovira and Vallejo 2002; Corbeels et al. 2003; O'Connell et al. 2003), and rapid incorporation of the forest floor material (Ashagrie et al. 2003; Fritzsche et al. 2005b) increases the soil N pool in the studied plantation (Lisanework and Michelsen 1994), facilitated by the rich understorey and the tree root distribution (Abate 2004). A high closed layer of herbaceous dicots induces a favourable micro-climate and provides above- and belowground inputs of high quality, presumably promoting gross microbial transformation and thereby stabilization of N from litter (Briones and Ineson 1996; Schwendener et al. 2005). On the other hand, the superficial density of low-N tree fine roots was very low for *E. globulus* (Abate 2004; Fritzsche et al. 2005a), reducing extraction of nutrients and water, while deep roots potentially scavenge deep N pools (Schroth et al. 1999; Jobbagy and Jackson 2004). Besides effects of litter quality (Satti et al. 2003; Booth et al. 2005), lower biological activity and less N-demanding trees (Abate 2004) might be responsible for higher N concentrations in the *C. lusitanica* plantation. The seasonal maximum of soil C and N after the large rainy season probably reflects an increase in litterfall (Lisanework and Michelsen 1994) and incorporation, as well as the response of plant internal C allocation to the root systems (including rhizodeposition) constantly adapting to dwindling moisture (Fritzsche et al. 2005a). The increase in belowground C is mirrored by a decrease in leaf C concentration (not shown), pointing towards export of C stored in the aboveground biomass. A similar maximum in C, N and C/N ratios after the dry season has been observed in a Mediterranean shrubland by Monokrousos et al. (2004).

Measured N concentrations of the sampled, lively leaves were rather high and appeared inversely related with leaf longevity. They were similar for the long-lived leaves, while the more ephemeral leaves of the understorey and the soft big leaves of the deciduous pioneer *Croton macrostachys* had much higher N concentrations, probably due to higher physiological activity of unit mass (Hiremath 2000; Lüttge et al. 2003).

Extractable Nitrogen

While being the prime fraction for plant uptake, the concentration of N_{ei} reacts sensitively to sample treatment and is analytically influenced by amino acids, attributable N_{eo} (Herrmann et al. 2005). A better estimate of the biologically active N pool is attained by the additional quantification of N_{eo} (Zhong and Makeschin 2003). In tropical soils, this fraction largely constitutes mobile N with fast nitrification and N immobilization (Lehmann et al. 2004). The concentrations of the single extractable species are quantitatively in the range of published data (Matsumoto et al. 2000; Erickson et al. 2002; Fierer and Schimel 2002).
Seasonality of the extractable species was pronounced, resulting from the changing balance of ammonification, nitrification, nitrate reduction and N immobilization, plant uptake and leaching. The rapid response of microbial activity to soil wetting (García-Méndez et al. 1991; Cui and Caldwell 1997; BassiriRad et al. 1999) has a particularly high effect on mineralization in fine-textured soils of dry environments (Austin et al. 2004). Nitrification is very fast under the tropical climate (Lehmann et al. 2004) and favourable soil pH of 6 – 7 in the topsoil, making NO_3^- the dominant free inorganic N species. Although nitrate reduction in micro-sites might in part reverse nitrification (Silver et al. 2001; Burger and Jackson 2004), the concentration of the more transitional NH_4^+ should be controlled by adsorption in the high-CEC topsoils and diffusion, buffering variability. We attribute the increase in NO_3^- in the dry season to a high nitrification in the well-aerated topsoil at a time of low N export. In contrast, with the begin of the rainy season nitrate depletion occurred in the order *E. globulus* > *P. falcatus* > *C. lusitanica*. As soil moisture decreased in the same order, we interpret this as a hint to denitrification (Hooda et al. 2003), supported by the observations by Andersson et al. (2003) in similar soils from western Ethiopian forests. The seasonality of N_{eo} is likely to be associated with that of microbial biomass (Matsumoto et al. 2000; Zhong and Makeschin 2003). So Michelsen et al. (2004) reported higher levels of microbial biomass in an Ethiopian forest soil for the rainy season. Similar observations were described by Yavitt et al. (2004) for neotropical forests.

The highest proportion of extractable N (Table 4-3) supports the above-stated hypothesis of greater biological activity in the natural forest. It concurs with the wet-chemical and spectroscopic characterization of the topsoils by Solomon et al. (2002; 2005) who found soil C of the natural forest more labile and microbially-influenced than in the *C. lusitanica* plantation. More intense nutrient cycling under natural vegetation was also concluded by Lian and Zhang (1998) from a comparative study in subtropical China, with monocultures of conifers being least active. A litter bag decomposition experiment study by Lisanework and Michelsen (1994) ranked the forest types *E. globulus* > natural forest = *C. lusitanica* plantation regarding their loss of mass. Considering the balance of N in that experiment, however, the natural forest showed an initial gain, thereby indicating a high internal cycling. Similar evidence was obtained from an *in-situ* incubation study, mixing isotopically labelled litter into the topsoil near the plots of our study (A. Johann, unpublished thesis). Incorporation of added N into the more stable heavy fraction took place within one month and ranked *E. globulus* > *C. lusitanica* > natural forest. At the same time overall N losses from the topsoil after a one year incubation decreased in the order *E. globulus* > natural forest > *C. lusitanica*. These observations are complemented by the maximum increase in extractability in the subsoil of *E. globulus*. That implies two distinct soil N pools, one being rapidly stabilised and the other one being highly mobile and thus prone to be lost from the system. In contrast, soil N pools of the natural forest appear to be highly coupled at high internal turnover and better conserving this pool, as visible from a low NO_3^- concentration in subsoil solution (Y. Ashagrie, unpublished data). The minimum increase in N extractability with depth in the *C. lusitanica* stand might be attributable to the general vertical displacement of the mobile N_e pool (visible from equal ratios for N_{ei} and N_{eo}), located relatively lower than the corresponding immobile insoluble pool. Superficial root activity (see below Fig. 4-3) and low microbial activity concentrated in the topsoil result in a basically homogeneous topsoil N pool and low subsoil N turnover letting N_e pass unaffected. This is mirrored by NO_3^- concentrations in the subsoil solution 15 times higher than in the natural forest (Y. Ashagrie, unpublished data).

Strong correlations between N_{eo} and NH_4^+ (Table 4-4) underline the function of N_{eo} as a substrate for ammonification. In contrast, correlations are much weaker with NO_3^- concentration, which is controlled by other factors like climate and plant uptake. The similarly high correlations of C, total N, NH_4^+ and N_e in both layers of the natural forest support the hypothesis of close coupling and a conservative N cycling. Association with C emerges even more intimate in the *E. globulus* topsoil, with a large pool of total N seemingly similar to N_{eo}. Yet in the subsoil of both plantations and to a minor extent in the *C. lusitanica* topsoil, the majority of C and N appears to be present in stable forms that are largely decoupled from the dynamics of the soluble species and thus show no correlation. This corroborates the hypothesis of low biological activity in the *C. lusitanica* plantation.

Table 4-4: Correlation matrices (R_s) of bulk C, bulk N and extractable N species (ammonium, nitrate, total extractable N and extractable organic N) for two soil depth layers (0 – 30 cm and 30 – 60 cm) of three forest types.

	0-30 cm depth					**30-60 cm depth**				
	C	NH_4^+	NO_3^-	N_e	N_{eo}	C	NH_4^+	NO_3^-	N_e	N_{eo}
C. lusitanica **plantation**										
NH_4^+	0.26					0.02				
NO_3^-	0.32*	0.53**				-0.07	0.32*			
N_e	0.30*	0.92**	0.63**			-0.06	0.87**	0.56**		
N_{eo}	0.26	0.89**	0.44**	0.96**		-0.01	0.86**	0.31*	0.95**	
N	0.98**	0.27*	0.33*	0.30*	0.26	0.98**	-0.02	-0.05	-0.09	-0.06
P. falcatus **natural forest**										
NH_4^+	0.37**					0.32*				
NO_3^-	0.35*	0.14				0.41**	0.16			
N_e	0.39**	0.73**	0.56**			0.43**	0.85**	0.38**		
N_{eo}	0.27*	0.68**	0.29*	0.93**		0.35**	0.79**	0.15	0.95**	
N	0.98**	0.38**	0.32*	0.36**	0.24	0.97**	0.31*	0.40**	0.40**	0.33*
E. globulus **plantation**										
NH_4^+	0.54**					0.19				
NO_3^-	0.39**	-0.01				0.25	0.21			
N_e	0.68**	0.82**	0.36**			0.22	0.82**	0.45**		
N_{eo}	0.62**	0.81**	0.05	0.93**		0.18	0.82**	0.19	0.95**	
N	0.99**	0.53**	0.40**	0.68**	0.61**	0.98**	0.18	0.24	0.20	0.15

* P < 0.05, ** P < 0.01; n = 56, except for 30 – 60 cm (n = 55 for *E. globulus* and n = 54 for *P. falcatus*).

High correlations of the extractable N species from the upper 30 cm with the layer beneath (Table 4-5) indicate subsoil concentrations to be controlled by the topsoil for *C. lusitanica*, presumably due to leaching. Correlations for N_{eo} are second in the natural forest which fits into the picture of both layers constituting one dynamic system. High correlations for N_{ei} in the *E. globulus* stand can be explained by nutrient leaching, with high biological activity rapidly transforming N_{eo}.

Table 4-5: Correlations (R_s) of extractable N species between soil layers within three forest types: upper layer (0 - 30 cm) values with lower layer (30 - 60 cm).

		C. lusitanica			*P. falcatus*			*E. globulus*		
		upper			upper			upper		
		NH_4^+	NO_3^-	N_{eo}	NH_4^+	NO_3^-	N_{eo}	NH_4^+	NO_3^-	N_{eo}
lower	NH_4^+	0.54^{**}	0.20	0.60^{**}	0.35^{**}	0.06	0.39^{**}	0.37^{**}	-0.27^{*}	0.26
	NO_3^-	0.10	0.50^{**}	0.13	-0.26	0.31^{*}	-0.31^{*}	-0.21	0.46^{**}	-0.27^{*}
	N_{eo}	0.56^{**}	0.16	0.67^{**}	0.48^{**}	0.20	0.52^{**}	0.36^{**}	-0.13	0.26

* $P < 0.05$, ** $P < 0.01$, n = 56 (*C. lusitanica*) n = 54 (*P. falcatus*) and n = 55 (*E. globulus*).

Isotopic evidence

The range of natural-abundance $\delta^{15}N$ values is in line with published data for natural forests and plantations in South Ethiopia (Eshetu and Högberg 2000; Eshetu 2004). The higher ^{15}N abundance in the plantations is a sign of a more open nutrient cycling (Högberg 1990; Högberg and Johannison 1993). This can be an effect of N losses during the establishment phase. Still, similar patterns with constantly equal $\delta^{15}N$ differences for leaves (Fischer, unpublished thesis) and bulk soil through the whole dataset, rather imply an effect of recent processes, namely biological N fixation and long-term, specific export of depleted species. A substantial N_2 fixation can only be expected in the natural forest, as its diverse understorey also comprises legumes (Abate 2004), while strongly fractionating denitrification should primarily affect the *E. globulus* plantation with high soil moisture (Fritzsche et al. 2005a). A high degree of decomposition (visible from the low C/N ratios) is commonly associated with high $\delta^{15}N$ values (Högberg 1997). While the $\delta^{15}N$ values of the two layers are virtually identical within the natural and *E. globulus* forests, the separation of topsoil and subsoil N pools under *C. lusitanica* is also reflected in its $\delta^{15}N$ signature. We ascribe this to N washed down from the topsoil during the rainy seasons, lowering the subsoil values, which are generally higher, probably from the conversion phase. Subsoil N dynamics also strongly differ. The peak in $\delta^{15}N$ of subsoil N_{ei} after the dry season (28 ‰) coincides with a decrease in the topsoil bulk $\delta^{15}N$. This indicates a downward movement of enriched N_{ei}. The strong dry season decline in N_{eo} as a source for N_{ei} signifies a higher degree of mineralization, during which ^{15}N gets enriched. In the *E. globulus* plantation, topsoil δ^{15}N values also of N_{ei} are higher than in the other forests. Unlike under *C. lusitanica*, this high-δ^{15}N material seemingly takes part in the actual nutrient cycle. The seasonality in the subsoil again indicates N dynamics in between *C. lusitanica* with dry season solute transport close to zero and the natural forest with the most balanced soil hydrology (Fritzsche et al. 2005a).

The high extent of ^{15}N depletion in the leaves is a sign of nitrate nutrition, comprising the effects of ^{15}N discrimination during nitrification and intra-plant nitrate reduction (Högberg 1997). *C. lusitanica* with slightly higher leaf δ^{15}N seems to take up a higher proportion of NH_4^+, probably owing to lower nitrification and highly competitive superficial root mats (Abate 2004).

Labelling with ^{15}N gave additional information to the evidence from N pool sizes and natural-abundance δ^{15}N, enabling us to validate our hypotheses on processes and identify the vegetation effect. Early values of the soil time series, however, should be viewed with caution, as the inherent methodical problem of inhomogeneous tracer distribution in the clay soil after injection might have led to an underestimation in the auger samples. Theoretically, ^{15}N labelling should have resulted in δ^{15}N values of 15 – 25 ‰ (*E. globulus* < *C. lusitanica* < natural forest) for the topsoil labelling and 32 – 34 ‰ for the 40 cm injection; yet these values were only approached for the 0 cm plots at the end of the experiment.

The maximum tracer signal in the topsoil of *E. globulus* after superficial labelling fits into the picture of a high topsoil rate of N stabilization. In the *P. falcatus* natural forest, the equal but low effect of superficial ^{15}N application on both layers supports the hypothesis of high biological activity. Initial plant uptake and immobilization appear high, but during the dry season a considerable amount is recycled in both layers, as visible from N_{ei}. The same pattern can be found in the *E. globulus* plantation, although less expressed. The identical pattern of δ^{15}N of topsoil N_{ei} for these two stands indicates similar turnover rates of this pool, given the similar pool size. The initial response of the *C. lusitanica* soil to labelling was minimal, but the later return of ^{15}N into both layers suggests plant uptake and subsequent rhizodeposition of remobilized plant N. However, the distinct rise in δ^{15}N of subsoil N_{ei} after the rainy season also signals N leaching. After the 40 cm tracer injection, the natural forest soil again emerged as the most active one with high initial cycling in the available fraction also of the upper layer and later immobilization in the lower layer. Nutrient return from the vegetation is reflected in rising topsoil $\delta^{15}N$ after 388 days. *C. lusitanica* is again the other extreme with gradually rising values and a high proportion of tracer in subsoil N_{ei}.

Plant N dynamics

Tracer incorporation into leaves (Fig. 4-2) exhibited large differences in extent and temporal course among the sampled vegetation elements. For most species, uptake took place very rapidly and increased after short rains. A rapid increase in ^{15}N uptake at enhanced water availability was also observed by BassiriRad et al. (1999) on two desert shrubs, being highly species-dependent. Our data supported the hypothesis by Lehmann et al. (2001) that plants with high nitrogen concentrations take up more tracer N. In contrast to investigations from Amazonia (Lehmann et al. 2001; Dinkelmeyer et al. 2003), leaf $\delta^{15}N$ values often increased until the end of the study period. Leaf samples should well represent plant uptake, as studies on *E. globulus* showed a high internal N cycling from mature leaves (Pate and Arthur 2000). Foliage is the by far most important aboveground N sink (Nissen et al. 1999), yet on whole-plant level tracer allocation to roots can be expected highest (Dyckmans and Flessa 2001).

Neighbour trees from the dominant species showed the expected minor extent of uptake, while regardless of the depth pioneer *Croton macrostachys* trees appeared more competitive, especially compared to *E. globulus*. The grass *Oplismenus compositus* effectively intercepted superficial N in all three forest types. *Rubus steudneri* was very active in the lower layer. Whereas the instant response with high $\delta^{15}N$ values is no surprise considering the low mass, the high competence of understorey plants was also found in hydroponic experiments for boreal species (Hangs et al. 2003b). For the understorey the decrease of density in the order natural forest ≥ *E. globulus* plantation >> *C. lusitanica* plantation has to be noted, with the highest diversity in the natural forest likely to increase nutrient competition (Hooper and Vitousek 1998).

Relating the uptake from the two depth layers (Fig. 4-3) reveals that *Oplismenus compositus* root activity is confined to the topsoil in the *C. lusitanica* plantation, while it can also access deeper pools in the other forests. This underlines the interaction of this grass with the root system of the dominant species. Nonetheless, this superficial N uptake is in part an effect of its strategy, visible from the understorey species *Rubus steudneri*, which largely extracted deeper layers. Competitive in quick uptake from the surface, *P. falcatus* on the long run extracted more tracer from the deeper layer. *C. lusitanica* took up N from the upper layer at high soil moisture, while *E. globulus* almost exclusively scavenged deep N pools. However, *Eucalyptus* spp. have been shown to also extract nutrients by forming superficial root mats at a juvenile stage (Adams et al. 2003) and under less favourable soil conditions (Laclau et al. 2004). Moreover, the sub-humid climate might play an important role by forcing root activity to deeper layers at least seasonally.

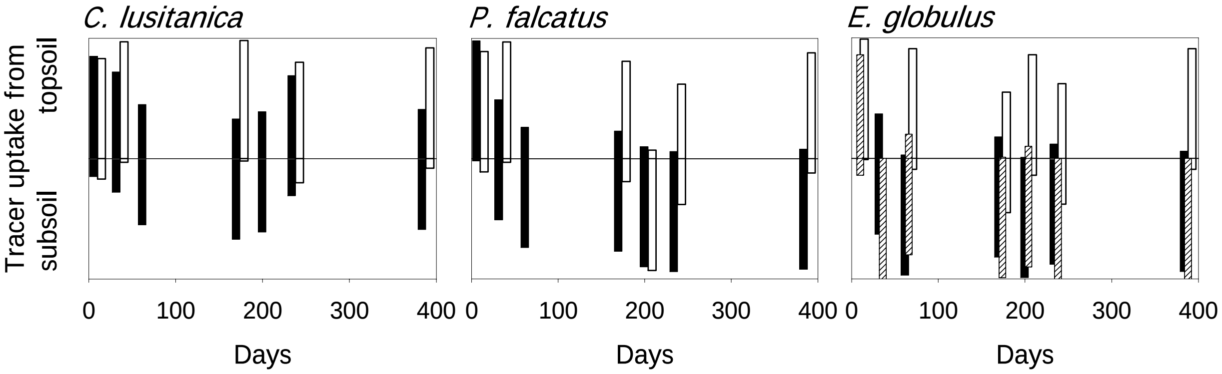

Fig. 4-3: Relative root activity of the dominant trees (filled bars) as well as understorey *Oplismenus compositus* (open bars) and *Rubus steudneri* (hatched bars, only under *E. globulus*): Distribution of tracer uptake between 0 cm and 40 cm soil depth in three forest types.

Conclusions

The study of soil N pools in two layers together with their natural δ^{15}N signatures and tracer dynamics gives complementary evidence about N cycling in the natural forest and the two plantations. It also allows to separate effects from forest conversion and actual ecosystem processes. The topsoil N enrichment in the plantations is such an inherited feature in the *C. lusitanica* forest, but N stabilization appears still relevant in the *E. globulus* stand. The understorey vegetation played an important part in N cycling, as it rapidly took up and returned nutrients from the active pool, which is likely to endorse nutrient conservation.

Nitrogen redistribution seems largely controlled by root distribution and thereby reflects its response to changes in soil moisture. The most balanced moisture conditions in the natural forest was mirrored by a reduced seasonality. *P. falcatus* and particularly *E. globulus* were efficient in recovering N from deeper layers. This ability of *E. globulus* did not affect other plants negatively, its low topsoil root activity even seemed to favour understorey growth.

The natural forest emerged as a system with high biological activity and N turnover in the upper 60 cm. High internal cycling is advantageous concerning nutrient conservation, soil quality and plant growth during all seasons. However, disturbance through grazing or selective logging might open nutrient cycling and trigger instantly high N losses. Afforestation with *C. lusitanica* in the practised form cannot be regarded as sustainable and apparently leads to the confinement of soil life to a thin superficial layer. This in turn bears the danger of high, irreversible nutrient losses at high rainfall. In the *E. globulus* stand, N cycling appears to involve a higher proportion of higher-molecular organic species, but is highly active though it may specifically suppress microbial communities (Souto et al. 2001). This system might thus be more robust to disturbances, yet N leaching from the subsoil could be considerable. While not necessarily transferable to highly differing sites, plantations of *E. globulus* appear as a nutrient-conserving way to secure wood supply. Mixture with other species could improve productivity (Garcia-Montiel and Binkley 1998; Forrester et al. 2005) and ecological value, and the promotion of naturally regenerating indigenous trees (Feyera et al. 2002), namely *P. falcatus*, opens a chance to gradually restore natural vegetation.

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References

Abate A (2004) Biomass and nutrient studies of selected tree species of natural and plantation forests: Implications for a sustainable management of the Munessa-Shashemene Forest, Ethiopia. PhD dissertation. Faculty of Biology, Chemistry and Geosciences. University of Bayreuth, Bayreuth, Germany, 163 p

Adams PR, Beadle CL, Mendham NJ, Smethurst PJ (2003) The impact of timing and duration of grass control on growth of a young *Eucalyptus globulus* Labill. plantation. New Forests 26:147-165

Aggangan RT, O'Connell AM, McGrath JF, Dell B (1999) The effects of *Eucalyptus globulus* Labill. leaf litter on C and N mineralization in soils from pasture and native forest. Soil Biol Biochem 31:1481-1487

Andersson M, Kjoller A, Struwe S (2003) Soil emissions of nitrous oxide in fire-prone African savannas. J Geophys Res-Atmos 108: No. 4630

Ashagrie Y, Zech W, Guggenberger G, Teketay D (2003) Changes in soil organic carbon, nitrogen and sulphur stocks due to the conversion of natural forest into tree plantations (*Pinus patula* and *Eucalyptus globulus*) in the highlands of Ethiopia. World Resource Review 15:462-482

Ashagrie Y, Zech W, Guggenberger G (2005) Transformation of a *Podocarpus falcatus* dominated natural forest into a monoculture *Eucalyptus globulus* plantation at Munesa, Ethiopia: soil organic C, N and S dynamics in primary particle and aggregate-size frations. Agriculture, Ecosystems and Environment 106:89-98

Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA, Schaeffer SM (2004) Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221-235

BassiriRad H, Tremmel DC, Virginia RA, Reynolds JF, de Soyza AG, Brunell MH (1999) Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. Plant Ecology 145:27-36

Benvenuti M, Carnicelli S, Belluomini G, Dainelli N, Di Grazia S, Ferrari GA, Iasio C, Sagri M, Ventra D, Atnafu B, Kebede S (2002) The Ziway-Shala lake basin (main Ethiopian rift, Ethiopia): a revision of basin evolution with special reference to the Late Quaternary. Journal of African Earth Sciences 35:247-269

Bigelow SW, Ewel JJ, Haggar JP (2004) Enhancing nutrient retention in tropical tree plantations: No short cuts. Ecol Appl 14:28-46

Binkley D, Resh SC (1999) Rapid changes in soils following *Eucalyptus* afforestation in Hawaii. Soil Science Society of America Journal 63:222-225

Booth MS, Stark JM, Rastetter E (2005) Controls on nitrogen cycling in terrestrial ecosystems: A synthetic analysis of literature data. Ecol Monogr 75:139-157

Briones MJI, Ineson P (1996) Decomposition of eucalyptus leaves in litter mixtures. Soil Biol Biochem 28:1381-1388

Burger M, Jackson LE (2004) Plant and microbial nitrogen use and turnover: rapid conversion of nitrate to ammonium in soil with roots. Plant and Soil 266:289-301

Corbeels M, O'Connell AM, Grove TS, Mendham DS, Rance SJ (2003) Nitrogen release from eucalypt leaves and legume residues as influenced by their biochemical quality and degree of contact with soil. Plant and Soil 250:15-28

Cuevas E, Lugo AE (1998) Dynamics of organic matter and nutrient return from litterfall in stands of ten tropical tree plantation species. Forest Ecol Manag 112:263-279

Cui MY, Caldwell MM (1997) A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. Plant and Soil 191:291-299

Davidson EA, Hart SC, Firestone MK (1992) Internal cycling of nitrate in soils of a mature coniferous forest. Ecology 73:1148-1156

Di HJ, Cameron KC, McLaren RG (2000) Isotopic dilution methods to determine the gross transformation rates of nitrogen, phosphorus, and sulfur in soil: a review of the theory, methodologies, and limitations. Australian Journal of Soil Research 38:213-230

Dinkelmeyer H, Lehmann J, Renck A, Trujillo L, da Silva JP, Gebauer G, Kaiser K (2003) Nitrogen uptake from ^{15}N-enriched fertilizer by four tree crops in an Amazonian agroforest. Agroforestry Systems 57:213-224

Dyckmans J, Flessa H (2001) Influence of tree internal N status on uptake and translocation of C and N in beech: a dual ^{13}C and ^{15}N labeling approach. Tree Physiology 21:395-401

Erickson H, Davidson EA, Keller M (2002) Former land-use and tree species affect nitrogen oxide emissions from a tropical dry forest. Oecologia 130:297-308

Eshetu Z, Högberg P (2000) Effects of land use on ^{15}N natural abundance of soils in Ethiopian highlands. Plant and Soil 222:109-117

Eshetu Z (2004) Natural ^{15}N abundance in soils under young-growth forests in Ethiopia. Forest Ecol Manag 187:139-147

Evans RD (2001) Physiological mechanisms influencing plant nitrogen isotope composition. Trends in Plant Science 6:121-126

FAO, ISRIC, ISSS (1998) World reference base for soil resources. Food and Agriculture Organization of the United Nations, Rome, Italy

FAO (2003) State of the world's forests, 2003. In. Food and Agriculture Organization of the United Nations, Rome

Feyera S, Beck E, Lüttge U (2002) Exotic trees as nurse-trees for the regeneration of natural tropical forests. Trees - Structure and Function 16:245-249

Fierer N, Schimel JP (2002) Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. Soil Biol Biochem 34:777-787

Forrester DI, Bauhus J, Cowie A (2005) On the success and failure of mixed-species tree plantations: lessons learned from a model system of *Eucalyptus globulus* and *Acacia mearnsii*. Forest Ecol Manag In press

Fritzsche F, Abate A, Fetene M, Beck E, Weise S, Guggenberger G (2005a) Soil-plant hydrology of indigenous and exotic trees in an Ethiopian montane forest. Tree Physiology:(submitted)

Fritzsche F, Solomon D, Tichomirowa M, Guggenberger G (2005b) Sulfur cycling in natural forest versus plantations: a ^{34}S litter-labelling experiment in a South-Ethiopian montane forest. Oecologia:(submitted)

Fritzsche F, Zech W, Guggenberger G (2005c) Soils of the Main Ethiopian Rift Valley: a catenary study. Catena:*(submitted)*

García-Méndez G, Maass JM, Matson PA, Vitousek PM (1991) Nitrogen transformations and nitrous oxide flux in a tropical deciduous forest in Mexico. Oecologia 88:362-366

Garcia-Montiel DC, Binkley D (1998) Effect of *Eucalyptus saligna* and *Albizia falcataria* on soil processes and nitrogen supply in Hawaii. Oecologia 113:547-556

Hangs RD, Knight JD, Van Rees KCJ (2003a) Nitrogen accumulation by conifer seedlings and competitor species from ^{15}Nitrogen-labeled controlled-release fertilizer. Soil Science Society of America Journal 67:300-308

Hangs RD, Knight JD, Van Rees KCJ (2003b) Nitrogen uptake characteristics for roots of conifer seedlings and common boreal forest competitor species. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 33:156-163

Hart SC, Myrold DD (1996) ^{15}N tracer studies of soil nitrogen transformations. In: Boutton TW, Yamasaki SI (eds) Mass Spectrometry of Soils. Dekker, New York, pp 225-246

Herrmann A, Willett VB, Stockdale EA, Jones DL (2005) Interference by amino acids during the determination of ^{15}N ammonium in soil. Soil Biol Biochem 37:1747-1750

Hiremath AJ (2000) Photosynthetic nutrient-use efficiency in three fast-growing tropical trees with differing leaf longevities. Tree Physiology 20:937-944

Högberg P (1990) Forests losing large quantities of nitrogen have elevated ^{15}N/^{14}N ratios. Oecologia 84:229-231

Högberg P, Johannison C (1993) ^{15}N abundance of forests is correlated with losses of nitrogen. Plant and Soil 157:147-150

Högberg P (1997) ^{15}N natural abundance in soil-plant systems. New Phytologist 137:179-203

Hooda AK, Weston CJ, Chen D (2003) Denitrification in effluent-irrigated clay soil under *Eucalyptus globulus* plantation in south-eastern Australia. Forest Ecol Manag 179:547-558

Hooper DU, Vitousek PM (1998) Effects of plant composition and diversity on nutrient cycling. Ecol Monogr 68:121-149

IAEA Analytical Quality Control Services (2004) Reference Materials Catalogue 2004-2005. In. IAEA, Vienna, Austria, p 115

Jobbagy EG, Jackson RB (2004) The uplift of soil nutrients by plants: biogeochemical consequences across scales. Ecology 85:2380-2389

Knicker H, Gonzalez-Vila FJ, Polvillo O, Gonzalez JA, Almendros G (2005) Fire-induced transformation of C- and N-forms in different organic soil fractions from a Dystric Cambisol under a Mediterranean pine forest (Pinus pinaster). Soil Biol Biochem 37:701-718

Laclau JP, Deleporte P, Ranger J, Bouilleti JP, Kazotti G (2003) Nutrient dynamics throughout the rotation of *Eucalyptus* clonal stands in Congo. Annals of Botany 91:879-892

Laclau JP, Toutain F, M'Bou AT, Arnaud M, Joffre R, Ranger J (2004) The function of the superficial root mat in the biogeochemical cycles of nutrients in Congolese *Eucalyptus* plantations. Annals of Botany 93:249-261

Lehmann J, Muraoka T (2001) Tracer methods to assess nutrient uptake distribution in multistrata agroforestry systems. Agroforestry Systems 53:133-140

Lehmann J, Muraoka T, Zech W (2001) Root activity patterns in an Amazonian agroforest with fruit trees determined by ^{32}P, ^{33}P and ^{15}N applications. Agroforestry Systems 52:185-197

Lehmann J, Lilienfein J, Rebel K, Lima SD, Wilcke W (2004) Subsoil retention of organic and inorganic nitrogen in a Brazilian savanna Oxisol. Soil Use Manage 20:163-172

Lemenih M, Itanna F (2004) Soil carbon stocks and turnovers in various vegetation types and arable lands along an elevation gradient in southern Ethiopia. Geoderma 123:177-188

Lemenih M, Olsson M, Karltun E (2004) Comparison of soil attributes under *Cupressus lusitanica* and *Eucalyptus saligna* established on abandoned farmlands with continuously cropped farmlands and natural forest in Ethiopia. Forest Ecol Manag 195:57-67

Lian YW, Zhang QS (1998) Conversion of a natural broad-leafed evergreen forest into pure and mixed plantation forests in a subtropical area: effects on nutrient cycling. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 28:1518-1529

Lipson D, Nasholm T (2001) The unexpected versatility of plants: organic nitrogen use and availability in terrestrial ecosystems. Oecologia 128:305-316

Lisanework N, Michelsen A (1993) Allelopathy in agroforestry systems: the effects of leaf extracts of *Cupressus lusitanica* and *Eucalyptus* spp. on four Ethiopian crops. Agroforestry Systems 21:63-74

Lisanework N, Michelsen A (1994) Litterfall and nutrient release by decomposition in three plantations compared with a natural forest in the Ethiopian highland. Forest Ecol Manag 65:149-164

Lüttge U, Berg A, Fetene M, Nauke P, Peter D, Beck E (2003) Comparative characterization of photosynthetic performance and water relations of native trees and exotic plantation trees in an Ethiopian forest. Trees - Structure and Function 17:40-50

Matsumoto S, Ae N, Yamagata M (2000) Extraction of mineralizable organic nitrogen from soils by a neutral phosphate buffer solution. Soil Biology and Biochemistry 32:1293-1299

Mead DJ, Preston CM (1994) Distribution and retranslocation of ^{15}N in lodgepole pine over eight growing seasons. Tree Physiology 14:389-402

Michelsen A, Lisanework N, Friis I, Holst N (1996) Comparisons of understorey vegetation and soil fertility in plantations and adjacent natural forests in the Ethiopian highlands. J Appl Ecol 33:627-642

Michelsen A, Andersson M, Jensen M, Kjoller A, Gashew M (2004) Carbon stocks, soil respiration and microbial biomass in fire-prone tropical grassland, woodland and forest ecosystems. Soil Biol Biochem 36:1707-1717

Monokrousos N, Papatheodorou EM, Diamantopoulos JD, Stamou GP (2004) Temporal and spatial variability of soil chemical and biological variables in a Mediterranean shrubland. Forest Ecol Manag 202:83-91

Nissen TM, Midmore DJ, Cabrera ML (1999) Aboveground and belowground competition between intercropped cabbage and young *Eucalyptus torelliana*. Agroforestry Systems 46:83-93

O'Connell AM, Grove TS, Mendham DS, Rance SJ (2003) Changes in soil N status and N supply rates in agricultural land afforested with eucalypts in south-western Australia. Soil Biol Biochem 35:1527-1536

Pate JS, Arthur DJ (2000) Uptake, partitioning and utilization of carbon and nitrogen in the phloem bleeding tree, Tasmanian blue gum (*Eucalyptus globulus*). Aust J Plant Physiol 27:869-884

Piirainen S, Finer L, Mannerkoski H, Starr M (2002) Effects of forest clear-cutting on the carbon and nitrogen fluxes through podzolic soil horizons. Plant and Soil 239:301-311

Pohjonen V, Pukkala T (1990) *Eucalyptus globulus* in Ethiopian forestry. Forest Ecol Manag 36:19-31

Prieto-Fernandez A, Carballas M, Carballas T (2004) Inorganic and organic N pools in soils burned or heated: immediate alterations and evolution after forest wildfires. Geoderma 121:291-306

Proe MF, Mead DJ, Byrne D (2000) Effect of pruning on nitrogen dynamics within crowns of *Pinus radiata*. Tree Physiology 20:653-661

Rovira P, Vallejo VR (2002) Labile and recalcitrant pools of carbon and nitrogen in organic matter decomposing at different depths in soil: an acid hydrolysis approach. Geoderma 107:109-141

Rowe EC, van Noordwijk M, Suprayogo D, Hairiah K, Giller KE, Cadisch G (2001) Root distributions partially explain ^{15}N uptake patterns in *Gliricidia* and *Peltophorum* hedgerow intercropping systems. Plant and Soil 235:167-179

Satti P, Mazzarino MJ, Gobbi M, Funes F, Roselli L, Fernandez H (2003) Soil N dynamics in relation to leaf litter quality and soil fertility in north-western Patagonian forests. J Ecol 91:173-181

Schroth G, da Silva LF, Seixas R, Teixeira WG, Macedo JLV, Zech W (1999) Subsoil accumulation of mineral nitrogen under polyculture and monoculture plantations, fallow and primary forest in a ferralitic Amazonian upland soil. Agriculture Ecosystems & Environment 75:109-120

Schwendener CM, Lehmann J, de Camargo PB, Luizao RCC, Fernandes ECM (2005) Nitrogen transfer between high- and low-quality leaves on a nutrient-poor Oxisol determined by ^{15}N enrichment. Soil Biol Biochem 37:787-794

Seleshi Y, Zanke U (2004) Recent changes in rainfall and rainy days in Ethiopia. International Journal of Climatology 24:973-983

Silvanova (1996) Enterprise formations of the Munessa-Shashemene State Forestry Project. Oromia Bureau of Agriculture Development, Addis Ababa, Ethiopia

Silver WL, Herman DJ, Firestone MK (2001) Dissimilatory nitrate reduction to ammonium in upland tropical forest soils. Ecology 82:2410-2416

Soil Survey Staff (2003) Keys to Soil Taxonomy, Ninth edn. United States Department of Agriculture, Natural Resources Service, Washington, USA

Solomon D, Fritzsche F, Tekalign M, Lehmann J, Zech W (2002) Soil organic matter composition in the subhumid Ethiopian highlands as influenced by deforestation and agricultural management. Soil Science Society of America Journal 66:68-82

Solomon D, Lehmann J, Kinyangi J, Liang BQ, Schafer T (2005) Carbon K-edge NEXAFS and FTIR-ATR spectroscopic investigation of organic carbon speciation in soils. Soil Science Society of America Journal 69:107-119

Souto XC, Bolano JC, Gonzalez L, Reigosa MJ (2001) Allelopathic effects of tree species on some soil microbial populations and herbaceous plants. Biol Plantarum 44:269-275

Stark JM, Hart SC (1996) Diffusion technique for preparing salt solutions, Kjeldahl digests, and persulfate digests for nitrogen-15 analysis. Soil Science Society of America Journal 60:1846-1855

Vervaet H, Boeckx P, Boko AMC, Van Cleemput O, Hofman G (2004) The role of gross and net N transformation processes and NH_4^+ and NO_3^- immobilization in controlling the mineral N pool of a temperate mixed deciduous forest soil. Plant and Soil 264:349-357

Yavitt JB, Wright SJ, Wieder RK (2004) Seasonal drought and dry-season irrigation influence leaf-litter nutrients and soil enzymes in a moist, lowland forest in Panama. Austral Ecology 29:177-188

Yirdaw E (2001) Diversity of naturally-regenerated native woody species in forest plantations in the Ethiopian highlands. New Forests 22:159-177

Yirdaw E, Luukkanen O (2003) Indigenous woody species diversity in *Eucalyptus globulus* Labill. ssp globulus plantations in the Ethiopian highlands. Biodivers Conserv 12:567-582

Yu Z, Zhang Q, Kraus TEC, Dahlgren RA, Anastasio C, Zasoski RJ (2002) Contribution of amino compounds to dissolved organic nitrogen in forest soils. Biogeochemistry 61:173-198

Zeller B, Colin-Belgrand M, Dambrine E, Martin F (2001) Fate of nitrogen released from ^{15}N-labelled litter in European beech forests. Tree Physiology 21:153-162

Zhong Z, Makeschin F (2003) Soluble organic nitrogen in temperate forest soils. Soil Biology and Biochemistry 35:333-338

Study 5:

Sulfur cycling in natural forest versus plantations: a ^{34}S litter-labelling experiment in a South-Ethiopian montane forest

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Abstract

Plantations of fast-growing exotic trees are promoted to mitigate the ongoing destruction of tropical forests, but knowledge gaps regarding processes and rates of nutrient cycling hinder the rating of sustainability. We thus aimed at elucidating species-dependent sulfur (S) dynamics in soil pools and vegetation. We employed a novel approach of *in-situ* ^{34}S isotope labelling in a natural forest dominated by indigenous *Podocarpus falcatus* and two plantations of exotics (*Cupressus lusitanica*, *Eucalyptus globulus*) in South Ethiopia. Litter of the respective species was labelled through stem injection of $K_2{}^{34}SO_4$ and spread under other individuals. For 14 months, S concentration and δ^{34}S values were monitored in organic layer and topsoil profiles (bulk S = S_b and KH_2PO_4 extractable S = S_e) and in plant leaves including the understorey. Unlike S_b, S_e concentrations greatly varied between the species, increasing with depth under *P. falcatus* and *C. lusitanica*, but decreasing under *E. globulus*; seasonality was minimal. Natural δ^{34}S values covered a small range of c. 4 ‰. ^{34}S labelling yielded a consistent picture of ecosystem S dynamics. Under *C. lusitanica*, extractability of litter-derived S was highest, making this forest susceptible to solute transport and leaching. The other treatments exhibited δ^{34}S values of S_e only slightly enriched to S_b. Under *E. globulus*, incorporation into soil and immobilization were rapid. S turnover was highest under *P. falcatus*, visible from a high proportion of S_e and similar δ^{34}S for S_e and S_b. While steadily increasing for both other species, leaf δ^{34}S of *C. lusitanica* peaked after the first rainy season, attributable to its shallow roots and nutrient recirculation. Uptake patterns of neighbouring trees and the understorey varied by species. Proving a powerful approach to ecosystem S dynamics, *in-situ* ^{34}S labelling revealed distinct influences of species and understorey on S dynamics and elucidated processes that may induce S losses.

Keywords:

Cupressus lusitanica, *Eucalyptus globulus*, extractable sulfur, plant uptake, *Podocarpus falcatus*, understorey.

Introduction

Sulfur (S) is essential for all kind of organisms. It is constituent of membrane-forming sulfolipids and the proteinogenic amino acids methionine and cysteine, whose disulfide bridges are essential for the tertiary structure of proteins. Physiological redox reactions in both photosynthesis and respiration require S, and S-containing phytochelatins help detoxify heavy metals in plants, while sulfoxides, sulfonates and isothiocyanates play a prominent role in their secondary metabolism (Marschner 1995). Yet S has moved into the focus of plant nutrition only recently, following the success in reducing atmospheric deposition of S in the industrialized world (Zhao and McGrath 1994). In the tropics, S deficiency has been a greater issue because of high leaching at low deposition rates and strong adsorption of sulfate in oxide-rich soils.

A particular challenge to conserving ecosystem S is posed by commercial forestry in the tropics. Like other plants, tree species specifically influence biogeochemical cycling of nutrients (Lisanework and Michelsen 1994; Garcia-Montiel and Binkley 1998; Hiremath and Ewel 2001), including S (Eviner and Chapin 2003). Their longevity multiplies this influence, and nutrient replenishment through fertilization is often not practical. However, knowledge gaps still exist even on popular exotic tree species (Cuevas and Lugo 1998). We thus conducted a comparative study on S dynamics in native and planted forests of the South-Ethiopian highlands. Like many other tropical regions, Ethiopia has a rural structure with its population heavily dependent on forest products, making it the African country with the highest fuelwood consumption (FAO 2003). As a response to century-long over-exploitation of natural forests, fast-growing exotic species, mainly from the genus *Eucalyptus*, were introduced around 1900 and now form the backbone of commercial forestry, both at small and large scale (Pohjonen and Pukkala 1990).

The biogeochemical cycling of S is quite complex, as this element is subject to a multitude of redox reactions and physico-chemical processes. Albeit industrial and volcanic activity can regionally result in high atmospheric deposition, the main primary source of S are S-bearing minerals such as sulfides. Nevertheless, the bulk of terrestrial biospheric S is recycled from organic S structures of the soil (Biederbeck 1978; Novak et al. 2003). Under aerobic humid conditions, these comprise primarily thioles, sulfonic acids and sulfate-esters (Strickland et al. 1986). Size and turnover of different S pools as well as the transfer between them are determinants in sustaining S availability while avoiding excessive losses.

While conventional methods can give information on net element fluxes (e. g. Piirainen et al. 2004), isotope techniques are the method of choice in studies on nutrient dynamics: They provide a minimally-invasive way to track nutrients through different ecosystem pools - and thereby give rapid evidence about shifts in equilibria. The short-lived radio-isotope ^{35}S has been successfully utilized to elucidate S adsorption and microbial transformation both in laboratory experiments (Bettany et al. 1974; McLaren et al. 1985; Spratt 1997; Houle et al. 2001) and *in situ* (Strickland et al. 1986). Some investigations included plants in the laboratory (Nziguheba et al. 2005) and in the field (Garten 1988; Cape 1993). Beyond that, S occurs in four stable isotopes (32, 33, 34, 36); they are not subject to particular environmental or temporal limitations and thus suited for long-term field experiments like the present study. The use of ^{34}S labelling in biology has been acknowledged quite some time ago (North and White 1951), but experiments involving non-radioactive S tracers have been rare. Whereas naturally occurring ^{34}S tracers require high doses (Eriksen 1996; Mayer et al. 2001), even minimal amounts of highly-enriched ^{34}S give clear isotope signals. However, availability of such chemicals has restricted their application to recent microcosm studies (Awonaike et al. 1993; Monaghan et al. 1999; Zhao et al. 2001; Trivelin et al. 2002; Tea et al. 2003).

In previous work from the same area, we presented evidence about the chemical bonding of S in different forest types, showing different proportions of C-bonded, sulfate-ester and sulfate S (Solomon et al. 2001). In this study, we aimed at following the biogeochemical S cycle in the ecosystem, starting from litterfall. Specific litter highly enriched in ^{34}S was added to the natural litter of three forest types, in order to minimize alteration of natural ecosystem and physiological processes, neither by fertilization nor by application of plant material with an uncharacteristic chemical makeup (Cuevas and Lugo 1998), which can strongly affect S dynamics (McLaren et al. 1985). Up to now, such biomass decomposition studies have only employed ^{15}N labelling (Zeller et al. 2001; Chintu and Zaharah 2003). All studies involving ^{34}S labelling were conducted on nutrient uptake of herbaceous species; no studies on nutrient cycling involving trees have been published so far.

Since only the small fraction of inorganic soil S is readily available for plants, a sort of pool separation is imperative when tackling ecosystem S cycling. KH_2PO_4 extractable S fairly represents the available (inorganic) and potentially available (mineralizable organic) soil S pool (Watkinson and Kear 1996), and was identified as a kind of yardstick for S sustainability (Spratt 1997). Technically, it can well be combined with isotope methods - including isotope labelling, as under natural conditions extractable soil S (by water) isotopically resembles bulk soil (Zhang et al. 1998; Fox et al. 2004).

In this paper we present an *in-situ* ^{34}S mineralization experiment on three contrasting tree species - two widely-planted exotics (the conifer *Cupressus lusitanica* and broad-leafed *Eucalyptus globulus*) and the indigenous conifer *Podocarpus falcatus*. The objectives of this study were: (i) to develop and test a new method to trace S in natural bonding through an ecosystem, (ii) to gain insight into the temporal dynamics of S mobilization from litter, (iii) to trace the transfer of S through different soil compartments (bulk and mineral/mineralizable S of topsoil layers) into plants, and (iv) to identify vegetation-dependent differences in S cycling.

Materials and Methods

Study area

The study was carried out in the Munessa-Shashemene Forest (7° 26' N 38° 52' E) at the eastern escarpment of the Main Ethiopian Rift Valley. The escarpment extends from the Rift Valley Lakes at about 1600 m asl to more than 3500 m asl at the marginal volcano structures. Natural vegetation includes various altitudinal belts of savannah woodland and closed forest. Starting from the 1970s, large plantations of *Eucalyptus* spp., *Pinus* spp., and *Cupressus lusitanica* have been established systematically, making the Munessa-Shashemene Forest a proper research site with a mosaic of plantation forest and remnant natural forest.

The study site at 2280 m asl has a mean annual temperature of 15 °C, annual rainfall is about 1500 mm (Fritzsche et al. 2005). A small rainy season from March to May is rather unreliable, while the large rainy season usually lasts from July to September. Natural vegetation is a semi-deciduous afromontane forest, dominated by *Podocarpus falcatus* (Thunb.) Mirb. and including *Croton macrostachys* Hochst. ex Del., *Olea europaea* ssp. *cuspidata* (Wall. Ex. DE) Cifferri, *Schefflera abyssinica* Harms, and *Allophyllus abyssinica* (Hochst.) Radlkofer (Abate 2004). The bedrock of intermediate Pliocene to Pleistocene volcanites is covered by Mollic Nitisols (Typic Paleudalfs); they appear homogeneous at the study site, with minor differences attributable to vegetation effects (F. Fritzsche, unpublished manuscript).

Our experimental plots were within 1000 m distance from each other in gently sloping terrain, one in a degraded natural forest stand dominated by *Podocarpus falcatus* (Thunb.) Mirb., and two in plantations of *Cupressus lusitanica* Mill. aged 20 years and of *Eucalyptus globulus* Labill. aged 21 years. The plantations, established after clearing of the natural forest, were even-aged monocultures with about 600 trees ha^{-1}. Canopy of *C. lusitanica* was very dense and dark, understorey vegetation was very sparse; the other stands were more open, allowing more light and precipitation to pass to the ground, sustaining a rich understorey vegetation (Michelsen et al. 1996; Abate 2004; Lemenih et al. 2004; Yirdaw and Luukkanen 2004).

Methodology

Tracer material for ^{34}S labelling was obtained by dry combustion of elemental ^{34}S (99,5% ^{34}S, Chemotrade, Düsseldorf, Germany): Elemental S was heated in a glass tube under O_2 in a vacuum line. SO_2/SO_3 was trapped in a gas-washing bottle, oxidation to sulfate was completed by H_2O_2, which was then dried as K_2SO_4. This K_2SO_4 was applied through stem injection (Horwath et al. 1992) on one tree individual of each *P. falcatus*, *C. lusitanica* and *E. globulus* with adult foliage to obtain a similar amount of labelled litter. The assumption of a uniform labelling of the litter appeared justified, as all the three species have diffuse-porous transport systems (Horwath et al. 1992). In order to access the xylem for injection of the tracer solution, a hole was drilled into each stem under water and immediately plugged with a Teflon tube, which was then sealed with hemp fibres and epoxy glue. Air was pressed out with a syringe and bottles containing the $K_2{}^{34}SO_4$ solution were connected to the tubes by injection needles. Trees were watered regularly to enhance transpiration under the rather dry conditions of the sub-humid environment. One week after completing the injection, the trees were wrapped in gas-tight plastic sheets and about 200 ml of ethene were applied daily for six consecutive days to induce senescence. The involved recirculation of nutrients from the leaves (Tyler 2005) should make them more comparable to natural litterfall. The foliage was harvested after one week manually; much of it had fallen down following the ethene treatment. This litter was air-dried and weighed. Between 1.6 kg (*P. falcatus*) and 1.8 kg (*E. globulus* and *C. lusitanica*) of litter dry mass was obtained from each tree individual.

After sampling for the natural δ^{34}S isotope abundance, this litter was applied on permanent research plots of each species (*P. falcatus*, *E. globulus* and *C. lusitanica*), on which we also studied other ecosystem parameters (Fritzsche et al. 2005), posing limitations to sampling. The respective litter was uniformly distributed around the central trees on a 4 m-diameter octagon (13.25 m^2) in July 2002, resulting in an addition of 136 g m^{-2} for *C. lusitanica* and *E. globulus*, and 120 g m^{-2} for *P. falcatus*.

Samples from soil, organic layer and leaves were collected on 11 July 2002 (prior to the organic-layer labelling), on 10 August 2002 at the beginning of the long rainy season, on 9 November 2002 at the end of the long rainy season, on 19 March 2003 at the beginning of the short rainy season, and on 25 October 2003 after the long rainy season (Fig. 5-1). Organic layer samples were taken in triplicate around the respective tree at a distance of 1 m to 1.5 m using a 10 cm diameter steel ring. Mineral soil cores of 20 cm length (5 cm diameter) from the same points were cut into four layers (0 - 5 cm, 5 - 10 cm, 10 - 15 cm and 15 - 20 cm) in order to resolve the movement of labelled litter-derived material into the topsoil. Composite leaf samples were taken from the central trees on the plots. To get more comprehensive information on ecosystem S dynamics, we included other plant functional types. Starting from October 2002, leaves were collected of the trees *Croton macrostachys* Hochst. ex Del. and *Bersama abyssinica* Fresen., of the herbaceous species *Oplismenus compositus* (L.) P. Beauv. and *Bothriocline* *schimperi* Oliver & Hiern ex Benth., *Rubus steudneri* Schweinf. and of the shrub *Carissa edulis* Vahl. All samples were air-dried at 45 °C.

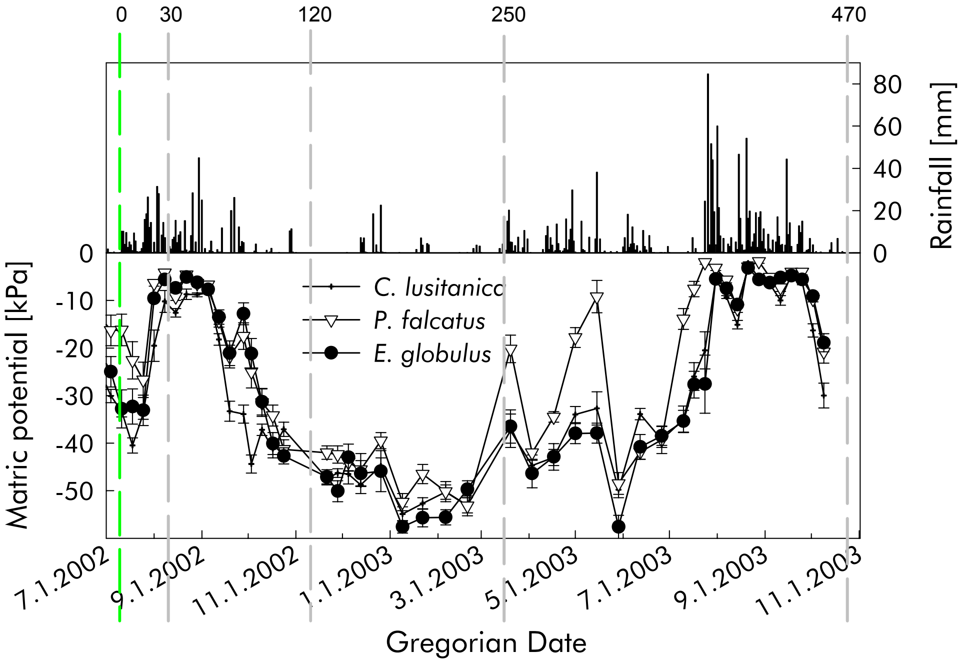

Fig. 5-1: Rainfall and soil moisture (tensiometric potential in 20 cm depth) for the study period (means ± standard error, n = 9), sampling dates are marked by dashed lines with the number of days starting from the label application.

For the determination of extractable S (S_e), 6 g of soil were extracted with 0.1 M KH_2PO_4 solution at pH 7 with a soil : extractant ratio of 1 : 5 (m/v), and 1 : 10 for the organic layer (Watkinson and Kear 1996). The concentration of 0.1 M was chosen after preliminary tests in order to achieve complete extraction of mineral S while minimizing contamination from the extractant (Kowalenko 1993). An aliquot of the KH_2PO_4 extracts was taken to determine total S by ICP-AES (Prietzel et al. 1996), with the rest freeze-dried for δ^{34}S isotope analysis.

The δ^{34}S isotope ratios of the ground samples and the KH_2PO_4 extracts were determined at the Institute of Mineralogy of the TU Bergakademie Freiberg (Germany) using a ThermoFinnigan Delta^{plus} isotope ratio mass spectrometer (Thermo Electron, Bremen, Germany). SO_2 generated in an elemental analyzer was analyzed after on-line concentration adjustment, enabling us to measure small amounts of less than 5 µg S matrix-independently at high sample throughput (Fritzsche and Tichomirowa 2005). Isotope ratios at low enrichment were expressed as δ^{34}S values according to the VCDT standard of the IAEA. The average standard error of the δ^{34}S determination for the natural-abundance samples from the bulk S and extractable S was 0.6 ‰ and 0.4 ‰ δ^{34}S, respectively (n = 45), corresponding with values reported by Norman et al. (2002). Variability was least for the homogeneous *C. lusitanica* stand and greatest for the diverse natural forest.

For comparing the δ^{34}S values, normalized isotope ratios ($\delta^{34}S_i^*$) were calculated from each measured value $\delta^{34}S_i$ with reference to *P. falcatus*, in order to obtain an equal isotope enrichment in equal litter mass, using a correction factor Fac_{spec} for each species (foliar S levels were similar):

$$Fac_{spec} = \frac{M_{spec} \cdot at\%ex_{spec}}{M_{Pf} \cdot at\%ex_{Pf}}$$

$$\delta^{34}S_{ti}^* = Fac_{spec} \cdot \left(\delta^{34}S_{ti} - \delta^{34}S_{0i}\right) + \delta^{34}S_{0i}$$ with *i*: depth layer of one species

t: sampling date

with M_{spec} being the mass of litter applied under *C. lusitanica* and *E. globulus*, respectively, and $at\%ex_{spec}$ being the absolute enrichment of the litter in at% above natural abundance. The respective values for *P. falcatus*, M_{Pf} and $at\%ex_{Pf}$, were serving as a reference. The correction is only necessary for the excess ^{34}S from the labelling, thus the natural-abundance value $\delta^{34}S_{0i}$ has to be excluded from the correction. After correction, equal mixing ratios of tracer in the studied ecosystem compartments are reflected in equal δ^{34}S values.

Statistical analysis

Spatial heterogeneity of the tracer application and mineralization tends to produce outliers, revoking the assumption of a statistical distribution required for a meaningful error analysis. Thus, we displayed median values (n = 3) of the δ^{34}S values of S_b, S_e and the central trees. The overall validity of the dataset is corroborated by the systematic behaviour of the time series of δ^{34}S values. Statistical calculations (ANOVA and Tukey's HSD test for S concentrations, Pearson's correlation coefficient R) were performed using the SPSS for Windows 10.0 software package (SPSS Inc., Chicago, USA).

Results

Bulk S content and extractable S

Bulk S (S_b) concentration was highest under *E. globulus* in both organic layer and topsoil, showing significant ($P < 0.05$) differences from the other forest types in the upper 10 cm of the mineral soil, and from *P. falcatus* in 10 - 15 cm (Table 5-1). Temporal differences in S_b were generally not significant. No correlation was found between the concentrations of S_b and the extractable fraction, S_e.

Table 5-1: Mean S concentrations in bulk soil (S_b) and KH_2PO_4 extracts (S_e), proportion of S_e to S_b for the three forest types over the whole study period (Cl: *Cupressus lusitanica*; Pf: *Podocarpus falcatus*; Eg: *Eucalyptus globulus*).

	Cl	**Pf**	**Eg**	**Cl**	**Pf**	**Eg**	**Cl**	**Pf**	**Eg**
		S_b			**S_e**			**S_e / S_b**	
		mg kg^{-1}			mg kg^{-1}			%	
O horizon	1462	1533	1639	44.5^{b*}	58.6^{ab}	67.7^{a}	3.0	3.8	4.1
0 – 5 cm	948^{b}	903^{b}	1264^{a}	29.7	35.9	40.9	3.1	4.0	3.2
5 – 10 cm	489^{b}	359^{b}	796^{a}	36.3	34.8	32.6	7.4	9.7	4.1
10 – 15 cm	329^{ab}	272^{b}	541^{a}	47.7^{ab}	53.8^{a}	34.9^{b}	14.5	19.8	6.5
15 – 20 cm	287	254	428	66.0^{a}	73.1^{a}	40.1^{b}	23.0	28.8	9.4

[*] Different letters indicate significant differences between the forest types for one parameter ($P < 0.05$, Tukey's HSD test, $n = 15$). Other differences are not significant.

Concentrations of S_e extracted from the organic layer were highest under *E. globulus* (Table 5-1). Seasonal variability of S_e among the species (Fig. 2) was not significant and only visible as a minimal trend for the 5 – 20 cm layers, suggesting lower levels of mineralizable S_e during the dry season. Differences at the first two sampling dates might be a result of different sampling distance from the boles, thus only visible for the homogeneous plantations. Organic layer S_e under *E. globulus* had the largest inter-replicate and annual variation (Fig. 5-2).

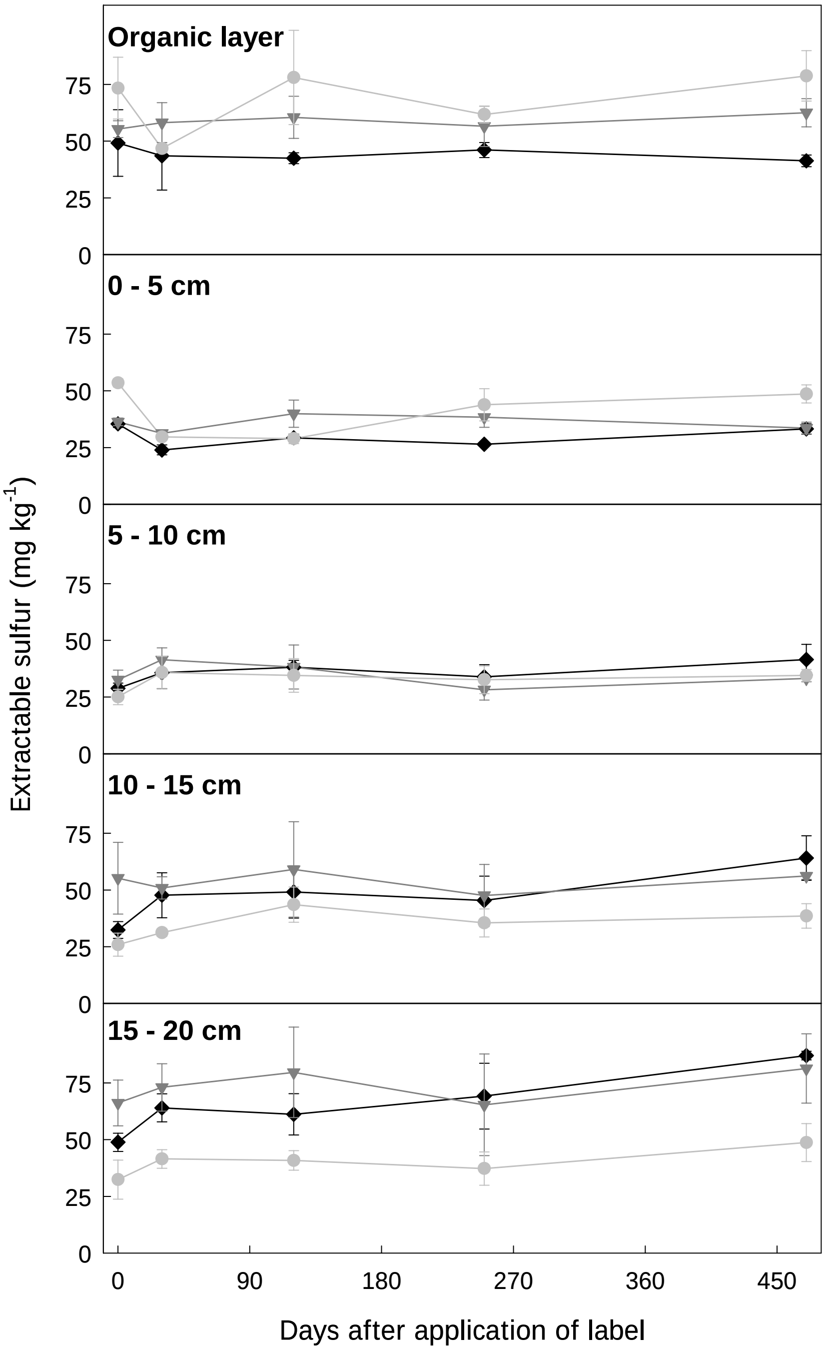

Fig. 5-2: Time series of extractable S (S_e) concentration under (♦) *Cupressus lusitanica*, (▼) *Podocarpus falcatus* and (●) *Eucalyptus globulus* by depth layers (means ± standard error, n = 3).

However, in the 4 mineral soil layers beneath, levels remained at 30 - 40 mg kg^{-1} at low variability. In contrast, S_e increased with depth under *C. lusitanica* and *P. falcatus* to concentrations around 70 mg kg^{-1} in 15 - 20 cm depth, even higher than in the organic layer with 45 mg kg^{-1} for *C. lusitanica* and 60 mg kg^{-1} for *P. falcatus*. In 5 - 10 cm depth, the concentration of S_e was virtually identical for the three treatments, amounting to 25 - 45 mg kg^{-1}. The annual range of the means at 5 - 10 cm depth was about 10 mg kg^{-1} for all species. While not significant, lowest values were consistently observed after the dry season and maxima in the main rainy season. Inter-replicate variability was highest in 10-20 cm depth under *P. falcatus*. This species also had the greatest proportion of mineral soil S_e (Table 5-1), increasing with depth to 20 - 30 %; S_e/S_b was lower under *C. lusitanica* by 20 %. Showing the highest proportion of S_e in the forest floor, the *E. globulus* treatment reached only one third of the *P. falcatus* values below 10 cm.

Plant labelling by $K_2{}^{34}SO_4$

Stem injection of $K_2{}^{34}SO_4$ was suited for all three tree species to label the litter applied on the plots (Table 5-2). As we intended for experimental reasons, the amount of litter obtained from the respective individuals was similar, with only minor differences in S content. Leaf S concentration was not affected by induced senescence, which is in line with published data on *Fagus sylvatica* (Tyler 2005) and on *Eucalyptus* spp. in Australia (McIvor 2001). However, the isotopic enrichment varied considerably after injecting similar amounts of $K_2{}^{34}SO_4$ solution, a common crux of the matter with biomass isotope labelling (e. g. Swanston and Myrold 1998). Correction factors for $\delta^{34}S$, necessary to express an equal proportion of label-derived S as equal $\delta^{34}S^*$ values, are displayed in Table 5-2 (normalization to *P. falcatus*). We assume that virtually all ^{34}S incorporated into the plants was present in organic form, as inorganic sulfate is only found under excess S availability (Trust and Fry 1992).

Table 5-2: Properties of the label applied under the three tree species: dry litter mass (M_{spec}), S content and ^{34}S isotope enrichment, applied isotope tracer per area and correction factor (Fac_{spec}) for equalization of label for the 3 tree species.

Species	**M_{spec}** g	**S content** g kg^{-1}	**enrichment** at% ex ^{34}S	**S label** mg ^{34}S ex m^{-2}	**Fac_{spec}**
Cupressus lusitanica	1710	1.4	12.08	22	0.391
Podocarpus falcatus	1510	1.4	5.34	9	1.000
Eucalyptus globulus	1710	1.5	6.77	13	0.697

δ^{34}S of bulk soil

The δ^{34}S values of S_b at natural abundance varied at 9 - 13 ‰ (open circles in Fig. 5-3, left row). The organic layer of the conifers was slightly depleted in ^{34}S to the 0 – 5 cm layer, in the mineral soil δ^{34}S values tended to decrease with depth. The enrichment in the uppermost mineral soil seemed most pronounced under *P. falcatus*, while the gradient under *E. globulus* was very little.

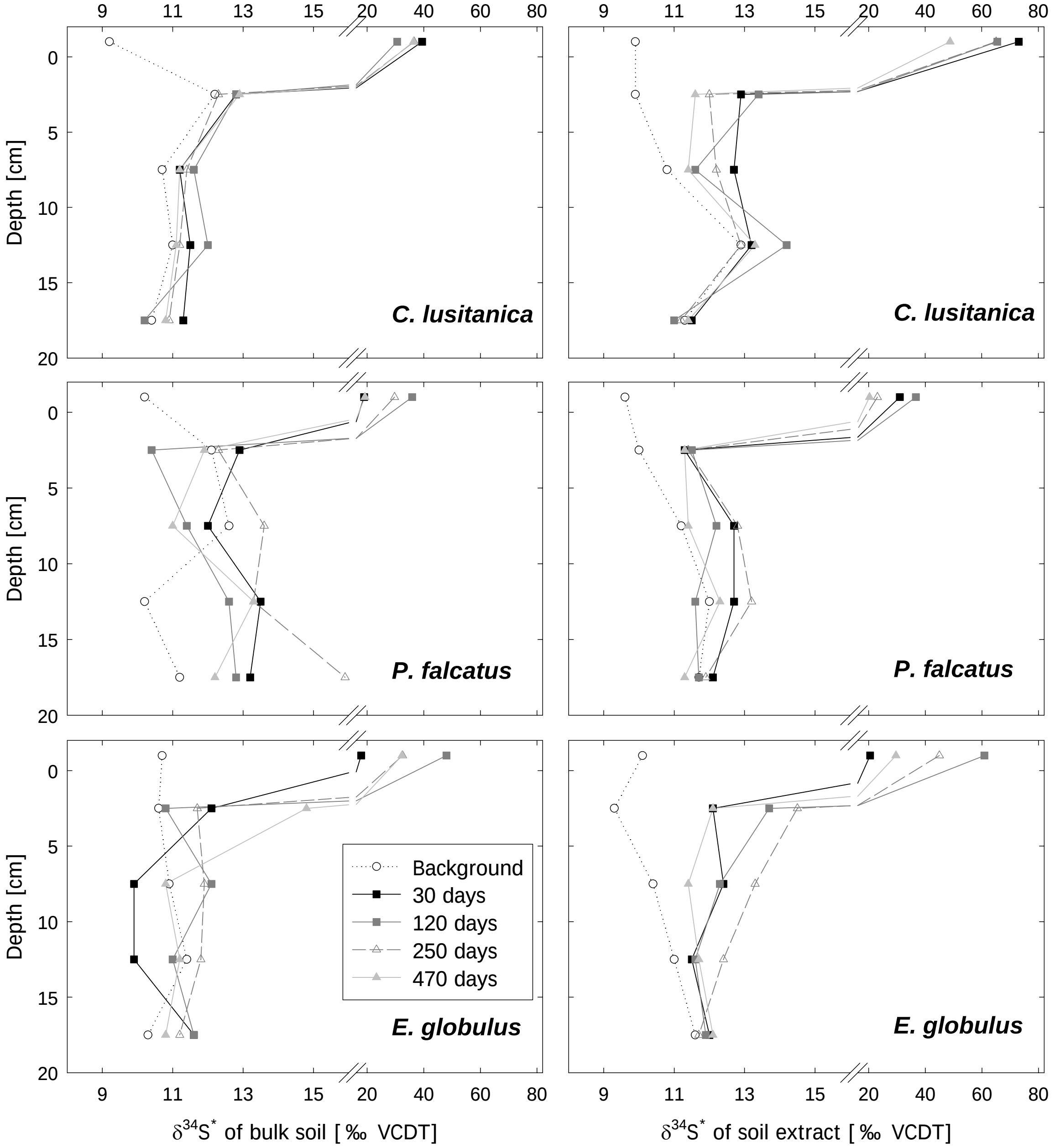

Fig. 5-3: Time series of corrected δ^{34}S depth profiles after labelling in the respective forest stands (median values, n = 3): bulk soil (S_b, left column) and soil extracts (S_e, right column).

Isotope labelling brought about a strong ^{34}S pulse in the organic layer of all treatments. The signal was most pronounced under *C. lusitanica*, reaching values of up to 100 ‰ δ^{34}S, followed by *E. globulus* and *P. falcatus*. After normalization to the enrichment of the label, all species showed similar $\delta^{34}S^*$ values (Fig. 5-3, left row). As was to be expected assuming constant dissipation of the tracer, under *C. lusitanica* this signal was strongest on the first sampling date. The other two species exhibited the highest enrichment only at the second date, which might be an artefact from including some material of the A horizon in the organic layer samples. Under all species, the relaxation of the tracer signal and its progression to the depth was visible. The isotopic shift with depth was small and quite uniform under *C. lusitanica*, and it diminished with time. Mineral soil under *P. falcatus* exhibited a less systematic pattern with highest isotope enrichment in the deeper layers. The tracer effect under *E. globulus* was quite variable in the mineral soil, where the signal reached its maximum after 250 days.

δ^{34}S of soil extracts

Isotope ratios of the KH_2PO_4 extracts yielded a much clearer pattern than the bulk soil samples (Fig. 5-3, right row). Natural-abundance values (open circles) were very similar for all three treatments, with slight gradients towards a heavier isotopic composition at greater depth. Only under *C. lusitanica* a clear δ^{34}S maximum occurred in 10 – 15 cm depth.

Tracer application resulted in strongly elevated δ^{34}S values of S_e from the organic layer, reaching more than 200 ‰ δ^{34}S under *C. lusitanica*. As for S_b, a constant depletion could be observed from the organic layer. However, enrichment of the extracts showed a clear species effect: While the S_e $\delta^{34}S^*$ values under *P. falcatus* hardly differed from the values for S_b, the enrichment under *C. lusitanica* was nearly twice. *E. globulus* was more similar to *P. falcatus*, but the signal faded faster.

The tracer signal in the mineral soil under *C. lusitanica* was highest after 30 days, fading slightly faster in the uppermost layers. Under *P. falcatus*, the δ^{34}S value in the 0 – 5 cm layer remained constantly enriched by 1.4 ‰, while below 5 cm the tracer effect had lowered in the wake of the rainy seasons (after 120 and

470 days). Unlike S_b, the tracer signal was pronounced in S_e in the plantation of *E. globulus*, showing a gradual increase in δ^{34}S during the first 250 days, declining with depth. After the second rainy season, much of the tracer had disappeared again from below 5 cm. For all tree species, S_e at 20 cm depth appeared unaffected by the labelling.

Correlation of the δ^{34}S values of S_b and S_e (Fig. 5-4) yielded lowest values (Pearson's R) for *P. falcatus*, followed by *E. globulus* and *C. lusitanica*, overall R for all treatments was 0.92. Regression slope was steepest for *C. lusitanica*, indicating a strong response of the extractable fraction. *E. globulus* was intermediate, and *P. falcatus* had a slope around one, indicating either equilibrium of S_b and S_e or fast leaching of the enriched fraction.

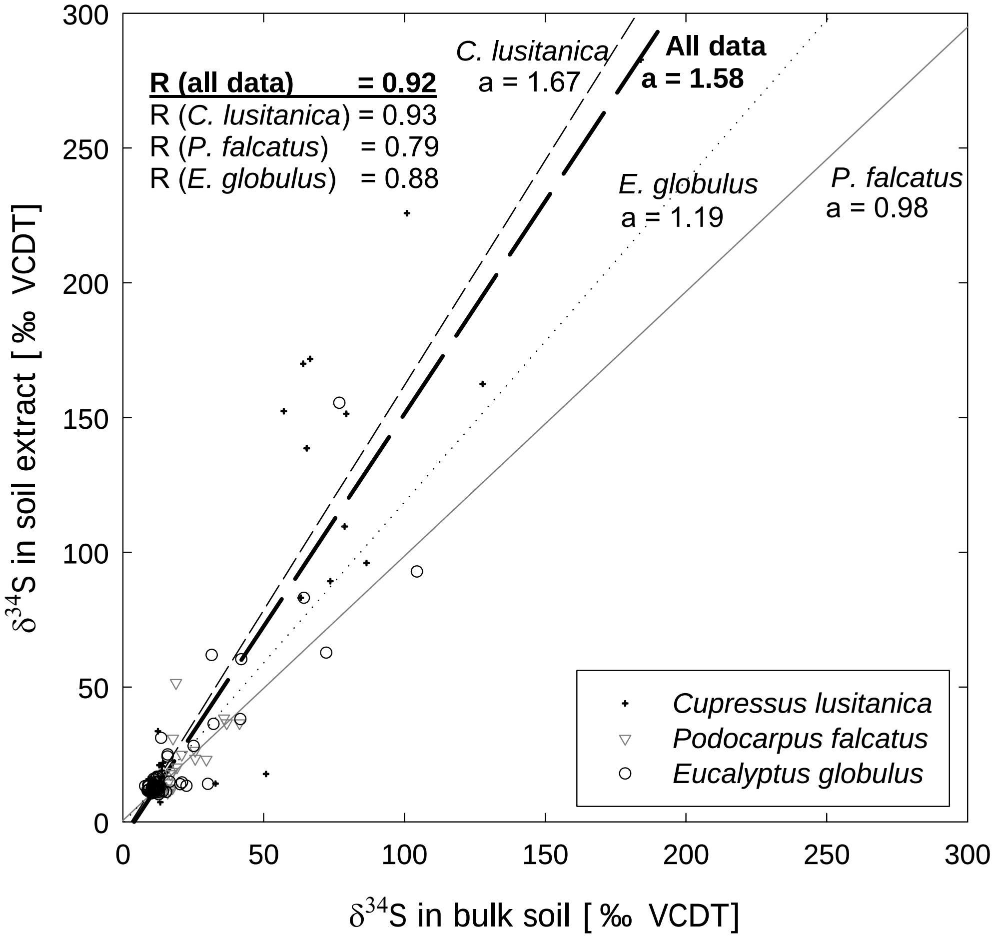

Fig. 5-4: Correlation of δ^{34}S in bulk soil (S_b) and KH_2PO_4 extracts (S_e) after labelling (regression lines for the respective species separately and for all data, including slope a and Pearson's correlation R; all correlations are significant at $P < 0.01$).

Tracer uptake by vegetation

The uptake of mineralized tracer S by the central trees of the plots is depicted as normalized δ^{34}S values in Fig. 5-5. As it is nearly impossible to estimate the S pool of the trees, we have to restrict ourselves essentially to a description of the temporal dynamics of S uptake. Leaf samples from all three dominant species exhibited a similar $\delta^{34}S^*$ increment after 30 days. While *P. falcatus* and *E. globulus* continued to take up the mineralized tracer slowly at similar rates, leaves of *C. lusitanica* showed a high maximum after the first rainy season. Yet after the second rainy season the proportion of tracer in the leaf samples of *C. lusitanica* had continually declined to values below the other two species, but still above natural abundance.

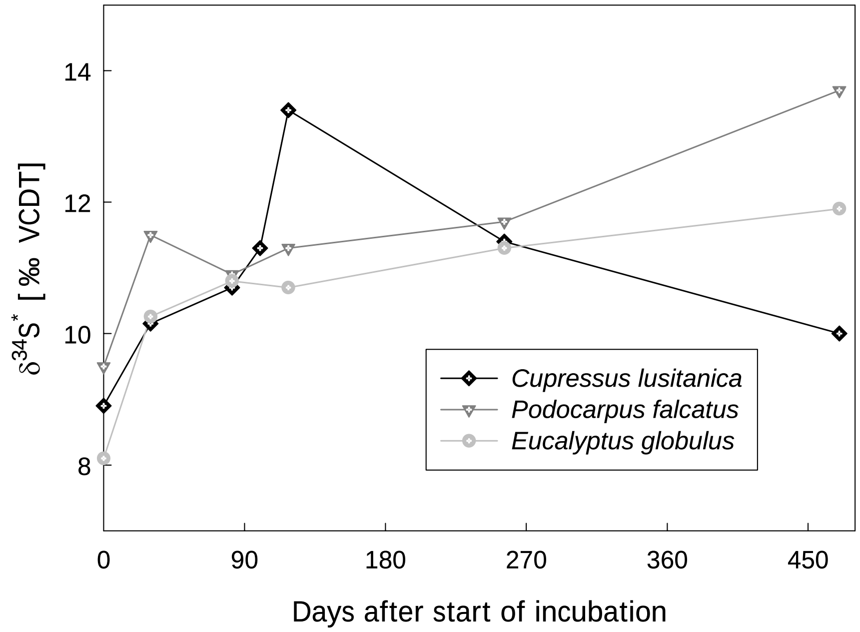

Fig. 5-5: Plant uptake of mineralized ^{34}S tracer: Time series of the normalized δ^{34}S values for the respective species (central trees).

Neighbouring trees and understorey vegetation showed differing patterns of tracer uptake (Table 5-3). Natural δ^{34}S variation of control samples from unlabeled plots was only minor. Tracer incorporation into leaves of the same age class from the grass *Oplismenus compositus* appeared inconsistent among the treatments. Therophytic *Bothriocline schimperi* exhibited a high ^{34}S enrichment in the first growing season, reduced by 60 % in the following year. The tracer signal in *Rubus* was very small with a rising trend towards the end of the study period. S uptake from the label by neighbouring shrubs and trees also depended on the species. Neighbouring *Croton macrostachys* trees varied in the speed and extent of tracer uptake, but consistently showed an effect. The tracer signal in the shrub *Carissa edulis* under *P. falcatus* declined continually during the year after the first rainy season to nearly natural abundance. Leaves of a small *Bersama abyssinica* in the *E. globulus* stand had quite high enrichment, which remained unchanged during the dry season.

Table 5-3: Plant uptake of mineralized S from label by trees and understorey plants by forest types: δ^{34}S values normalized to the label of *Podocarpus falcatus*.

	Days after labelling	**87**	**104**	**118**	**148**	**256**	**286**	**320**	**470**
C. lus.	*Oplismenus* label	38.8	10.4		22.3	33.9			15.4
	Oplismenus control		9.7			10.3			10.0
P. falcatus	*Oplismenus* label	15.7		13.2		11.8			16.1
	Oplismenus control	9.7		9.7		10.2			10.4
	Croton	10.4		11.8			10.7		11.1
	Carissa	12.4		11.3		10.3			10.4
E. globulus	*Oplismenus* label	15.3		12.2		12.8			14.4
	Oplismenus control	10.3		9.9		11.0			9.7
	Bothriocline label	24.4		23.5					15.2
	Bothriocline control	10.0	9.6	9.8					
	Rubus label	11.3		11.4		11.2		12.1	11.7
	Rubus control	10.2		11.4		10.1			
	Croton	11.1		11.6			11.5		11.9
	Croton	12.8		12.0			11.0		11.4
	Bersama	13.6		12.9		13.4			

Discussion

We conducted our study on S dynamics on neighbouring plots with an identical long-term site history and comparable site conditions (Ashagrie, unpublished thesis). Consequently, specific effects of litter quality, water regime etc. can hardly be separated. However, our dataset can give insight into the overall S cycling in the respective forest ecosystems. A precondition for isotope tracer studies utilizing only one isotope ratio, in our case $\delta^{34}S$, is that large natural isotopic shifts can be excluded. Only anaerobic S metabolism is accompanied by large fractionations (Mitchell et al. 1998), but under the sub-humid climate of the study site topsoil conditions can always be regarded as oxic. To date, no isotope labelling studies are available on natural soil-plant S dynamics to relate our results to as a whole. Published investigations were all conducted outside the tropics and focussed on plant uptake under small-scale controlled-environment conditions involving herbaceous species *ex situ*, or on effects of excessive S deposition.

Concentrations of S_b only differed between *E. globulus* on the one hand and the conifers on the other hand. We attribute the higher S concentration under *E. globulus* to the higher foliage S level (Abate 2004) and faster incorporation of the broadleafed litter into the mineral soil, as the organic layer amounted to only 60 % of the mass under the conifers (Y. Ashagrie, unpublished data). Overall concentrations of S_e correspond well with published data from different biomes and land uses (Zhao and McGrath 1994; Watkinson and Kear 1996; Norman et al. 2002; Yavitt et al. 2004). Seasonality of S_e was weak, contrary to findings from Panama by Yavitt et al. (2004), but also reported from German forests (Norman et al. 2002). The proportion of S_e was in the range expected for the chosen extractant (Watkinson and Kear 1996). Relating amounts of S_e to our previous work (Solomon et al. 2001) shows that about one third is made up of sulfate-S. The slight depletion of the organic layer relative to the mineral soil in natural-abundance $\delta^{34}S$ with lower differences for the extractable fraction is a commonly observed phenomenon (Fuller et al. 1986; Giesemann et al. 1995; Norman et al. 2002; Novak et al. 2003), presumably caused by kinetic discrimination of ^{34}S and preferential adsorption of $^{34}SO_4^{2-}$ leading to lower plant uptake. Natural depth gradients in

Munessa were low, attributable to fast nutrient turnover in the tropical climate and low atmospheric deposition (Y. Ashagrie, unpublished data).

Preparation of the ^{34}S litter label by stem injection did not yield the same isotope enrichment for all three species. This was no great surprise, given the architecture of both whole plants and leaves, which highly differed among the treated species. This again involves differences in S allocation and redistribution (Garten 1990), including the response to the ethene gassing (Abeles et al. 1992). *E. globulus* was more than twice as high as the others, and the broad base of the *C. lusitanica* leaves might particularly hinder abscission of the leave tissue from twigs. This could be seen from the fact that the leaves of *P. falcatus* and *E. globulus* fell down readily with the trees recovering later – contrary to the broad-based leaves of *C. lusitanica*.

In order to validate plot labelling by litter application, we compared the O horizon mass calculated from isotope dilution with gravimetric analysis. The mass by isotope dilution from the 120-days δ^{34}S values (after one rainy season) amounted to 9.32 kg m^{-2} for *P. falcatus*, 10.75 kg m^{-2} for *C. lusitanica* and 5.53 kg m^{-2} for *E. globulus*, exceeding the gravimetrically determined S stocks (Y. Ashagrie, unpublished data) with a factor of 2.2, 3.0 and 2.3, respectively. These figures only show tendencies, but they are internally consistent and match with the other results. We thus take them as a starting point for discussing the dynamics of the ^{34}S label.

The calculated differences in O horizon mass might be a consequence of (a) the determination of cumulative litter mass vs. actual litter mass, and (b) an overestimation due to preferential depletion of fresh litter-derived S through plant uptake or leaching. The latter is supported by calculations for S in Panamanian rainforests of Yavitt et al. (2004), who estimated longer residence times for bulk forest floor mass and N than for S, which was around 150 days.

This residence time as well as the half-life of mass of harvested senescent leaves from the same species decomposing in litter bags ranging around five months (Lisanework and Michelsen 1994) are well in line with our findings for the *P. falcatus* dominated forest. Comprising the high-decomposition rainy season, it indicates a rather tight S cycling without excessive fluxes between other ecosystem compartments. The higher difference under *E. globulus* is probably to be ascribed to fast decomposition (Lisanework and Michelsen 1994), reflected in the high superficial contents of S_e and the thin organic layer. Moreover, minimal depth gradients in natural ^{34}S abundance point towards a close coupling of organic layer and mineral soil, leading to an S accumulation in the mineral soil. The faster incorporation into the soil also extends to soil fractions, as microcosm incubations in the same forest stands indicated, making *E. globulus* the treatment with the highest S retention (A.C. Johann, unpublished thesis).

For *C. lusitanica*, microcosm *in-situ* incubation confirmed the maximum S losses from litter mixed into the topsoil (A.C. Johann, unpublished thesis). Other mechanisms appear responsible for the difference in mass estimates in this plantation. Litter washed down by the first strong rains can suddenly increase litter mass causing strong cumulative effects, as dry leaves stay longer on the branches of this species. Furthermore, the leaves of this species might contain a higher quantity of mobile and labile S compounds in the leaves, which is implied by the steep regression slope of $\delta^{34}S$ from S_b and S_e (Fig. 5-4), and has also been found in the comparative study on other macro-nutrients in the same forest types by Lisanework and Michelsen (1994). This fraction can be leached or taken up by plants. Leaching of soluble S was indicated by maximum $\delta^{34}S$ values of soil extracts from 30-60 cm soil depth occurring under *C. lusitanica* that were elevated by up to 4 ‰ (data not shown). Owing to its superficial root mats, *C. lusitanica* is probably more competitive in nutrient uptake from the forest floor versus microbial immobilization, which is reflected in the high leaf tracer signal for the discussed date (Fig. 5-5).

The incorporation of $^{35}SO_4^{2-}$ tracers into organic structures of organic layers and topsoils has been repeatedly investigated. In an exemplary laboratory incubation study, Houle et al. (2001) observed an immobilization of more than 70 % of the added sulfate in the organic layer within 4 days at 20 °C, reaching less than a quarter in the mineral soil at only a fraction of the speed. Although dealing with samples from a boreal Podzol, the incubation study gives an estimate about the speed of turnover of roughly half the sulfate pool per day. This evidence of rapid transformation and immobilization concurs with incubation studies employing inorganic ^{35}S addition (Nziguheba et al. 2005), as well as organic S amendments (Strickland et al. 1986; Wu et al. 1993), both for agricultural and forest soils. This high turnover acts equilibrating and thus explains the even isotope signature of S_e. In our study, the S_e tracer signal proved to be a sensitive indicator for S dynamics, even reflecting seasonal effects. In contrast to the concentrations, its more intense isotope depletion in the open canopies after the rainy seasons was a sign of substantial washing of the soil by the rains. Relating the ^{34}S enrichment of S_e and S_b (Fig. 5-4) can help elucidate processes leading to the conservation and dissipation of S due to differences in either chemical stability of the label or soil properties affecting transport. As under *C. lusitanica* $\delta^{34}S$ values of S_b and to a lesser extent of S_e hardly changed below 10cm, we suppose solute transport as the primary transport mechanism, in agreement with the high tracer signal in the subsoil. Under *E. globulus*, adsorption of S_e washed down through the mineral soil appears important, as the isotope signal is much less reflected in the bulk soil. Increasing $\delta^{34}S$ values of S_e with time indicate that plant nutrient uptake from the surface might not intercept mineralized S efficiently - which is not surprising for a species with a low superficial fine root density (Fritzsche et al. 2005). Under *P. falcatus*, a major proportion of S leaves the organic layer, causing only minor effects in the 0 – 5 cm layer. A greater effect in S_b at 20 cm points towards fast particulate transport or bio-chemical immobilization of the leached S_e, which is in line with the higher variability in the $\delta^{34}S$ profile of S_b, in S_e concentration and in the soil water tension (Fig. 5-1). The increasing proportion of S_e with depth (Table 5-1) and the consistently moderate isotope enrichment in S_e are signs for high S mineralization and turnover. The high diversity of the natural forest in canopy structure and plant functional types strongly affects soil life through micro-climate, litter quality and rhizodeposition (Hooper and Vitousek 1998), as indicated by a ^{15}N labelling study on the same plots (Fischer et al. 2005), concurring with results from a similar experimental design by Lian and Zhang (1998). It might thus be essential to keep S turnover – and thereby S availability – high, and to prevent S losses. The opposite can be seen for the mono-structured, comprehensively shaded ecosystem of *C. lusitanica*, where low biological activity is probably responsible for the slow relaxation of the tracer signal in the organic layer (Fig. 5-3).

As stated above, literature on *in situ* S dynamics of natural ecosystems by isotope tracers is missing. Still, some similarities with our evidence have been found in an irrigation experiment on atmospheric deposition employing a lowly-enriched sulfate tracer that included five German forest sites (Mayer et al. 2001). In sesqui-oxide-rich Luvisols and Cambisols, maximum isotopic enrichment of both total S and sulfate occurred at around 15 cm depth in nearly all cases, to decline again sharply below. This corresponds to our data of a tracer signal vanishing at 20 cm depth despite lower S_b contents and backs our sampling design. Since plant uptake was excluded, adsorption of inorganic S was identified by Mayer et al. (2001) as the main mechanism of retention in the mineral soil. Similar patterns were found by Novak et al. (2003) in soils from Central Europe.

Tree leaf samples were naturally depleted in δ^{34}S compared to the soil (Fig. 5-3), which was also reported by Giesemann et al. (1995). Plant uptake of S from the label highly depended on the species. *P. falcatus* and *E. globulus* appeared to constantly incorporate tracer S into foliage, a result that was similarly found after ^{35}S radio-labelling in temperate forests (Garten 1988; Cape 1993). Reduced availability of S from the label with progressing time, as well as recirculation explain the diminishing slope. For *C. lusitanica*, the decline after a peak in the first rainy season is likely to be connected to the high δ^{34}S of S_e, to higher remobilization of S from plant tissue, and to its root activity concentrated near the surface. This also led to the lowest recovery of N tracer under *C. lusitanica* in our ^{15}N tracer study (Fischer et al. 2005), while uptake patterns of ^{15}N applied beneath the litter layer for the dominating species generally resembled the results from the presented study. In contrast, deep rooting might be the reason for the steady uptake by the other two species, buffering seasonality (Fritzsche et al. 2005) and recovering leached S (Hansen 1974; Jobbagy and Jackson 2004).

Specimens of *Croton* showed seasonal variations, as the understorey did. This is not surprising, as this deciduous pioneer species might have a higher turnover of nutrients. The shallow-rooted grass *Oplismenus* got most tracer under *C. lusitanica*, probably due to high enrichment of S_e and the low covering by the grass. In the open canopies, *Oplismenus* took up a similar amount of tracer in the second year, and thus appeared to rely on lower-turnover S. A pronounced decline in dry-season δ^{34}S for the open canopies indicates reduced mineralization from the organic layer and uptake from the lower, moister layers. Similar patterns were observed for understorey N uptake (Fischer et al. 2005). Keeping its foliar δ^{34}S values constant, *Rubus* appears much less affected by the dry season, probably due to its root activity in deeper layers (Fischer et al. 2005). Annual *Bothriocline* seems to have tapped an easily available fraction of the S tracer that was already depleted in the second growing season.

Conclusions

Ecosystem S dynamics proved greatly affected by forest type, owing to differences in stand structure and species, i.e. chemical characteristics of the plant tissue and plant architecture. A higher diversity in plant functional groups is postulated to promote conservative nutrient cycling (Hooper and Vitousek 1998; Hiremath and Ewel 2001) by temporal and spatial partitioning of resources (Eviner and Chapin 2003). Consequently, nutrient losses should increase in the order *Podocarpus falcatus* < *Eucalyptus globulus* < *Cupressus lusitanica*, as reported by Lisanework and Michelsen (1994), which was also indicated by our study. Nutrient use greatly varied among the treatments: S turnover appeared highest under *P. falcatus*, retention was high under *Eucalyptus globulus*, maybe replenished from deep resources. Uptake was striking under *Cupressus lusitanica*, signifying a high plant-level nutrient use efficiency as indicated by work of Abate (2004); still, nutrient retention of this forest type and ecosystem nutrient use efficiency were low.

Our study demonstrates the use of labelling with highly-enriched ^{34}S in element transfer studies and its applicability *in situ* as a sensitive tool to visualize S cycling. Optimization of this method can give an isotope signal sharp enough to calculate exact rates of transfer and turnover under natural conditions, while avoiding alteration of ecosystem processes. S cycling has been suggested to be rather independent of soil conditions in tropical forests (Yavitt 2000), possibly making studies of the kind presented here widely transferable. Given the close association of organic carbon and S cycling (Novak et al. 2003), the method might moreover help to gain insight into soil organic matter dynamics in general, and to assess ecosystem vulnerability.

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References

Abate A (2004) Biomass and nutrient studies of selected tree species of natural and plantation forests: Implications for a sustainable management of the Munessa-Shashemene Forest, Ethiopia. PhD dissertation. Faculty of Biology, Chemistry and Geosciences. University of Bayreuth, Bayreuth, Germany, 163 p

Abeles FB, Morgan PW, Saltweit MEJ (1992) Ethylene in plant biology, 2nd edn. Academic Press, New York

Awonaike KO, Danso SKA, Zapata F (1993) The use of double isotope (^{15}N and ^{34}S) labelling technique to assess the suitability of various reference crops for estimating nitrogen fixation in *Gliricidia sepium* and *Leucaena leucocephala*. Plant and Soil 155/156:325-328

Bettany JR, Stewart JWB, Halstead EH (1974) Assessment of Available Soil Sulfur in an ^{35}S Growth Chamber Experiment. Canadian Journal of Soil Science 54:309-315

Biederbeck VO (1978) Soil organic sulfur and fertility. In: Schnitzer M, Khan SM (eds) Soil Organic Matter. Elsevier, Amsterdam, pp 273-310

Cape JN (1993) The Use of ^{35}S to Study Sulfur Cycling in Forests. Environmental Geochemistry and Health 15:113-118

Chintu R, Zaharah AR (2003) Nitrogen uptake of maize (*Zea mays*. L) from isotope-labeled biomass of *Paraserianthes falcataria* grown under controlled conditions. Agroforestry Systems 57:101-107

Cuevas E, Lugo AE (1998) Dynamics of organic matter and nutrient return from litterfall in stands of ten tropical tree plantation species. Forest Ecol Manag 112:263-279

Eriksen J (1996) Incorporation of S into soil organic matter in the field as determined by the natural abundance of stable S isotopes. Biology and Fertility of Soils 22:149-155

Eviner VT, Chapin FS (2003) Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. Annual Review of Ecology Evolution and Systematics 34:455-485

FAO (2003) State of the world's forests, 2003. In. Food and Agriculture Organization of the United Nations, Rome

Fischer H, Fritzsche F, Zech W, Guggenberger G (2005) Nitrogen dynamics in three forest types of the South-Ethiopian highlands. Plant and Soil:(submitted)

Fox MA, Zhao FJ, McGrath SP (2004) A new method for the determination of the ^{34}S/^{32}S ratio of water-soluble sulphur in soil. International Journal of Environmental Analytical Chemistry 84:323-329

Fritzsche F, Abate A, Fetene M, Beck E, Weise S, Guggenberger G (2005) Soil-plant hydrology of indigenous and exotic trees in an Ethiopian montane forest. Tree Physiology:(submitted)

Fritzsche F, Tichomirowa M (2005) Signal improvement in elemental analyzer-continuous flow isotope ratio mass spectrometry for samples with low sulfur contents by on-line concentration adjustment. Chemical Geology:(submitted)

Fuller RD, Mitchell MJ, Krouse HR, Wyskowski BJ, Driscoll CT (1986) Stable sulfur isotope ratios as a tool for interpreting ecosystem sulfur dynamics. Water Air Soil Poll 28:163-171

Garcia-Montiel DC, Binkley D (1998) Effect of *Eucalyptus saligna* and *Albizia falcataria* on soil processes and nitrogen supply in Hawaii. Oecologia 113:547-556

Garten CT (1988) Fate and distribution of ^{35}S in Yellow Poplar and Red Maple trees. Oecologia 76:43-50

Garten CT (1990) Foliar leaching, translocation, and biogenic emission of ^{35}S in radiolabeled Loblolly Pines. Ecology 71:239-251

Giesemann A, Jager HJ, Feger KH (1995) Evaluation of sulfur cycling in managed forest stands by means of stable S-isotope analysis. Plant and Soil 169:399-404

Hansen P (1974) Drainage depth for apple trees. Tidsskrift for Planteavl 78:46-52

Hiremath AJ, Ewel JJ (2001) Ecosystem nutrient use efficiency, productivity, and nutrient accrual in model tropical communities. Ecosystems 4:669-682

Hooper DU, Vitousek PM (1998) Effects of plant composition and diversity on nutrient cycling. Ecol Monogr 68:121-149

Horwath WR, Paul EA, Pregitzer KS (1992) Injection of N-15 into trees to study nitrogen cycling in soil. Soil Science Society of America Journal 56:316-319

Houle D, Carignan R, Ouimet R (2001) Soil organic sulfur dynamics in a coniferous forest. Biogeochemistry 53:105-124

Jobbagy EG, Jackson RB (2004) The uplift of soil nutrients by plants: biogeochemical consequences across scales. Ecology 85:2380-2389

Kowalenko CG (1993) Extraction of available sulfur. In: Carter MR (ed) Soil sampling and methods of soil analysis. Lewis Publishers, Boca Raton, FL, pp 65-74

Lemenih M, Gidyelew T, Teketay D (2004) Effects of canopy cover and understory environment of tree plantations on richness, density and size of colonizing woody species in southern Ethiopia. Forest Ecol Manag 194:1-10

Lian YW, Zhang QS (1998) Conversion of a natural broad-leafed evergreen forest into pure and mixed plantation forests in a subtropical area: effects on nutrient cycling. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 28:1518-1529

Lisanework N, Michelsen A (1994) Litterfall and nutrient release by decomposition in three plantations compared with a natural forest in the Ethiopian highland. Forest Ecol Manag 65:149-164

Marschner H (1995) Mineral nutrition of higher plants. Elsevier, Amsterdam

Mayer B, Prietzel J, Krouse HR (2001) The influence of sulfur deposition rates on sulfate retention patterns and mechanisms in aerated forest soils. Appl Geochem 16:1003-1019

McIvor JG (2001) Litterfall from trees in semiarid woodlands of north-east Queensland. Austral Ecology 26:150-155

McLaren RG, Keer JI, Swift RS (1985) Sulfur transformations in soils using sulphur-35 labeling. Soil Biol Biochem 17:73-79

Michelsen A, Lisanework N, Friis I, Holst N (1996) Comparisons of understorey vegetation and soil fertility in plantations and adjacent natural forests in the Ethiopian highlands. J Appl Ecol 33:627-642

Mitchell MJ, Krouse HR, Mayer B, Stam AC, Zhang Y (1998) Use of stable isotopes in evaluating sulfur biogeochemistry of forest ecosystems. In: Kendall C, McDonnell JJ (eds) Isotope Tracers in Catchment Hydrology. Elsevier, Amsterdam, pp 489-518

Monaghan JM, Scrimgeour CM, Stein WM, Zhao FJ, Evans EJ (1999) Sulphur accumulation and redistribution in wheat (*Triticum aestivum*): A study using stable sulphur isotope ratios as a tracer system. Plant, Cell and Environment 22:831-839

Norman AL, Giesemann A, Krouse HR, Jager HJ (2002) Sulphur isotope fractionation during sulphur mineralization: results of an incubation-extraction experiment with a Black Forest soil. Soil Biol Biochem 34:1425-1438

North ED, White RR (1951) Separation of the stable isotope of sulfur-34. Ind Eng Chem 43:2390-2397

Novak M, Buzek F, Harrison AF, Prechova E, Jackova I, Fottova D (2003) Similarity between C, N and S stable isotope profiles in European spruce forest soils: implications for the use of δ^{34}S as a tracer. Appl Geochem 18:765-779

Nziguheba G, Smolders E, Merckx R (2005) Sulphur immobilization and availability in soils assessed using isotope dilution. Soil Biol Biochem 37:635-644

Piirainen S, Finer L, Mannerkoski H, Starr M (2004) Effects of forest clear-cutting on the sulphur, phosphorus and base cations fluxes through podzolic soil horizons. Biogeochemistry 69:405-424

Pohjonen V, Pukkala T (1990) *Eucalyptus globulus* in Ethiopian forestry. Forest Ecol Manag 36:19-31

Prietzel J, Cronauer H, Strehl C (1996) Determination of dissolved total sulfur in aqueous extracts and seepage water of forest soils. International Journal of Environmental Analytical Chemistry 64:193-203

Solomon D, Lehmann J, Tekalign M, Fritzsche F, Zech W (2001) Sulfur fractions in particle-size separates of the sub-humid Ethiopian highlands as influenced by land use changes. Geoderma 102:41-59

Spratt HG (1997) Microbial sulfur transformations in A-horizon soils of a Missouri Ozark forest managed for timber production by clear-cutting. Soil Biol Biochem 29:1639-1646

Strickland TC, Fitzgerald JW, Swank WT (1986) *In situ* mobilization of ^{35}S-labeled organic sulfur in litter and soil from a hardwood forest. Soil Biol Biochem 18:463-468

Swanston CW, Myrold DD (1998) Evaluation of the stem injection technique and subsequent ^{15}N partitioning in red alder crowns. Plant and Soil 198:63-69

Tea I, Genter T, Naulet N, Morvan E, Kleiber D (2003) Isotopic study of post-anthesis foliar incorporation of sulphur and nitrogen in wheat. Isot Environ Healt S 39:289-300

Trivelin PCO, Bendassolli JA, Muraoka T, Carneiro F, Jr. (2002) Sulfur utilization by rice and *Crotolaria juncea* from sulfate - ^{34}S applied to the soil. Scientia Agricola 59:205-207

Trust BA, Fry B (1992) Stable sulphur isotopes in plants: a review. Plant, Cell and Environment 15:1105-1110

Tyler G (2005) Changes in the concentrations of major, minor and rare-earth elements during leaf senescence and decomposition in a Fagus sylvatica forest. Forest Ecol Manag 206:167-177

Watkinson JH, Kear MJ (1996) Sulfate and mineralisable organic sulfur in pastoral soils of New Zealand. II. A soil test for mineralisable organic sulfur. Australian Journal of Soil Research 34:405-412

Wu J, O`Donnell AG, Syers JK (1993) Microbial-growth and sulfur immobilization following the incorporation of plant residues into soil. Soil Biol Biochem 25:1567-1573

Yavitt JB (2000) Nutrient dynamics of soil derived from different parent material on Barro Colorado Island, Panama. Biotropica 32:198-207

Yavitt JB, Wright SJ, Wieder RK (2004) Seasonal drought and dry-season irrigation influence leaf-litter nutrients and soil enzymes in a moist, lowland forest in Panama. Austral Ecology 29:177-188

Yirdaw E, Luukkanen O (2004) Photosynthetically active radiation transmittance of forest plantation canopies in the Ethiopian highlands. Forest Ecol Manag 188:17-24

Zeller B, Colin-Belgrand M, Dambrine E, Martin F (2001) Fate of nitrogen released from ^{15}N-labelled litter in European beech forests. Tree Physiology 21:153-162

Zhang YM, Mitchell MJ, Christ M, Likens GE, Krouse HR (1998) Stable sulfur isotopic biogeochemistry of the Hubbard Brook Experimental Forest, New Hampshire. Biogeochemistry 41:259-275

Zhao F, McGrath SP (1994) Extractable sulphate and organic sulphur in soils and their availability to plants. Plant and Soil 164:243-250

Zhao FJ, Verkampen KCJ, Birdsey M, Blake-Kalff MMA, McGrath SP (2001) Use of the enriched stable isotope ^{34}S to study sulphur uptake and distribution in wheat. Journal of Plant Nutrition 24:1551-1560

General conclusions

Methodological aspects

The advances in stable-isotope methodology of S achieved in this work open new perspectives for *in-situ* studies on nutrient cycling, as it can provide process-related evidence. The analytical improvement allows the fast and precise analysis of the isotope signature of S in small concentrations and in organic matrices. This is a precondition for ecosystem studies which generally require large sample sets to tackle spatial variability. But the technique might also be of great value for other disciplines. While availability of homogeneous sample material is not the sticking point in geochemistry, samples with low S concentration require a time-consuming off-line preparation to achieve satisfactory concentrations. After all this frequently involves contamination and isotope fractionations as well. Measuring the sandstone samples used in the methodological work of Study 2 proved highly problematic when using conventional methods.

The KH_2PO_4 extraction of soil N and S (Studies 4, 5) yielded sound data on the dynamics of these nutrients in a more sensitive pool. This mineralizable organic fraction may give a better estimate of the active fraction than the inorganic species of N and S, particularly under tropical conditions. Additionally, it is more robust to sample treatment and easier to handle for isotope analysis.

The catenary study through Munessa Forest (Study 1) showed that soil development is controlled by climate and relief, while the influence of bedrock is minimal. The systematic pattern of internally homogeneous sites is an important prerequisite for ecological research, both on gradients and within one geo-ecological unit.

The co-occurrence of different forest types in some of these units allows to work out specific traits of plants and vegetation in comparative studies, which can be related to "reference species". This was of great use in the experiments of the present study (Studies 3 – 5), as the fair knowledge on *E. globulus* could be related to the other species, which increases the transferability of in-depth studies like the ones presented to a broad range of site conditions.

The single-tree centred experimental design implemented on the permanent plots of the different forest types emerged appropriate for the purpose of identifying species effects. The assumption that the identified differences were really attributable to the effect of the central trees was corroborated by the ^{15}N uptake pattern and by equal variability of extractable N species for all three stands. While influences by neighbouring trees will naturally be greater than zero, the chosen design allowed work to out traits of *P. falcatus* under the given conditions and in comparison with the plantation species. Slight differences might appear in canopies with a different composition, but neither pristine natural forests nor monocultures like the two plantations appear as the key to sustainable forest utilization in Ethiopia. Likewise, a variation in site conditions will change the quantity of ecosystem fluxes, but the processes and physiological responses can be expected to stay the same at a wider ecological spectrum.

Carrying out all experiments for Studies 3 - 5 on the same plots required careful management of the experimental sites and sometimes posed some constraints to the sampling design. However, using identical plots and plant individuals for different experiments yields a sharper picture on functional relationships.

Ecological implications

The comparative studies conducted on the permanent plots link the dynamics of water, N and S, the soil internal cycling and nutrient recycling from organic matter. This revealed general differences between the tree species under study, as well as differing seasonal patterns, referring both to water uptake and nutrient cycling. The different root systems plaid a prominent role in water transfer and soil nutrient dynamics, but specific effects of plant-internal nutrient cycling and litter quality were also important.

The extended, high-biomass root system of *P. falcatus* appeared to play a major role in soil water redistribution, with a balancing influence on soil conditions. The strong positive response of transpiration to soil moisture kept soil conditions even more constant, but will also minimize its photosynthetic yield. Consequently, seasonality was less pronounced in the soil of the natural forest. The mineral soil of the natural forest had the largest active proportion of N and S with a strong internal coupling and fast turnover. Nutrient uptake by *P. falcatus* was equally strong from topsoil and subsoil.

The striking feature of *C. lusitanica* was the comprehensive control on the topsoil through its dense, superficial root mats. These were highly efficient in uptake of superficial water, N and S, leaving little space for understorey plants. However, nutrients that had passed this barrier were likely to be lost through leaching, as subsoil biological activity appeared very low. Dry conditions during the dry season made this plantation highly problematic under the given conditions. Dry-season adaptation occurred in form of a relocation of the root system to deeper layers and reduced transpiration. Recirculation of S from the foliage of *C. lusitanica* was pronounced, and a greater proportion of labile S compounds in the litter extended this to soil processes.

E. globulus had a very expansive, low-biomass root system. In spite of its response to dry season conditions by strongly enhancing transpiration, soil drying was not severe in normal years, which was due to its aseasonal reliance on deep water resources. Still an influence on deeper resources cannot be excluded. Nutrients (N) were taken up from deeper layers as well throughout the year, leaving the topsoil to the understorey plants and thereby promoting natural regeneration. Litter incorporation into the mineral soil was most rapid under *E. globulus*. In contrast to the other species, biological activity appeared to decrease in the mineral soil, with a marked stabilization of N.

These findings suggest that planting *C. lusitanica* is not recommendable in Munessa Forest, as it promotes nutrient losses and as it suppresses soil life and understorey, which emerged very important for retaining nutrients while keeping them available. The natural forest appears as the most sustainable system. However, production aspects will favour *E. globulus*, although this species has some adverse effects on soil organic matter quality and a higher leaching intensity. Nevertheless, its deep roots contribute to nutrient recycling and interfere to a lesser extent with regenerating species.

Research perspectives

The studies presented in this dissertation can only shed light on limited aspects of ecosystem sustainability. In order to obtain a really comprehensive view, they need to be merged with other investigations on the ecology of natural and plantation forests, above all the ecosystem flux study currently under way on the same plots in Munessa Forest. But some further investigations appear necessary as well.

Root activity and exudation should be further addressed, as they are intimately linked to soil life, as should be the effect of the low fine root biomass of *E. globulus* on soil structure (Bewket and Stroosnijder 2003).

The influences of canopy structure and silviculture need to be addressed, as diversification of the plantations could largely compensate the negative impacts of individual species. Other trees might attain a better rating in sustainability, but this has still to be found out. Finally, mixed stands might be a sustainable and still productive alternative to pure natural forests (Khanna 1997), but special attention has to be paid to the right composition (Garnier et al. 1997). As the rehabilitation of natural forests has to be one primary goal in forest policy, the gradual conversion of plantations has to be addressed, particularly the natural regeneration of indigenous species (Parrotta et al. 1997). Natural regeneration in plantations of *E. globulus* is quite high (Michelsen et al. 1996; Feyera et al. 2002), but the responsible factors are not yet identified. These include above all seedling establishment and seed dispersal, but also more hidden aspects like the mycorrhizal community, which may be decisive for forest regeneration (Wubet et al. 2003).

For a better transferability, all investigations should be put into the framework of site conditions, as done by Rückamp and Abate in a study on site-vegetation interaction (unpublished, 2004).

From the methodological point of view, the presented ^{34}S tracer method should be optimized, as it can also give evidence about the cycling of organic matter, the dynamics of which has been shown to be closely coupled to those of N and S (Novak et al. 2003). This can extend our knowledge on C sequestration and dynamics of soil organic C, which is the prominent agent of nutrient retention in the high-turnover topsoil of tropical soils, lending them further quality as indicators of overall ecosystem nutrient cycling and sustainability.

Finally, it has to be borne in mind that forest plantations can never serve all the benefits arising from natural forests, like their biodiversity providing non-wood forest products, let alone the individual face of natural forests.

References

Bewket W, Stroosnijder L (2003) Effects of agroecological land use succession on soil properties in Chemoga watershed, Blue Nile basin, Ethiopia. Geoderma 111:85-98

Feyera S, Beck E, Lüttge U (2002) Exotic trees as nurse-trees for the regeneration of natural tropical forests. Trees - Structure and Function 16:245-249

Garnier E, Navas ML, Austin MP, Lilley JM, Gifford RM (1997) A problem for biodiversity-productivity studies: how to compare the productivity of multispecific plant mixtures to that of monocultures? Acta Oecol 18:657-670

Khanna PK (1997) Comparison of growth and nutrition of young monocultures and mixed stands of *Eucalyptus globulus* and *Acacia mearnsii*. Forest Ecol Manag 94:105-113

Michelsen A, Lisanework N, Friis I, Holst N (1996) Comparisons of understorey vegetation and soil fertility in plantations and adjacent natural forests in the Ethiopian highlands. J Appl Ecol 33:627-642

Novak M, Buzek F, Harrison AF, Prechova E, Jackova I, Fottova D (2003) Similarity between C, N and S stable isotope profiles in European spruce forest soils: implications for the use of $\delta^{34}S$ as a tracer. Appl Geochem 18:765-779

Parrotta JA, Turnbull JW, Jones N (1997) Introduction - Catalyzing native forest regeneration on degraded tropical lands. Forest Ecol Manag 99:1-7

Wubet T, Kottke I, Teketay D, Oberwinkler F (2003) Mycorrhizal status of indigenous trees in dry Afromontane forests of Ethiopia. Forest Ecol Manag 179:387-399

Declaration

Hiermit erkläre ich, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe. Ich habe an keiner anderen Hochschule als der Universität Bayreuth ein Promotionsverfahren begonnen.

Bayreuth, 28. Juni 2005