SUMMARIZING SYNTHESIS

The overall goal of the present study was to determine the below-ground carbon dynamics as a function of climate variably in undisturbed soils of a wet tropical rain forest. The measurements were conducted in the old-growth forests of La Selva Biological Station in the Caribbean lowlands of Costa Rica. Six plots were selected for the various measurements: three plots on 'old alluvium' soils and three plots on 'residual' soils.

1 EFFECTS OF SOIL WATER CONTENT ON SOIL CO_2 EFFLUX

The focus of Chapter 3 was on the quantification of soil CO_2 efflux. In particular, the CO_2 emission of two soil types was compared and the factors controlling the CO_2 flux were shown and discussed. Soil CO_2 efflux was measured from eight permanent soil chambers on each of the six study sites. Bi-weekly soil CO_2 efflux measurements were carried out since April 1998 using a portable infrared analyzer with datalogger. The CO_2 flux was calculated from the linear regression of increasing CO_2 concentration in the chamber headspace versus time. At the same time soil water content and soil temperature were estimated. The total amount of CO_2 emitted per year was calculated by multiplying the mean annual hourly CO_2 soil flux rates by the number of hours per year.

Between 'old alluvium' sites, the three-year average CO_2 flux rates ranged from 11 to 12 Mg C ha^{-1} $year^{-1}$. Higher soil CO_2 flux occurred on the 'residual' sites (12 to 16 Mg C ha^{-1} $year^{-1}$). Spatial differences in CO_2 efflux were related to fine root biomass, soil carbon and phosphorus concentration but also to soil water content. During the 3rd year, efflux rates from 'old alluvium' sites were elevated with reference to the first two years of this study. No inter-annual variation in soil CO_2 efflux was detected for 'residual' sites. Soil respiration is different in different types of ecosystems and varies with environmental conditions (RAICH & SCHLESINGER 1992). Published measurements of annual soil CO_2 efflux in tropical and subtropical moist/humid forests range from 8.9 - 14.5 Mg C ha^{-1} $year^{-1}$ (RAICH & SCHLESINGER 1992). Differences in the magnitude of soil CO_2 efflux between the wet and 'drier' season were not found. Studies from tropical moist forests show a clear seasonal trend with lower CO_2 emission during dry hot periods (RAJVANSHI & GUPTA 1986, FEIGL et al. 1995).

The CO_2 flux data obtained in the present study represent an integrated measure of root and heterotrophic respiration as well as gas diffusion. All these processes may respond differently to biotic and abiotic factors. Thus, it is difficult to obtain a strong correlation between soil CO_2 efflux and a single factor. Although the sampling occurred across a large area with substantial spatial variation, soil water content explained between 20 and 50 % of the seasonal variation in soil CO_2 efflux rates. The relationship between soil CO_2 efflux and the volumetric water content was best described as a parabolic function. This reflects the general observation that CO_2 flux declined in both saturated and in very dry soils. Rising soil CO_2 efflux rates caused by an increase in soil water content suggests that soil moisture may be a factor limiting root and microbial respiration. During periods of high soil water contents, CO_2 emission decreased probably due to lower diffusion and CO_2 production rates. The apparent effect of temperature on soil CO_2 efflux was probably the result of the covariance between soil temperature and soil water content.

High spatial variability of CO_2 efflux has been reported (RAICH et al. 1990, HANSON et al. 1993). Until now, the CO_2 efflux measurements at La Selva were concentrated on a few replicated sites to assess the factors influencing soil CO_2 emission in this wet tropical environment. However, to understand carbon exchange in forest ecosystems, knowledge of landscape scale dynamics of soil CO_2 emission is important. Determination of soil CO_2 efflux on a landscape-scale level should therefore be the subject of further studies.

The present study is the only published study in the wet tropics, which reports on more than one year of soil CO_2 efflux measurements. Some extreme climate effects like ENSO and the observed interannual variation in soil CO_2 efflux indicate the necessity for long-term monitoring. Only long-term monitoring on a landscape scale basis can give a better insight into interannual variation of soil CO_2 efflux and the factors controlling temporal variation of soil CO_2 emission.

2 CO_2 PRODUCTION IN DEEPLY WEATHERED SOILS OF THE WET TROPICS

In Chapter 4, the estimates of CO_2 production rates were presented. Special attention was paid to the relationship between environmental factors and CO_2 production. Diffusion coefficients, which were needed to calculate the CO_2 production rates, were derived from empirical formulas and validated using radon measurements. In addition long-term spatial and temporal

variations in soil profile temperature, soil water content and soil air CO_2 concentrations were examined.

I found that the La Selva soils are vertically organized into two layers of a different CO_2 regime. In the upper 0.5 m, where 85 –90 % of the CO_2 is produced, fluxes of CO_2 are large as a result of higher diffusion rates. Consequently, the concentration of CO_2 remains small. In deeper layers, where the production rates are generally low, diffusivity is low as well and CO_2 concentrations are elevated. Based on long-term field observations of CO_2 concentrations in soil air I concluded that transport of CO_2 within the profile played an important role in the formation of the observed CO_2 depth profiles.

CO_2 transport occurred mainly in the gas phase. However, soil water content in the investigated sites was high and the proportion of the CO_2 in the gaseous phase became smaller whereas the proportion of the dissolved CO_2 content became larger with depth. Below 1 m depth around 95 % of the total CO_2 content in bulk soil was dissolved in the liquid phase. This implies that soil water is an important reservoir of CO_2 (HAMADA 1999). It was observed that soil CO_2 content and CO_2 production varied less widely in deeper layers than in the topsoil. This may be explained by the fact that environmental parameters fluctuated also within a small range. The temporal variation of the total content of CO_2 may also be mitigated by the amount of CO_2 dissolved in the liquid phase. Thus, the liquid phase in not only important as a storage medium for CO_2 but also as a 'buffer'. It can be concluded that the CO_2 content in the liquid phase must be taken into account in order to clarify the dynamic of CO_2 in soil profiles.

Soil CO_2 concentrations and empirical estimated diffusion rates were used to calculate the CO_2 production rates as a function of depth. Before the CO_2 production rates were estimated, the utility of two diffusion models (non-aggregated and aggregated model) was examined. It was shown that the diffusion values derived from the aggregated soil model provided significantly better agreement with the observed ^{222}Rn activities through the profile. The non-aggregated model underestimated diffusivity which resulted in an overestimation of ^{222}Rn activities.

In both 'old alluvium' and 'residual' soils about 85 to 90 % of the CO_2 production (10 to 13 Mg C ha^{-1} $year^{-1}$) occurred in the top 0.5 m of the soil (including the litter layer). Spatial differences in CO_2 production were related to the carbon input of fine litterfall, fine root biomass, soil carbon content and basal respiration. Around 5 % (1.5 Mg C ha^{-1} $year^{-1}$) of the CO_2 was produced between 0.5 and 3.0 m depth.

The total amount of CO_2 produced in 2.0 - 3.0 m depth was < 2 % of the total CO_2 efflux. Yet, especially on 'old alluvium' sites, CO_2 production in this layer appeared to be more temperature sensitive than in the above laying horizons. This observation made clear that deep soil processes have to be assessed and monitored to get reliable information on below-ground carbon dynamics. Even small changes in temperature may cause an increase in deep soil CO_2 production because of the exponential temperature response. The effect of soil temperature on deep soil CO_2 production makes the system susceptible to changes in climate. An increase in soil temperature would lead to a higher annual turnover of deep soil carbon and subsequent carbon loss.

The present study showed that temporal variation in soil CO_2 efflux and CO_2 production can be explained to some extent by soil temperature and soil water content. Moreover, it was observed that fine litterfall and fine root biomass have a certain influence on the spatial variation between sites. I assume that both the timing of litterfall inputs to the forest floor and the fine root growth pattern also influence the temporal variation in CO_2 production and soil CO_2 efflux. To resolve this issue, future research in the area should include studies on the seasonal dynamics of fine litterfall and fine root production. In addition, studies have to be done on the turnover rate of litter and roots. In the present study no attempt was made to separate the contribution of root respiration and heterotrophic respiration to total CO_2 production. Root respiration has been considered to contribute between 10 to 90 % of total soil CO_2 efflux (BOWDEN et al. 1993, THIERRON & LAUDELOUT 1996, HANSEN et al. 2000). Therefore, particular attention should also be paid to the magnitude of root respiration and its temporal variation. Isotope techniques (^{13}C, ^{14}C) have to be applied to solve this problem. In addition, ^{14}C inventories are needed to evaluate soil carbon dynamics.

3 DYNAMICS OF DISSOLVED ORGANIC MATTER AND DISSOLVED INORGANIC NITROGEN

Besides soil organic carbon and soil CO_2, the amount of dissolved organic carbon contributes to the below-ground carbon budget of an ecosystem. Chapter 5 focused on the quantification of dissolved organic matter (DOM) and dissolved inorganic nitrogen (DIN) in throughfall and soil solution. The objectives study were: (i) to quantify the contribution of dissolved organic carbon and nitrogen to the total aboveground litter inputs of carbon and nitrogen, (ii) to track changes in DOM biodegradability and DOC composition, and (iii) to determine the importance of sorption in regulating DOC concentrations. I measured dissolved organic

matter (DOM) and dissolved inorganic nitrogen (DIN) in throughfall, litter leachate and soil solution over one year. Laboratory experiments were carried out to quantify the portion of rapidly biodegradable DOM and to estimate the sorption capacity of the soil. Finally, chemical and isotopic composition of DOC was measured using fractionation and mass spectrometry.

Fluxes of dissolved organic carbon (DOC, 277 kg C ha^{-1} $year^{-1}$) and dissolved organic nitrogen (DON, 13 kg N ha^{-1} $year^{-1}$) were highest in the litter leachate. The amount of DOC and DON decreased with soil depth. We estimated that approximately 50 kg C ha^{-1} $year^{-1}$ (DOC) and 1 kg N ha^{-1} $year^{-1}$ (DON) were leached from the soil. The fraction of biodegradable DOM in throughfall (23 %) and litter leachate (33 %) was lower than in the soil solution (41 – 46 %). Chemical composition of DOM changed as water was percolating through the soil. DOC in litter leachate was characterized by a high proportion of humic substances (80 %) of high aromaticity. In contrast, soil solution contained less humic substances of lower aromaticity. Partition coefficients (m) of up to 0.93 indicate that the clay and sesquioxide-rich La Selva soils have a high affinity for DOC. Sorption of DOC by the soil matrix has probably led to large soil organic carbon stores in the subsoil. There is, however, no indication that this process will increase as a result of elevated CO_2 and increased N-deposition in the near future.

The present study showed that the majority of N in soil solution was in the dissolved mineral form, particularly NO_3^--N. Similar results have been reported from other highly N saturated forest ecosystems.

4 BELOW-GROUND CARBON POOLS AND FLUXES

All essential carbon input and output fluxes as well as the soil organic carbon stocks, which were monitored and estimated in the course of the present study, are summarized in Figure 6.1. Total soil organic carbon down to 3 m depth was higher for the ‘residual’ sites (330 Mg C ha^{-1}) than for the ‘old alluvium’ sites (213 Mg C ha^{-1}). This amount is about twice as high as the carbon stocks reported from tropical moist forests in the Amazon basin (TRUMBORE et al. 1995, SOMMER et al. 2000). The top 0.5 m contained between 1.2 Mg C ha^{-1} (‘old alluvium’) and 1.5 Mg C ha^{-1} in form of microbial biomass. Below 0.5 m depth (to 3.0 m depth) microbial biomass contributed approximately 1 Mg C ha^{-1} to the soil organic carbon pool (VELDKAMP et al. submitted). Using stable carbon isotopes VELDKAMP et al. (submitted)

estimated the decomposable (= labile) and passive (= stable) fraction of the soil organic carbon pool. They found that in 'old alluvium' sites 22 % and in 'residual' sites 30 % of the soil organic carbon stored in the topsoil (0 - 0.5 m depth) was decomposable. The proportion of labile carbon in deeper layers (0.5 - 3.0 m depth) ranged from 14 % ('residual') to 30 % ('old alluvium'). These results show that large stocks of relatively labile carbon are not limited to the upper soil horizons.

Total carbon storage in fine litter (and branches < 5 cm) is approximately 1.6 Mg C ha^{-1} (RAICH 1980). Carbon originating from large pieces of standing or fallen dead wood (known as coarse woody debris, CWD) amounted to 19 Mg C ha^{-1} on 'old alluvium' sites and 21 Mg C ha^{-1} on 'residual sites (CLARK et al. 2002). CWD at La Selva represented ca. 33 % of the above-ground biomass of live trees (CLARK & CLARK 2000). The fine root carbon stock (live and dead roots ≤ 5 mm) to a depth of 0.5 m was 1.3 Mg C ha^{-1} for 'old alluvium' and 1.9 Mg C ha^{-1} for 'residual' sites (OBERBAUER et al. 2002). Total root biomass below 2 m is very low in La Selva soils (VELDKAMP et al. submitted).

The major above-ground source of carbon input was litterfall. At La Selva, fine litterfall contributed between 3.9 Mg C ha^{-1} $year^{-1}$ ('old alluvium') and 4.8 Mg C ha^{-1} $year^{-1}$ ('residual') to the annual carbon input (DAVIDSON et al. 2002). Carbon from coarse woody debris was identified as another major source of input ('old allluvium' 1.7 Mg C ha^{-1} $year^{-1}$, 'residual' 3.1 Mg C ha^{-1} $year^{-1}$) (CLARK et al. 2002). Annual carbon input in form of DOC (< 0.35 Mg C ha^{-1} $year^{-1}$) was small compared to fine litter and coarse woody debris. To date no estimates are available on fine root production.

Soil CO_2 efflux was by far the single greatest carbon flux measured at both 'old alluvium' (11 Mg C ha^{-1} $year^{-1}$) and 'residual' sites (14 Mg C ha^{-1} $year^{-1}$). Annual total dissolved organic carbon lost from this forest was approximately 0.05 Mg C ha^{-1} $year^{-1}$. The magnitude of dissolved inorganic carbon transported into groundwater was approximately 1 % of CO_2 emitted into the atmosphere.

The amount of carbon emitted to the atmosphere was three times the input of carbon in form of fine litter. Allocation of carbon to roots often equals or exceeds aboveground litterfall C (DAVIDSON et al. 2002). RAICH & NADELHOFFER (1989) suggested that in steady state systems, the difference between soil respiration and litterfall C could be used to estimate the total below-ground carbon allocation (TBCA). According to this equation (TBCA = Soil respiration – litterfall C). 7.1 Mg ha^{-1} $year^{-1}$ ('old alluvium') and 9.2 Mg ha^{-1} $year^{-1}$ will be allocated to roots. Total below-ground C allocation in La Selva soils was approximately two

times the aboveground litterfall C. This is in agreement with TBCA data based on a analysis of forests from around the world (RAICH & NADELHOFFER 1989, DAVIDSON et al. 2002).

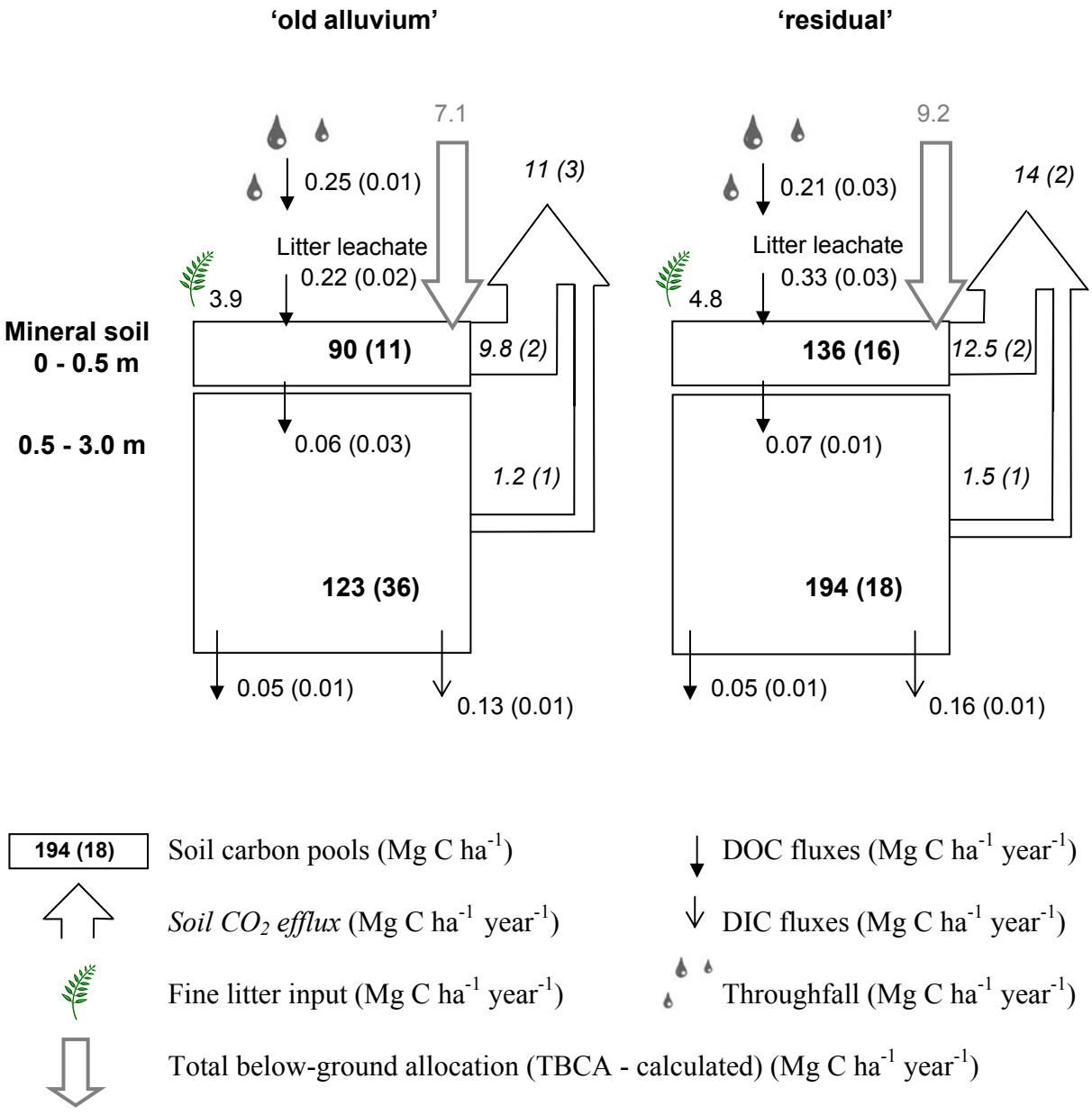

Figure 6.1: Below-ground carbon pools and fluxes in 'old alluvium' and 'residual' sites at the La Selva Biological Station, Costa Rica. DOC fluxes are expressed as the mean (± standard deviation from two study sites per soil type) of bi-weekly measurements taken between May 2000 - May 2001. Soil CO_2 efflux and DIC fluxes are expressed as the mean (± standard deviation from three study sites per soil type) of bi-weekly measurements taken from April 1998 - April 2001. Fine litter input was based on bi-weekly measurements taken between October 1998 and September 1999 (DAVIDSON et al. 2002).

The results from the present study and from VELDKAMP et al. (submitted) point out that up to 30 % of the soil organic carbon stored in deeper layers (0.5 - 3.0 m depth) was decomposable. That the soil apparently stored a large pool of carbon below the first meter raises important issues for global carbon budgets and for carbon sequestration strategies (BATJES 1996). Regardless of their size, deep soil carbon stocks are often considered unimportant, because of their fairly slow turnover (SOMBROEK et al. 1993). This would make them relatively insensitive to changes in climate or management. On the other hand, several investigations demonstrated that some proportion of deep SOC probably has a relatively fast turnover (TRUMBORE et al. 1995, VELDKAMP et al. submitted). Thus, deep soils might act as a carbon source if temperature increases or if the forest is cleared.

Moreover, the observed temperature dependence of CO_2 production, especially in 'old alluvium' sites, made clear that deep soil processes have to be assessed and monitored to get reliable information on below-ground carbon dynamics. Even small changes in temperature may cause an increase in deep soil CO_2 production because of the exponential temperature response. The effect of soil temperature on deep soil CO_2 production makes the system susceptible to changes in climate. An increase in soil temperature would lead to a higher annual turnover of deep soil carbon and subsequent carbon loss.

Global climate models predict an average annual mean increase in global temperatures of 1.3 - 2.3 °C for a doubling of atmospheric CO_2 (COX et al. 2000). If the increase in air temperature is translated into higher soil temperature, CO_2 production can be expected to increase as a response of the ecosystem to increased temperature. Strong temperature dependence of decomposition rates in labile SOM pools, coupled with the large amounts of labile carbon in tropical forest soils, could lead to large positive feedback between tropical forest SOM and global or regional temperature changes. However, to estimate this response, one needs to know the likely variations in other climate factors as well as biological inputs governing soil respiration and transport through the soil. CLARK et al. (submitted) reported a decline in productivity with rising mean night temperate. This may lead to a decrease in root respiration and annual litterfall. In this case the soil organic carbon pool will decrease in the future.

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