Factors controlling carbon turnover in forest soils

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Contents

Abstract

Soils store a large amount of carbon, which is estimated to be around 2000 Pg globally. In this context, soil respiration, the carbon dioxide flux released from the soil, plays an important role. It has two main sources: the decomposition of soil organic matter by microorganisms and the activity of roots and root-associated organisms. Changes in the amount of carbon cycling through the soil may provide feedbacks that are relevant for climate changes. Thus, the overall objectives of this study were to quantify the turnover of carbon in the soil and to identify its controls.

Turnover times of different soil organic matter fractions were estimated from their carbon-14 isotope ($\Delta^{14}C$) values combined with a model. The soil organic matter fractions were collected from 11 forest sites in northern Italy located along a mean annual temperature gradient from ~ 4 to 12 °C. Turnover times of the different fractions increased with increasing soil depth and ranged from 2-15, 25-150, and 50-900 years, for the labile, intermediate, and stabilized soil organic matter fraction, respectively.

Temperature sensitivities of the turnover times of the different soil organic matter fractions were investigated from correlation coefficients and regression analysis. The temperature sensitivity of the stabilized soil organic matter fraction was at least equal to that of the intermediate fractions, and possibly twice as high. A temperature sensitivity of the turnover times of the labile fraction could not observed here. Several factors may have influenced the results as observed here for the three soil organic matter fractions, for example the applied modeling assumptions, or the confounding effect of occasional summer drought at the warmer sites.

From the $\Delta^{14}C$-based turnover times and the carbon stocks of the different soil organic matter fractions respiration fluxes were calculated. Subsequently, this soil organic matter-derived respiration was subtracted from previously determined total annual soil respiration of the sites. The following partitioning of total soil respiration was found: ~ 30% from the decomposition of litter layers; less then 10% from the decomposition of soil organic matter in the mineral soil; and ~ 60% from the activity of roots, root-associated organisms, and the decomposition of organic matter that decomposes in less than one year after it has entered the soil. To subdivide the latter respiration source, respiration derived from the annual litterfall within the first year was estimated from an exponential decay function with a decomposition rate based on the $\Delta^{14}C$-based turnover times of the fresh litter.

Total soil respiration increased with increasing nitrogen content of the litter layers, this relationship explained 70% of variation in total soil respiration. The litter-derived and root-derived respiration both seemed to increase with increasing litter nitrogen. However, the occurrence of two outliers hampered interpretation of these latter results. Overall, the results suggested that at the sites a large fraction of the biological activity in the soil is located in or near the litter layers where the availability of nitrogen is high, and results suggested that plants may maintain a high availability of nitrogen in the soil through the production of litter with high nitrogen content.

This study contributed to research on soil carbon dynamics in that: (i) the temperature sensitivity of turnover times of different soil organic matter fractions were estimated using $\Delta^{14}C$ analyses, a method that quantifies soil organic matter turnover on a decadal scale; (ii) the use of $\Delta^{14}C$-based turnover times of soil organic matter to partition soil respiration was evaluated; and (iii) the effect of the availability of nitrogen in the soil on soil respiration was shown and discussed.

Zusammenfassung

Im Boden wird weltweit eine sehr große Menge Kohlenstoff (etwa 2000 Pg) in Form von organischer Substanz (Humus) gespeichert. Die Bodenatmung fungiert in diesem Zusammenhang als Fluss von Kohlenstoff in Form von CO_2 aus dem Boden in die Atmosphäre. Als die beiden Hauptquellen sind zu nennen: der Abbau von Humus durch Mikroorganismen und die Aktivität von Wurzeln und wurzelassoziierten Mikroorganismen. Veränderungen der Kohlenstoffumsetzung im Boden durch die Klimaveränderungen könnten dabei zu Rückkopplungen mit dem atmosphärischen Kohlenstoff und dem Klima selbst führen. Das Ziel dieser Arbeit ist die Quantifizierung der Kohlenstoffumsatzzeiten im Boden und die Bestimmung der dabei steuernden Variablen.

Hierzu wurden die Umsatzzeiten verschiedener Fraktionen der organischen Bodensubstanz geschätzt durch Ihren Kohlenstoff-14 Isotopen ($\Delta^{14}C$) Werten zu kombinieren mit einem Kohlenstoffumsatz-Modell. Die zugrunde liegenden Böden stammen aus 11 Waldstandorten in Norditalien mit unterschiedlichen Höhenlagen, die einem Temperaturgradienten mit mittleren Jahrestemperaturen von etwa 4 bis 12 ^{o}C entsprechen. Die Umsatzzeiten der unterschiedlichen Fraktionen der organischen Substanz nahmen mit zunehmender Bodentiefe zu, mit Werten von 2–15 Jahren für die labile Fraktion, 25–150 Jahren für die intermediäre Fraktion und 50-900 Jahren für die stabilisierte Fraktion.

Die Temperatursensitivität der Umsatzzeiten der unterschiedlichen Fraktionen wurde mit Korrelations- und Regressionsanalysen untersucht. Die Temperatursensitivität der stabilisierten Fraktion war mindestens ähnlich hoch wie die der intermediären Fraktion. Die Temperatursensitivität der labilen Fraktion konnte nicht ermittelt werden. Verschiedene Faktoren beeinflussten möglicherweise die Ergebnisse der Temperatursensitivität, zum Beispiel die verwendeten Modellannahmen oder die auftretende Sommertrockenheit an den wärmeren Standorten.

Aus den $\Delta^{14}C$-basierten Umsatzzeiten und den Vorräten der unterschiedlichen Fraktionen der organischen Substanz wurden Bodenatmungsflüsse berechnet. Diese wurden mit experimentell bestimmten Jahressummen der Bodenatmung der verschiedenen Standorte verrechnet. Dabei wurde folgende Aufteilung der Bodenatmungsquellen ermittelt: etwa 30% der Bodenatmung stammte von der Abbau der Streuauflage, weniger als 10% stammte aus der organischen Substanz des

Mineralsbodens und etwa 60% der Bodenatmung ließ sich auf die Aktivität der Wurzeln, der wurzelassoziierten Mikroorganismen sowie den Abbau leichtverfügbarer organischer Substanz (Umsatzzeit < 1 Jahr) zurückführen. Um die letztgenannte Bodenatmungsquelle weiter aufzuteilen wurde die Atmung aus der frischen Streu während des ersten Jahres mittels einer exponentiellen Abbaufunktion und den $\Delta^{14}C$-basierte Umsatzzeiten der frischen Streu abgeschätzt.

Die gesamte Bodenatmung nahm mit zunehmendem Stickstoffgehalt der Streuauflage zu. Diese Korrelation erklärte 70% der Variation der gesamten Bodenatmung. Die Stickstoffgehalte scheinen sowohl die Bodenatmung aus der Streuauflage als auch die Wurzelatmung positiv zu beeinflussen. Zwei Ausreißer in den Daten stellten diese Schlussfolgerung zwar in Frage, insgesamt deuten die Ergebnisse jedoch darauf hin, dass ein großer Teil der biologische Aktivität in oder nahe unter der Streuauflagen stattfindet und dass Bäume eine hohe Stickstoffverfügbarkeit im Boden durch die Produktion von Streu mit hohen Stickstoffgehalten gewährleisten.

Diese Arbeit leistete somit insgesamt folgenden Beitrag zur Bodenkohlenstoffforschung: (i) Die Temperatursensitivität der Umsatzzeiten unterschiedlicher Fraktionen der organische Substanz des Bodens wurde bestimmt mittels $\Delta^{14}C$ Analysen, ein Methode zur Quantifizierung von Umsatzzeiten auf Zeitskalen von Jahrzehnten; (ii); die Anwendung von auf $\Delta^{14}C$ basierte Umsatzzeiten der organischen Substanz zur Aufteilung von Bodenatmung in verschiedene Quellen wurde evaluiert; und (iii) der Einfluss der Verfügbarkeit vom Stickstoff im Boden auf die Bodenatmung wurde gezeigt und diskutiert.

1. Introduction

1.1 Motivation

Decomposition of soil organic matter (SOM) and the activity of roots and root-associated organisms result in a CO_2 flux emitted from the soil (hereafter: soil respiration). Changing environmental conditions like rising temperatures, increasing atmospheric CO_2 concentrations, and anthropogenic nitrogen deposition may change the rates at which those processes take place. Rising temperatures may enhance the rate of SOM decomposition, although they may also increase carbon input to the soil as a result of increased ecosystem productivity. Drought may slow down SOM decomposition, but may also reduce carbon input to the soil through reduced ecosystem productivity. Increasing nitrogen deposition may increase carbon input to the soil because nitrogen frequently limits ecosystem productivity, whereas the effects of nitrogen deposition on SOM turnover are variable. The additional CO_2 released from or sequestered in the soil as a result of such changes may be an important feedback mechanism for climate change, with both negative as well as positive feedbacks being possible (Lashof et al. 1997, Hyvönen et al. 2007, Heimann and Reichstein 2008). Therefore, a thorough understanding of processes regulating the global carbon cycle, including the turnover of carbon in the soil, is necessary. This may support policy makers in their decisions and allow more accurate predictions of the impact of changing environmental conditions on terrestrial ecosystems.

1.2 Controls on carbon turnover in soils

The amount of carbon stored in soils is the net result of litter accumulation and soil organic matter (SOM) decomposition. Through soil respiration, a flux globally estimated to be 80 Pg carbon (Raich et al. 2002), carbon is released from the soil to the atmosphere. Soil respiration consists of two main components: (1) respiration resulting from the decomposition of SOM, and (2) respiration from roots. Total soil respiration is thus the result of two distinct processes. The decomposition rate of SOM varies among different pools, with turnover times ranging from 1 to 1000 years or even longer (Chapin et al. 2002). Root-derived respiration on the other hand is directly linked to the photosynthetic activity of plants (Högberg et al. 2006), and thus represents a soil carbon pool that turns over relatively fast in comparison to the SOM pool. When SOM-derived respiration is approximately balanced by above- and

belowground litter production, the SOM pool is considered to be roughly in steady state (Raich and Nadelhoffer 1989).

A major abiotic control on microbial activity in the soil, and thus on SOM turnover, is *temperature*. A faster SOM turnover as a result of global warming may cause that additional CO_2 is released from soils (Davidson and Janssens 2006, Kirschbaum 2006). *Soil moisture* is another abiotic control on the SOM turnover. Microbial activity in the soil can be reduced during drought as well as during water saturation. Since soil moisture co-varies with temperature, observed temperature responses can be confounded by moisture limitation at higher temperatures (Reichstein and Beer 2008b).

There is a strong variation in the *chemical composition* of SOM, which is related to the initial litter composition (i.e. plant specie and type of tissue) as well as to microbial alterations that take place during SOM decomposition. The variation in chemical composition of SOM leads to quality differences, i.e. differences in the degree of decomposability, and thus the rate of turnover. *Quality* of aboveground litter and root litter is related to nutrient (e.g. nitrogen, phosphorus, and calcium) and lignin concentrations (Berg 2000, Silver and Miya 2001). In addition following properties of SOM can play a role (Chapin et al. 2002): (1) size of the molecules, which determines whether they can pass microbial membranes, (2) the strength of the chemical bindings, and (3) the molecular structure; many microbial enzymes can break down molecules that have a regular structure (e.g cellulose), but much less can break down molecules with irregular structures (e.g. lignin). After the initial decomposition stage, SOM does not contain recognizable plant tissue anymore and consists largely of humus. At this stage the SOM has been mixed with the mineral soil. Fractionation of SOM in an advanced decomposition stage, has shown that considerable differences in the age, and thus in the quality, exist within this SOM (Rasmussen et al. 2005, Mikutta et al. 2006).

Stabilization of SOM through associations with mineral particles occurs in soils as a result of chemical bindings or through formation of aggregates. The stronger the association between SOM and mineral particles, the more its turnover will be decreased by it. Chemical bindings between SOM molecules and the surfaces of mineral soil particles can stabilize SOM. Clay particles, iron- and aluminium oxides are the most important surfaces for such bindings. Aggregate formation is promoted by biologic activity in the soil e.g. the presence of earthworms. SOM

contained in aggregates is protected against microbial attack because it is less accessible and because conditions in the aggregates are less favourable for decomposition. (Krull et al. 2003, von Lützow et al. 2006)

Root-derived respiration on the other hand is dependent on *photosynthetic activity* during the growing season and on plants' *carbohydrate reserves* during spring and during unfavourable conditions (Ryan and Law 2005). An experiment in which the flow of photosynthates to the roots was terminated by girdling of tree stems, has shown a marked decrease in the total soil respiration (Högberg et al. 2001). Also several studies have shown increases in soil respiration with increasing *productivity* (Raich and Schlesinger 1992, Janssens et al. 2001, Hibbard et al. 2005). Furthermore, it has been shown that root-derived respiration increases with increasing root *nitrogen* content (Ryan et al. 1996, Pregitzer et al. 1998). Root-derived respiration, like SOM-derived respiration, also changes with *temperature*, which is partly a direct and partly an indirect response. The direct response of plant respiration, and thus root-derived respiration, to temperature is related to the capacity of enzymes and the supply of substrate in the plant (Atkin and Tjoelker 2003). On the other hand, the indirect response of root-derived respiration is related to seasonal trends in root growth, root maintenance, and substrate supply (Yuste et al. 2004, Davidson et al. 2006).

1.3 Quantification of SOM turnover using carbon-14 isotope analyses

Differences in the aforementioned controls on SOM turnover, both within a soil profile as well as on larger spatial scales, will lead to differences in SOM turnover times. Carbon-14 isotope ($\Delta^{14}C$) analyses of SOM can be applied to quantify such differences in SOM turnover. The use of $\Delta^{14}C$-analyses of SOM as applied in this study is based on the occurrence of high atmospheric $\Delta^{14}CO_2$ concentrations in the 1950s and 60s as a result of aboveground nuclear weapon testing (the so-called bomb-peak; see Figure 1.1a). This peak was followed by a gradual decrease of the atmospheric $\Delta^{14}CO_2$, mainly as a result of $\Delta^{14}CO_2$ uptake by the ocean. In addition, vegetation has also taken up part of this $\Delta^{14}CO_2$, which has labelled all the organic matter formed since then. Consequently, the input of this labelled organic matter (e.g. litterfall and root litter) to the soil has also labelled SOM pools. From the $\Delta^{14}C$ value of a SOM pool (which is its response to the bomb-peak) measured at some point in time, a turnover time of the SOM pool can be estimated by using a simple

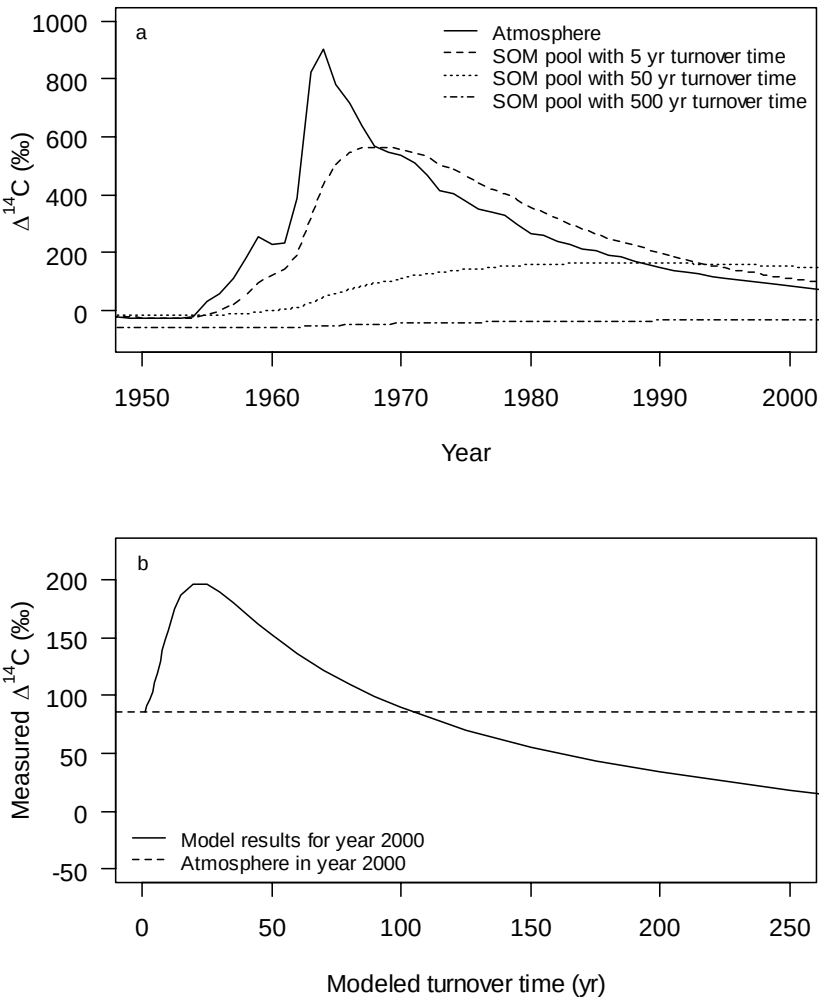

Figure 1.1: (a) Changes in the atmospheric $\Delta^{14}CO_2$ concentrations as a result of nuclear weapon testing (solid line) as well as the responses of different soil organic matter (SOM) pools (dashed lines) to the atmospheric $\Delta^{14}CO_2$. (b) Measured $\Delta^{14}C$ values of SOM and the corresponding turnover times as derived from a model for the year 2000. $\Delta^{14}C$ values of SOM higher than the atmospheric $\Delta^{14}CO_2$ in the year of sampling correspond to two possible turnover times. The effects of a lagged input of atmospheric $\Delta^{14}CO_2$ or implementation of an intermediate SOM pool, as applied in Chapter 2, are not included in this illustration.

model and a record of atmospheric $\Delta^{14}CO_2$ concentrations (Figure 1.1a). Details about the model can be found in Trumbore and Torn (in press) and in Chapter 2 of this thesis. The use of $\Delta^{14}C$ analyses has two major advantages. Firstly, the $\Delta^{14}C$ of SOM reflect the long-term result of litter accumulation and SOM decomposition. Secondly, the method does not require experimental manipulations or disturbances of the investigated ecosystem. The method however also has some disadvantages. Firstly, it is necessary to assume constant annual carbon inputs and steady-state SOM pools,

unless detailed management history is available upon which alternative scenarios of carbon input can be based. Secondly, ambiguous model results occur for $\Delta^{14}C$ that are above a specific value (Figure 1.1b), i.e. a single $\Delta^{14}C$ value can corresponds to two possible turnover times. Which of the two possible turnover times is the more plausible one, needs to be determined from additional data (see Chapter 2 or Trumbore 1996).

1.4 Objectives

The overall objective of the work presented here, is to identify controls on the turnover of carbon in forest soils. The next chapters have the following specific objectives: (i) to estimate the turnover times of different SOM fractions based on their $\Delta^{14}C$ values; (ii) to determine the response of SOM turnover times to variation in mean annual temperature; (iii) to calculate the contributions of SOM-derived and root-derived respiration to total soil respiration from $\Delta^{14}C$-based turnover times and carbon stocks of SOM pools; and (iv) to investigate and explain the effect of the availability of nitrogen on total soil respiration and on components of soil respiration.

1.5 Thesis outline

In Chapter 2 modelling of $\Delta^{14}C$ values of SOM, as introduced above, is applied to three different SOM fractions. The effects of temperature and some other site characteristics are investigated. The intermediate and stabilized SOM pools showed significant temperature responses. In a subsequent analysis, the temperature sensitivities of these two SOM fractions are quantified with different temperature sensitivity functions. Finally, difficulties associated with modelling of $\Delta^{14}C$ values of SOM, the absence of a temperature sensitivity for the labile SOM fraction, and the interpretation of observed temperature sensitivities of SOM turnover times are discussed.

In Chapter 3 carbon fluxes derived from the decomposition of the different SOM fractions are estimated by combining the turnover times of the different SOM fractions with their carbon stocks. Litter-derived respiration was 81% of the total $\Delta^{14}C$-based SOM-derived respiration. By subtracting the $\Delta^{14}C$-based SOM derived respiration from the sites' previously determined total soil respiration (see Rodeghiero and Cescatti 2005), respiration derived from recently fixed carbon was

determined, which was on average 62% of the total soil respiration. This respiration from recently fixed carbon was presumed to consist of root-derived respiration as well as respiration from a fraction litter that could not be included in the respiration based on $\Delta^{14}C$ values due to seasonal fluctuations in the litter stocks. Results of this partitioning were compared with alternative estimates of SOM-derived and root-derived respiration from two other studies.

In Chapter 4 nitrogen content of decomposed litter layers is presented as an important control on total soil respiration. Effects of nitrogen on litter quality, root respiration rates, and productivity are discussed as possible explanations for the increase of soil respiration with increasing nitrogen content. It is suggested that nitrogen content of canopy or litter might be useful to estimate total soil respiration at the landscape scale.

In Chapter 5 the main findings and conclusions of this study are summarized.

2. Temperature sensitivity of the turnover times of soil organic matter in forests

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Abstract

Soils represent the largest carbon pool in the terrestrial biosphere and climate change might affect the main carbon fluxes associated with this pool. These fluxes are the production of aboveground litter and root litter, and decomposition of the soil organic matter (SOM) pool by soil microorganisms. Knowledge about the temperature sensitivity of the decomposition of different SOM fractions is crucial in order to understand how climate change might affect carbon storage in soils. In this study, the temperature sensitivity of the turnover times of three different SOM fractions (labile, intermediate, and stabilized) were investigated for 11 forest sites along a temperature gradient. Carbon-14 isotope analyses of the SOM fractions combined with a model provided estimates of their turnover times. The turnover times of the labile SOM fraction were not correlated with mean annual soil temperature. Therefore it was not possible to estimate temperature sensitivity for the labile SOM fraction. Given considerable evidence elsewhere for significant temperature sensitivities of labile SOM, lack of temperature sensitivity for the labile SOM fraction here indicates most likely limitations of the applied methodology. The turnover times of the intermediate and the stabilized SOM fractions were both correlated with mean annual soil temperatures. The temperature sensitivity of the stabilized SOM fraction was at least equal to that of the intermediate SOM fraction and possibly more than twice as high. A correction for confounding effects of soil acidity and clay content on the temperature sensitivities of

the intermediate and stabilized SOM fractions was included in the analysis. The results as observed here for the three SOM fractions may have been influenced by: (1) modeling assumptions for the estimation of SOM turnover times of leaf and needle longevities, constant annual carbon inputs, and steady-state SOM pools, (2) the occurrence of summer drought at some sites, (3) differences between sites in quality of the SOM fractions, or (4) the relatively small temperature range. Our results suggested that a one degree increase in temperature could lead to decreases in turnover times of 4 to 11% and 8 to 16%, for the intermediate and stabilized SOM fractions, respectively.

Keywords
Soil organic carbon; soil organic matter; forest; litter; density fractionation; turnover time; decomposition; temperature gradient; ^{14}C; temperature sensitivity.

2.1 Introduction

Soil organic matter (SOM) is the largest carbon pool of the terrestrial biosphere with an amount of carbon estimated to be between 1.5 and 2.3 10^3 Pg (Jobbágy and Jackson 2000). The main carbon fluxes associated with the turnover of the SOM pool are aboveground litter and root litter production and their consequent decomposition to CO_2 by soil microorganisms. These fluxes are controlled by the physical, chemical, and biological conditions in ecosystems (Lavelle and Spain 2001, Chapin et al. 2002).

Climate change could affect the sizes of both of these main carbon fluxes and result in either a net release of carbon from the soil or a net sequestration of atmospheric CO_2 as SOM. Such changes in the global SOM balance could act as an important feedback mechanism to climate change (Lashof et al. 1997, Woodwell et al. 1998, Amundson 2001). Therefore the effect of temperature changes on SOM turnover has received considerable attention over the last decade (Kirschbaum 2006). Currently, the temperature sensitivities of the turnover of different SOM fractions (e.g. labile, intermediate, and stabilized) are under debate, because they could affect the magnitude of the aforementioned potential feedback (Fang et al. 2005, Knorr et al. 2005b, Reichstein et al. 2005a, Reichstein et al. 2005b, Conen et al. 2006, Davidson and Janssens 2006, Fang et al. 2006).

The "turnover time" is the average time that carbon resides in a (conceptual) SOM pool (also referred to as mean residence time). When analyses of radioactive carbon isotope content ($\Delta^{14}C$) of SOM are combined with a model, they can be used to

estimate a turnover time of SOM. The model describes the relationship between SOM turnover times and the changes in $\Delta^{14}C$ values of SOM due to the ^{14}C released into the atmosphere in the 1950s and 1960s by nuclear weapon testing (so-called bomb peak). In comparison with other methods to quantify SOM turnover, the approach described above has the advantage that the turnover times reflect long-term results of accumulation and decomposition of SOM in the field in undisturbed soils and without experimental manipulations. However modeling $\Delta^{14}C$ values of SOM often requires assumptions of steady state size SOM pools and constant annual carbon inputs, assumptions which usually cannot be verified. In addition, $\Delta^{14}C$ analysis with accelerator mass spectrometry has some disadvantages: the risks of unrepresentative measurements due to small sample sizes, the risk of sample contamination, and the high costs of the analysis (Trumbore 1996).

Studies along natural temperature gradients give the opportunity to observe the temperature sensitivity of SOM turnover without the use of experimental manipulations. The interpretation of results however may be difficult because of many other parameters varying along the same gradient (Garten et al. 1999, Garten 2004). Few studies exist in which $\Delta^{14}C$ analyses of SOM were used to investigate the change in SOM turnover times along a temperature gradient. Using $\Delta^{14}C$ values of bulk SOM and a three-pool SOM model, Townsend et al. (1995) observed a twofold change in turnover times of an intermediate SOM pool for a change in annual temperatures of 10 ^{o}C on the island of Hawaii. Trumbore et al. (1996) found that among three SOM fractions, the $\Delta^{14}C$-based turnover times of the most labile fraction were most sensitive to temperature. Turnover times and temperature sensitivity of the most stable SOM fraction however were not reported in these studies.

The objective of our study was to investigate the temperature sensitivities of the turnover times of three different SOM fractions along a temperature gradient in the southern Italian Alps. SOM in the mineral soil was separated using a density fractionation. We estimated the turnover times of the SOM fractions from their $\Delta^{14}C$ values and determined their correlations with mean annual soil temperatures as well as with some site characteristics that could have played a confounding role. Where significant correlations between turnover times and temperatures were present, temperature sensitivities were analyzed for differences between SOM fractions using three commonly used functions. Our results may contribute to a better understanding of

Table 2.1. Some characteristics of the 11 sites in the southern Italian Alps along an elevational gradient from 220 m to 1740 m above sea level (a.s.l.), listed by increasing elevation.

Site (abbreviation)	Latitude (deg)	Longitude (deg)	Elevation (m a.s.l.)	Aspect	Slope (%)	Mean annual temperature (ºC)		Precip. (mm/ year)
						Air	Soil	
Casteller (CaH)	46º01'20"	11º08'30"	220	SW	14	11.6	11.2	951
Toblino (ToO)	46º03'35"	10º58'33"	250	SE	18	11.8	11.9	879
Mattarello (MaP)	46º01'06"	11º08'46"	420	S	16	11	9.9	959
Lagolo P (LaP)	46º01'44"	10º59'49"	760	W	31	9.5	9.4	961
Lagolo B (LaB)	46º02'16"	11º00'25"	970	NW	27	8.5	7.6	967
Brigolina B (BrB)	46º03'58"	11º04'32"	1020	SW	36	8.6	7.2	976
Brigolina S (BrS)	46º03'47"	11º04'11"	1020	N	31	8.5	7.4	982
Vaneze (VaS)	46º02'54"	11º03'47"	1150	N	53	5.9	4.8	1015
Lavarone (LaF)	46º57'19"	11º17'04"	1370	SW	11	6.7	4.5	1085
Bondone (BoB)	46º01'04"	11º03'51"	1470	SE	62	6.2	7.2	1195
Renon (ReS)	46º35'15"	11º26'04"	1740	SE	36	4.2	3.9	1008

the impact of climate change on carbon storage in soils and they may be useful in studies modeling SOM turnover in forest ecosystems.

2.2 Methods

2.2.1 Study sites

The sites are forests located along an elevation gradient ranging from 220 to 1740 meter above sea level in the southern Italian Alps in the Autonomous province of Trento (Table 2.1, after Rodeghiero and Cescatti (2005)). Mean annual air and soil temperature (at 10 cm depth) of the sites ranged from 4.2 to 11.8 ^{o}C and 3.9 to 11.9 ^{o}C, respectively. Most soils of the study sites had a high stone content and were shallow (~ 60 cm), which is characteristic for mountain regions. At all sites, except one, soils were formed on calcareous parent material, with eolian deposits (loess) frequently present. Soils of site Renon are formed on rhyolitic parent material. The sites were located on slopes with inclinations ranging from 11 to 62%. Evidence of mass movement in the past was found at sites Brigolina S, Lavarone, and Renon. Evergreen trees dominate at seven sites, while deciduous trees dominate at four other sites. Mean tree age at the sites in 2001 was between 44 to 180 years and we considered this age to be the minimum age of the forests. The management history of the sites was not documented. At sites Casteller, Toblino, and Bondone most trees were cut to ground level every 15 to 25 years (coppice with standards). The other sites were managed as high forests or are in a transition from coppice to high forest. Four sites had a different land use in the past than at present,

Table 2.1. Extended

Site abbr.	Forest type	Dominant species	Litterfall (gC/ m2/ year) (SE)†	Forest manage-ment	Mean tree age (years)	Former land-use type ‡	Parent material	Soil type §
CaH	Hophorn beam	*Ostrya carpinifolia*	214(26)	coppice	44	n.a.	Calcareous	Calcaric Phaeozem
ToO	Holm oak	*Quercus ilex*	515(72)	coppice	45	n.a.	Calcareous	Leptic Calcaric Cambisol
MaP	Austrian pine	*Pinus nigra*	328(24)	high forest	44	n.a.	Calcareous	Calcaric Phaeozem
LaP	Scots pine	*Pinus sylvestris*	188(6)	high forest	69	n.a.	Calcareous	Calcaric Phaeozem
LaB	European beech	*Fagus sylvatica*	233(25)	high forest	61	n.a.	Calcareous	Calcaric Cambisol
BrB	European beech	*Fagus sylvatica*	257(31)	high forest	50	Woodland, ~50 years ago	Calcareous	Calcaric Cambisol
BrS	Norway spruce	*Picea abies*	275(21)	high forest	50	Pasture, ~ 100 years ago	Calcareous	Calcaric Cambisol
VaS	Norway spruce	*Picea abies*	147(17)	high forest	60	Pasture or arable land, ~100 years ago	Calcareous	Calcaric Skeletic Cambisol
LaF	Silver fir	*Abies alba*	254(12)	high forest	120	n.a.	Calcareous	Calcaric Cambisol
BoB	European beech	*Fagus sylvatica*	177(6)	coppice	60	n.a.	Calcareous	Calcaric Phaeozem
ReS	Norway spruce	*Picea abies*	115(12)	high forest	180	Woodland, ~ 50 years ago	Rhyolite	Podzol

†Data presented are means, with SE in parenthesis
‡ An entry of "n.a." indicates that data were not available
§ *Source*: FAO-WRB (1998)

given the sites' locations close to (former) pastures and/or the crown architecture of the older trees. We presumed that sites Brigolina S and Vaneze were pastures or arable land ~100 years ago and that sites Brigolina B and Renon were woodlands ~50 years ago with a more open canopy than at present.

2.2.2 Soil sampling

Soils at the study sites were sampled in August 2001. At nine sites (Casteller, Toblino, Mattarello, Lagolo P, Lagolo B, Brigolina B, Brigolina S, Vaneze, and Bondone) soil was sampled at three pits. At the two other sites, Lavarone and Renon, two pits were sampled. At nine sites the distance between pits was approximately five to ten meters. At sites Lavarone and Renon distances between the pits were approximately 30 and 50 m, respectively. Organic horizon and mineral soil up to a maximum depth of 30 cm were sampled from an area of 25 by 25 cm. The organic horizon was separated in the fresh litter layer (L layer) and the fermented and humified litter layers (F and H layers). At four sites the H layer was thick enough to be sampled separately from the F layer (sites Brigolina S, Vaneze, Lavarone, and Renon). The mineral soil was sampled in layers of 0-5, 5-10, 10-20 and, 20-30 cm below the mineral soil surface. Stone content of the excavated soil was assessed by volumetric measurements in order to include a correction for it in the calculation of carbon stocks. Due to very high stone content soil

layer 20-30 cm was not sampled at sites Toblino, Lagolo P, and Bondone. Next to the soil pit a sample for soil bulk density determination was taken for each soil layers with a 100 cm^3 core. Soil samples were packed in polyethylene bags and stored at -18 ^oC until further processing.

2.2.3 Sample processing

Dry weight of the litter layers samples was determined after drying them at 70 ^oC for at least 24 hours followed by cooling down in an exsiccator. If present, large stones and large pieces of wood were removed. Subsequently each litter sample or a representative amount was coarse sorted by removing woody pieces, roots, pine cones, small stones and mineral soil, and fresh green material like grass. If parts of litter samples contained a large amount of fungal hyphae, these parts were entirely removed from the sample. Sub-samples of the coarse sorted litter samples of approximately ten gram were fine sorted to remove any of the above mentioned materials still remaining in the sub-sample. Mineral soil samples were dried at 35 ^oC for several days, cooled down in an exsiccator, and then sieved to < 2 mm. Before carbon, nitrogen, and $\Delta^{14}C$ analyses all samples were ground in a ball mill.

2.2.4 Density fractionation

Before the density separation most bulk mineral soil samples of all sites except sites Lavarone and Renon were pooled by soil layer. For some sites we expected considerable differences between pits in $\Delta^{14}C$ values for some soil layers, on basis of differences in carbon to nitrogen ratios of corresponding bulk soil samples (personal observations). For these sites we kept all three samples separate or only pooled the samples of two pits (see Appendix A: Tables A1.2 and A1.3). To test the precision of the method, for sites Lavarone and Renon $\Delta^{14}C$ analyses were made in duplicate and without pooling the samples of both pits.

Bulk mineral soil was fractionated by density by suspending 10 to 15 g of the samples in a 1.6 g/cm^3 sodium polytungstate solution (Sometu, Berlin, Germany). The fraction with a density of 1.6 g/cm^3 or less (light SOM fraction) was considered to be organic carbon not associated with the mineral soil particles. The fraction with a density of more than 1.6 g/cm^3 (heavy SOM fraction) was considered to contain organic carbon associated with mineral soil particles (Trumbore and Zheng 1996) either due to occlusion in aggregates or inter-molecular interactions (von Lützow et al. 2006).

Suspended samples were gently horizontally shaken for circa 10 minutes on a shaker platform. No ultra-sonification was applied. The suspension was centrifuged at 3500 revs/minute for 30 minutes, after which the light SOM fraction was decanted. The whole procedure was repeated twice for the fraction with a density higher than 1.6 g/cm^3. Each separation was performed with a fresh sodium polytungstate solution to ensure clean separation. Fractions were washed with de-ionized water to remove all sodium polytungstate solution and freeze dried. Only pre-combusted glass equipment was used. Remaining fine roots in the heavy SOM fraction were removed during an examination of the samples under a binocular. Remaining fine roots were not removed from the light SOM, because they were considered to be part of it.

2.2.5 Chemical analysis

Total carbon and total nitrogen content of samples of the organic horizon, bulk mineral soil, and density fractions were measured in duplicate with a CN-analyzer (varioMax, Elementar, Hauna, Germany). Organic carbon content of bulk mineral soil and heavy SOM fraction was measured in duplicate with a CS-analyzer (CS-500, ELTRA, Neuss, Germany) after removal of lime by an acidification of the samples with a HCl solution of four molar.

Soil acidity was measured in a suspension of bulk mineral soil and de-ionized water with a soil to liquid mass ratio of 1 : 2.5, for all mineral soil layers. The suspensions were mixed in an end-over-end shaker for one hour and then allowed to settle for one hour. This procedure was repeated once and then the settled suspensions were decanted. Soil acidity was determined with a pH measurement of the decanted solution, measured with a standard pH meter with a glass electrode.

2.2.6 $\Delta^{14}C$ analysis

After sample processing and density fractionation, $\Delta^{14}C$ values of the SOM fractions were measured with accelerator mass spectrometry. Samples of the three SOM fractions (litter, light, and heavy SOM) were combusted to CO_2 in an elemental analyzer (NC2500, Carlo Erba Instruments, Milan, Italy) and a small part of the sample mass (< 10%) was analyzed for its stable carbon isotope ratio ($\delta^{13}C$) in an isotope ratio mass spectrometer (Delta Plus, ThermoQuest, Bremen, Germany). The remaining major part of the sample mass was collected in a cryogenic CO_2 trap. The trapped CO_2 was directed to reactors and graphitized by reduction with H_2. Steinhof et al. (2004) described the sample

preparation in detail. The samples were analyzed for $\Delta^{14}C$ either at the Leibniz AMS Laboratory, Kiel, Germany or at the Rafter Radiocarbon Laboratory, Lower Hutt, New Zealand. The expression of ^{14}C content as $\Delta^{14}C$ value was defined by Stuiver and Polach (1977). This expression includes a correction for the mass dependent isotopic fraction to a $\delta^{13}C$ value of -25 ‰ and a correction for radioactive decay of the standard since 1950.

The $\Delta^{14}C$ values of some heavy SOM samples were corrected for presence of a fraction of inorganic carbon (i.e. lime). Due to its high age this inorganic carbon fraction does not contain any ^{14}C. A lime correction was applied if the ratio of organic carbon to total carbon contents was 0.99 or lower for both heavy SOM sample as well as the corresponding bulk soil sample (16 heavy SOM samples in total, see Appendix A: Table A1.3). Assuming that the inorganic carbon fraction did not contain any ^{14}C, lime corrected $\Delta^{14}C$ values were calculated for these 16 samples from their measured $^{14}C/^{12}C$ isotope ratios divided by the fraction organic carbon in the samples.

2.2.7 Modeling SOM turnover times

In the 1960s the atmospheric $^{14}CO_2$ level had nearly doubled as compared to 1950, due to testing of nuclear weapons. After this so-called bomb peak, the atmospheric $^{14}CO_2$ level has been declining, mainly due to uptake of $^{14}CO_2$ into the ocean. As a consequence of the bomb peak, the $\Delta^{14}C$ values of SOM have been changing over time because vegetation has been producing litter with changing $\Delta^{14}C$ values.

We calculated turnover times of litter, light and heavy SOM fractions based on their $\Delta^{14}C$ values. When it is assumed that: (1) annual carbon inputs to SOM pool are constant, and (2) SOM pools are at steady state. Then the change in the $^{14}C/^{12}C$ isotope ratio of a SOM pool (R_{SOM}) over time can be described as (Gaudinski et al. 2000, Bird and Torn 2006):

$$R_{SOM}(t) = k \times R_{atm}(t) + R_{SOM}(t-1) \times (1-k-\lambda) \qquad \text{Equation 2.1}$$

This equation is based on the description of SOM decomposition as a process with first-order kinetics, formulated in a discrete form (i.e. a one year time step). Parameter k is the decomposition rate of SOM and λ is the radioactive decay constant of ^{14}C (0.000121 yr^{-1}). The turnover time τ of SOM is defined as the inverse of the decomposition rate k.

Parameter R_{atm} corresponds to $^{14}C/^{12}C$ isotope ratios of atmospheric CO_2 calculated from atmospheric $\Delta^{14}C$ values.

The $\Delta^{14}C$ values of SOM were modeled accordingly for the period 1900-2000. For each sample a decomposition rate k was calculated by fitting the model to the SOM's measured $\Delta^{14}C$ value. As estimation of the annual atmospheric $\Delta^{14}C$ values at the study sites (Equation 2.1) we used $\Delta^{14}C$ values from a tree-ring record for 1900-1954 (Stuiver et al. 1998), values given by a curve fitted to atmospheric measurements for 1955-1958 (Tans 1981), and values from direct atmospheric measurement for 1959-2000 (Levin and Kromer 2004). Due to the increase and followed decline of the atmospheric $\Delta^{14}C$ values (the bomb peak) for some $\Delta^{14}C$ values there were two possible model fits, and thus turnover times (see Results). Wang and Hsieh (2002) and Bruun et al. (2005) have reviewed the use of the bomb peak and other ^{14}C-based methods to estimate turnover times of SOM.

Since all samples were taken before the annual peak in litterfall in autumn, the modeled $\Delta^{14}C$ values of SOM were fitted to the measured $\Delta^{14}C$ values in the year 2000. For the samples of the litter layers, the input of ^{14}C from the atmosphere was lagged by taking into account leaf and needle longevity of the dominant tree species at site. Based on dominant tree species, the abundance of deciduous understory, and needle life spans at the sites (personal observations), following lag phases were estimated: zero year for sites Casteller, Lagolo B, Brigolina B, and Bondone (deciduous sites), two years for sites Toblino and Mattarello, three years for site Lagolo P, four years for site Brigolina S, five years for sites Vaneze and Lavarone. Site Renon had a patchy vegetation and different lag phases were assigned to the litter from the two soil pits. Litter samples from a plot with a leaf area index of four were assigned a lag phase of six years, whereas litter samples from a plot with a leaf area index of two were assigned a lag phase of four years, because the abundance of understory was presumed to be higher at the latter. No lag phase was applied for estimation of the turnover times of light and heavy SOM. Instead modeled $\Delta^{14}C$ values for an intermediate carbon pool with a turnover time of five years were used as input to the light and heavy SOM fraction. In this way a rough general correction was made for residence of ^{14}C in aboveground litter and living roots before entering the light or heavy SOM fractions.

For some sites more than one $\Delta^{14}C$ analysis per SOM fraction was made for certain soil layers. Where this was the case, a weighted average turnover time was calculated for each SOM fraction from the turnover times modeled for each $\Delta^{14}C$ value.

The number of pits that a $\Delta^{14}C$ value represented was the weight assigned to a modeled turnover time (see Appendix A: Tables A1.2 and A1.3). For sites were the H layer had been sampled separately from the F layer (Brigolina S, Vaneze, Lavarone, and Renon), the turnover time for the F+H layers was modeled from the weighted average $\Delta^{14}C$ value of the F and H layers. The carbon stocks of the F layer and H layer were used as the weights of their $\Delta^{14}C$ values.

2.2.8 Correlations

Pearson coefficients were calculated to determine whether a relationship between turnover times of the SOM fractions and mean annual soil temperatures was present. Because the turnover times of SOM fractions significantly increased with depth of the soil layer (see Results), a normalization of the turnover times was applied to remove the depth related differences. For a turnover time *TT* from SOM fraction f in litter or mineral soil layer *l*, the normalized turnover time TT_{norm} was:

$$TT_{norm} = \frac{TT - TT_{fl,avg}}{sd_{fl}} \qquad \text{Equation 2.2}$$

In which $TT_{fl,avg}$ and sd_{fl} are the average turnover time of SOM fraction *f* in soil layer *l* of all the sites and its standard deviation, respectively.

The correlations between the normalized turnover times and a number of possible confounding factors to which SOM turnover can be related were also calculated. And in addition the correlations between mean annual soil temperatures and the confounding factors were calculated. These confounding factors can affect microbial activity, are indicators of SOM quality, or can stabilize SOM (Lavelle and Spain 2001, Chapin et al. 2002). The confounding factors included were: (1) nitrogen content of the SOM fractions, (2) carbon to nitrogen ratio of the SOM fractions, (3) soil acidity, (4) annual precipitation, (5) average relative soil water content in summer months of 2001, and (6) an estimated clay content of the soil layers. The factors (1) to (3) were determined in this study. Factor (4) was taken from Rodeghiero and Cescatti (2005). Factor (5) was calculated from the measurements of Rodeghiero and Cescatti (2005). Factor (6) was the clay content of a sites' pedogenetic soil horizon as presented in Rodeghiero (2003), if the soil layer was completely within the horizon's upper and lower borders. If the soil layer

was crossing the border between two soil horizons, a weighted average clay content of the two pedogenetic soil horizons was calculated. The values for factors (3), (5), and (6) are given in Appendices B and C.

2.2.9 Temperature sensitivity functions

The turnover times of light and heavy SOM fractions, which showed significant correlation with temperatures (see Results), were analyzed in more detail using three commonly used functions. These were: the van 't Hoff, Arrhenius, and Lloyd and Taylor functions (see Davidson et al. 2006). The van 't Hoff function describes a constant temperature sensitivity of SOM turnover. The other two functions describe decreasing temperature sensitivities with increasing temperature.

The temperature sensitivity functions were fitted to the SOM turnover times using nonlinear regression. Analysis of variance (ANOVA) was applied to fitted regression models to determine if turnover times of different SOM fractions had significantly different temperature sensitivities. The reference values in the functions (corresponding to the α's in Davidson et al. (2006)) were used as fitting parameters for which a separate value was determined for each different combination of soil layer and SOM fractions. Parameters T_0 and E_0 in the Lloyd-Taylor function were correlated (i.e. changes in T_0 are compensated by changes in E_0 and vice versa) and T_0 was therefore fixed to a value of 227.13 K as determined by Lloyd and Taylor (1994). We presumed that a constant relative error in the SOM turnover times was more likely than a constant absolute error. Therefore log-transformed temperature sensitivity functions were fitted to log-transformed SOM turnover times. Transforming back to normal scale, the error term of the regression model becomes multiplicative (Draper and Smith 1998). This means that on the normal scale the errors were proportional to the fitted values and thus corresponded to relative errors. The log-transformation avoided a bias of the regression towards the higher SOM turnover times which would have been the case when absolute errors had been minimized.

To address the possible confounding effects of soil acidity and clay content on the temperature sensitivity (see Results), the regression and ANOVA were repeated with temperature sensitivity functions that accounted for effects of soil acidity and clay content on turnover times. The approach was analogue, for example, to that used by Reichstein et al. (2003) and Reth et al. (2005). The soil acidity function presented in the latter study was applied here. The parameter corresponding with the pH value optimal

for SOM turnover (*phOpt*) was set to a value of 7. The parameter representing the sensitivity of SOM turnover to deviation from the optimal pH value (*phSens*) was used as a fitting parameter and initially allowed to have different values for each SOM fraction. These values were however not significantly different and thus the *phSens* parameter was fitted having a single value. For the effect of clay content on the turnover of the heavy SOM fraction we used the clay function determined by Müller and Höper (2004) for wet, mild, mid-latitude climates. The clay function describes a nonlinear increase in turnover times with the clay content increasing from 0 to 25 %. Above a clay content of 25 % the effect of clay on turnover times remains constant. For the light SOM fraction, which is not associated with mineral soil particles, the clay function was set to a value of 1. In all the publications cited above, functions describe effects of temperature, soil acidity, or clay content on soil respiration. The functions can be rewritten for turnover times because their respiration terms can be considered as relative turnover rates (with unit 1/year) which are equal to the inverse of turnover times. Statistical analyses were done with the software package R 2.2.0 (R Development Core Team 2008) and its the additional packages Hmisc (Harrell et al. 2005) and nlme (Pinheiro et al. 2005).

2. 3 Results

2.3.1 Turnover times

Litter. — The $\Delta^{14}C$ values of all litter layers corresponded to two possible turnover times (hereafter referred to as short and long turnover time). We choose for the short turnover times as the more plausible ones because at ten study sites the annual aboveground litter input estimated with the short turnover times (i.e. the ratios of litter carbon stocks and short turnover times) were closer to the measured annual litterfall than the estimates with the long turnover times. The estimates with short turnover times corresponded to 49 to 142% of the measured annual litterfall (Rodeghiero and Cescatti 2005) whereas the estimates with long turnover times corresponded to 2 to 33% of the measured annual litterfall. At site Renon, the annual aboveground litter input estimated with the short turnover times was a factor 2.2 higher than the measured litterfall. Nevertheless we also choose for the short turnover times for this site because the long turnover times were unrealistically high and decreased with increasing stage of decomposition (67.8 and 44.5 years for the L and F+H layers, respectively). For the sites Lavarone and Renon for which $\Delta^{14}C$ analyses were made in duplicate, the maximum coefficient of variation for

turnover times of the litter SOM fraction was 57% (n = 4, see Appendix A: Table A1.1). The litter layers L and F+H had turnover times of several years, with a maximum of 15 years (Figure 2.1). The turnover time of the F+H layers was always longer than the turnover time of the corresponding L layer. Mean turnover times and their standard deviation (in parenthesis) of the L and F+H layers were 2.9 (1.1) and 7.5 (2.8) years, respectively. For the $\Delta^{14}C$ value of the L layer of site Mattarello no reasonable turnover time was found because it was lower than the $\Delta^{14}C$ value of the model input for the year of the measurement (two years lagged atmospheric $\Delta^{14}C$ value).

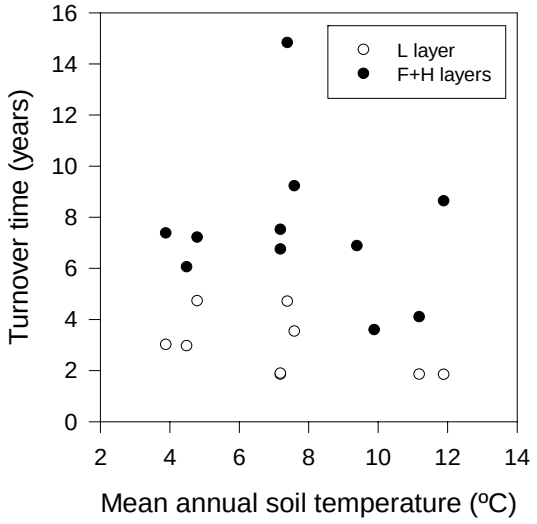

Figure 2.1. Turnover-times of fresh (L) and fermented and humified (F+H) litter layers at 11 forest sites in the southern Italian Alps based on their $\Delta^{14}C$ values plotted against sites' mean annual soil temperatures.

Light fraction. — The $\Delta^{14}C$ values of the light SOM fraction that were higher than 111 ‰ (63 % of the samples), corresponded to a short and a long turnover time. The long turnover times were chosen as the more plausible ones because the short turnover times (ranging between 1.1 and 13.1 years) seemed unrealistic given the following three considerations. First, the annual carbon inputs to the soil layers estimated with the short turnover times suggested belowground inputs that increased with soil depth. Second, in many cases this estimated annual carbon input was higher than the fine root biomass (diameter <2 mm) measured for ten of the sites in a later study (personal observations). Third, for soil layers with only a long turnover time for the light SOM fraction (samples with $\Delta^{14}C$ values < 111 ‰) choice of the short turnover time for its upper soil layer would have suggested a strong increase in light SOM turnover times (seven to 95 fold)

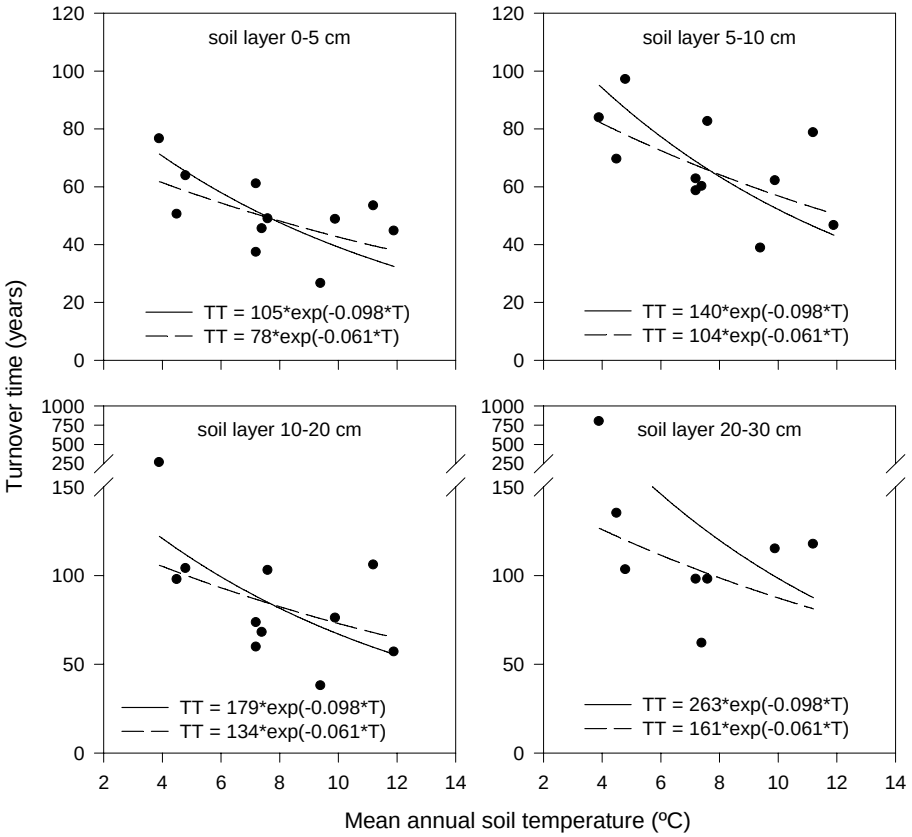

Figure 2.2 Turnover times (TT) of the light SOM fractions in four soil layers at 11 forest sites in the southern Italian Alps based on their $\Delta^{14}C$ values plotted against sites' mean annual soil temperatures (T). Lines represent the standard van 't Hoff temperature sensitivity functions as determined for each soil layer. Solid lines were determined using all turnover times of light and heavy SOM fractions (n = 82). Dashed lines were determined with two highly influential observations excluded. Results with the Arrhenius and Lloyd and Taylor temperature sensitivity functions differed only marginally from the results presented in this figure. Note the break in vertical axes of the two bottom panels.

within five to ten centimeters of soil depth. For the sites Lavarone and Renon for which $\Delta^{14}C$ analyses were made in duplicate, the maximum coefficient of variation for the long turnover times of the light SOM fraction was 100% (n = 4, see Appendix A: Table A1.2).

The turnover times of light fraction SOM ranged between 27 and 135 years, except for the two lowest soil layers at site Renon (Figure 2.2). Overall, the turnover times of light SOM fraction showed a tendency to increase with soil layer depth, although not to the same degree at every site. Average turnover times of the light SOM fraction and their standard errors (in parenthesis) were: 51 (13), 67 (16), 95 (58), and 191 (230) years for soil layers 0-5 cm, 5-10 cm, 10-20 cm, and 20-30 cm, respectively. For the coldest site (Renon) the light SOM fraction of soil layers 10-20 cm and 20-30 cm had turnover times and standard deviations (in parenthesis) of 264 (173) and 797 (800) years, respectively. The high standard errors of these turnover times were due to large

differences in $\Delta^{14}C$ values between samples of one soil layer. The model could not be fitted to the measured $\Delta^{14}C$ values of one of the light SOM samples from site Toblino representing soil layer 10-20 cm and to one of the duplicate measurements on the light fraction SOM samples from site Renon representing soil layer 10-20 cm. The measured $\Delta^{14}C$ values of these samples were equal to the atmospheric $\Delta^{14}C$ values of the early 1980s (220 to 235 ‰)

Heavy fraction. — Turnover times of the heavy SOM fraction ranged between 40 and 861 years, except for the soil layer 20-30 cm of site Renon (Figure 2.3). At all sites there was an increase in turnover times with an increase of soil layer depth. Average turnover times of the heavy fraction SOM and their standard deviations (in parenthesis) were: 100 (38), 166 (95), 319 (212), and 687 (446) years for soil layers 0-5 cm, 5-10 cm, 10-20 cm, and 20-30 cm, respectively. At site Toblino turnover times of the heavy fraction SOM increased from 85 years in soil layer 0-5 cm to more than 300 years in soil layers 5-10 and 10-20 cm. For site Renon the heavy SOM fraction of soil layer 20-30 cm had a turnover

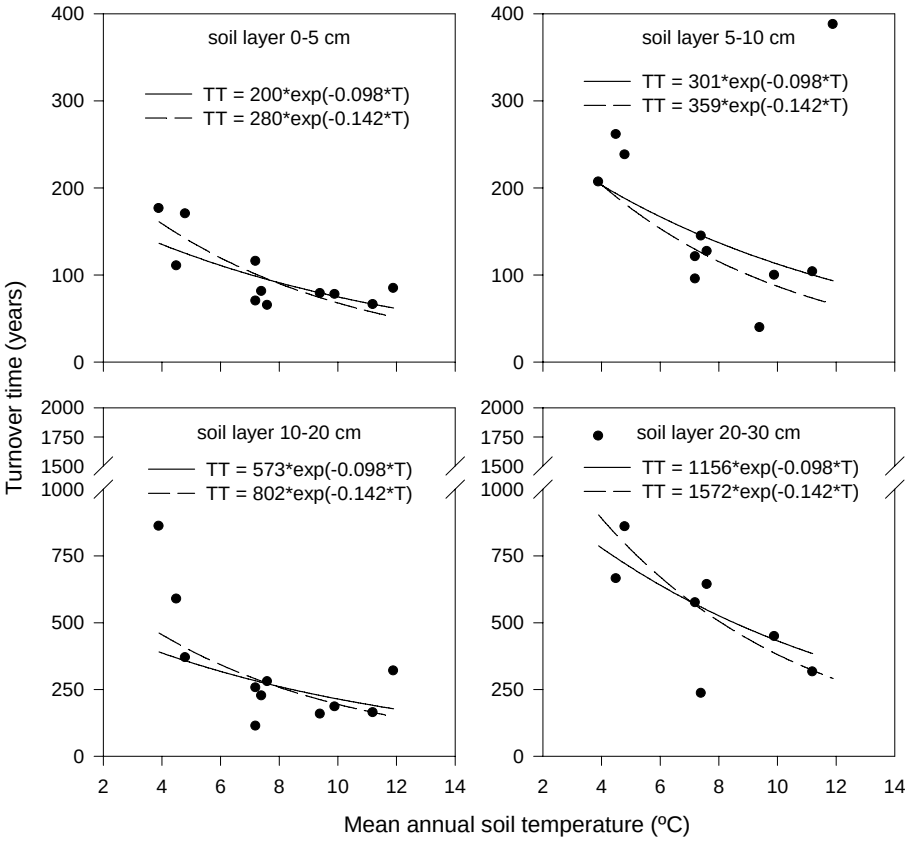

Figure 2.3. Turnover times (TT) of the heavy SOM fractions in four soil layers at 11 forest sites in the southern Italian Alps based on their $\Delta^{14}C$ values plotted against sites' mean annual soil tempertures (T). Format and explanations are as in Figure 2.2.

time of nearly 1800 years, almost twice as high as the second highest turnover time of the heavy fraction SOM. For the sites Lavarone and Renon for which $\Delta^{14}C$ analyses were made in duplicate, the maximum coefficient of variation for turnover times of the heavy SOM fraction was 74% (n = 4, see Appendix A: Table A1.3).

The $\Delta^{14}C$ values of the heavy SOM fraction that were higher than 111 ‰ (16 % of the samples), corresponded to a short and a long turnover time. The long turnover times were chosen as the more plausible ones, for the same reasons as for the light fraction SOM (see above). The model could not be fitted to the $\Delta^{14}C$ values of the heavy SOM fractions of soil layers 0-5 and 5-10 cm of one of the pits from site Brigolina S. The $\Delta^{14}C$ values of these samples (300 and 325 ‰) were equal to that of the atmosphere in the late 1970s.

2.3.2 Correlations

Normalized turnover times of the light and heavy SOM fractions were correlated with mean annual soil temperatures, whereas normalized turnover times of the litter SOM fraction were not (Table 2.2). Soil acidity was correlated with the normalized turnover times of all three SOM fractions as well as with mean annual soil temperatures. Soil water content in summer was correlated with the normalized turnover times of light and heavy SOM fractions (for both n = 41), but not correlated with mean annual soil temperatures (n = 11). Estimated clay content was correlated with normalized turnover times of the heavy SOM fraction as well as with mean annual soil temperatures (Table 2.2).

2.3.3 Temperature sensitivity

The temperature sensitivities of the turnover times of light and heavy SOM fractions were highly significant with all three functions ($P < 0.001$, ANOVA), both with the standard temperature sensitivity functions as well as with functions that accounted for effects of soil acidity and clay content. None of the functions showed significant differences in temperature sensitivity of light and heavy SOM fractions. Temperature sensitivity functions that accounted for effects of soil acidity and clay content did not explain a higher fraction of the variance than the standard functions did (R^2 between 0.75 and 0.77, Table 2.3). Effects of soil acidity and clay content were added to the temperature sensitivity functions because correlations coefficients (see Table 2.2) suggested that: (1) the temperature sensitivity of the turnover times of light and heavy

Table 2.2. Pearson correlation coefficients (r) calculated for the turnover times of three SOM fractions and mean annual soil temperature as well as some confounding factors. The turnover times were normalized to remove the effect of layer depth (see Equation 2.2). Also shown are the r's for mean annual soil temperature and some confounding factors.

	Litter SOM		Light SOM		Heavy SOM	
	TTnorm	Tsoil	TTnorm	Tsoil	TTnorm	Tsoil
Normalized SOM turnover time (TTnorm)		-0.32		-0.54***		-0.54***
Mean annual soil temperature (Tsoil)	-0.32		-0.54***		-0.54***	
Annual precipitation	-0.03	-0.57	0.06	-0.57	0.02	-0.57
Nitrogen content of SOM fraction	-0.41	0.31	-0.08	0.38*	0.00	-0.02
Carbon-to-Nitrogen ratio of SOM fraction	0.24	-0.20	0.20	-0.36*	0.17	-0.49**
Soil acidity (pH in water-soil suspension)‖	-0.49*	0.63*§	-0.37*	0.54***	-0.52***	0.54***
Clay content	†	†	†	†	-0.52***	0.46**
Site's soil water content in summer	-0.13	-0.43	0.70***	-0.43	0.51***	-0.43
n	20	11 or 20‡	41	11 or 41‡	41	11 or 41‡

* = P < 0.05, ** = P < 0.01, *** = P < 0.001.
‖ For the litter SOM fraction pH of soil layer 0-5 cm was used.
‡ The number observations (n) corresponds to the higher number, except for correlations between two site characteristic.
§ n = 11
† Not relevant

SOM fractions may have been partly resulting from the more acidic soils occurring at the colder sites which additionally slowed down SOM decomposition at these sites and (2) a stronger temperature sensitivity of the turnover times of heavy SOM fraction may have been masked by the higher clay content of soils occurring at the warmer sites which slowed down decomposition of heavy fraction SOM at these sites. With the standard functions, the parameter values corresponding to the temperature sensitivities had values for which a one degree increase in temperature resulted in a 9 to 11% decrease in turnover time. With functions that accounted for the effects of soil acidity and clay content, the parameter values corresponding to the temperature sensitivity were slightly lower (Table 2.3), and with these parameter values a one degree increase in temperature resulted in an 8 to 10% decrease in turnover time. A previous analysis in which the standard temperature sensitivity functions were fitted using linear regression had shown that two turnover times had an exceptionally high influence on the outcome of the linear regression i.e. they had Cook's statistics (Draper and Smith 1998) that were at

least a factor 12 higher than the average Cook's statistic (results not shown). The highly influential turnover times corresponded to the light SOM fraction of soil layer 20-30 cm from site Renon (see Figure 2.2, bottom right panel, T = 3.9 ^{o}C) and the heavy SOM fraction of soil layer 5-10 cm from site Toblino (see Figure 2.3, top right panel, T = 11.9 ^{o}C). The analysis of the temperature sensitivity was repeated with these two turnover times excluded from the data. After removing the two highly influential turnover times from the data, the light SOM fraction had a significantly lower temperature sensitivity than the heavy SOM fraction with all three functions, both with the standard temperature sensitivity functions ($P \leq 0.013$, ANOVA) as well as with the temperature sensitivity functions that accounted for effects of soil acidity and clay content ($P \leq 0.003$, ANOVA). After excluding the two turnover times from the data, the fraction of variance

Table 2.3. Parameter values and explained variance (R^2) of three temperature sensitivity functions. The values without brackets were obtained with the standard temperature sensitivity functions. The values in brackets were obtained with temperature sensitivity functions that accounted for effects of soil acidity and clay content.

Temperature sensitivity function	Parameter values and explained variance				
	Using all data		Two observation excluded		
	Light and heavy SOM	R^2	Light SOM	Heavy SOM	R^2
van 't Hoff	0.098	0.77	0.061	0.142	0.85
[β]	(0.087)	(0.75)	(0.045)	(0.149)	(0.83)
Arrhenius	65037	0.77	40223	93427	0.85
[E_a]	(57517)	(0.75)	(30283)	(98514)	(0.83)
Lloyd and Taylor	294.7	0.77	182.1	417.4	0.85
[E_0]	(267.9)	(0.76)	(143.2)	(446.3)	(0.84)

explained by the temperature sensitivity functions became slightly higher (R^2 between 0.83 and 0.85, Table 2.3) but as before the temperature sensitivity functions that accounted for effects of soil acidity and clay content did not explain a higher fraction of the variance than the standard functions did. With the standard functions, the parameter values corresponding to the temperature sensitivity of the light SOM fraction had values for which a one degree increase in temperature resulted in a 5 to 7% decrease in turnover time. With functions that accounted for the effects of soil acidity and clay content, the parameter values corresponding to the temperature sensitivity of the light SOM fraction became slightly lower and with these parameter values a one degree increase in temperature resulted in a 4 to 6% decrease in turnover time. With the standard functions, the parameter values corresponding to the temperature sensitivity of the heavy SOM fraction had values for which a one degree increase in temperature resulted in a 12 to 15% decrease in turnover time. With temperature sensitivity functions that accounted for the effects of soil acidity and clay content, the parameter values

corresponding to the temperature sensitivity of the heavy SOM fraction became slightly higher, and with these parameter values a one degree increase in temperature resulted in a 13 to 16% decrease in turnover time.

2.4 Discussion

2.4.1 Turnover times

The observed increase in turnover times in the order of litter, light, and heavy SOM fractions suggested that the SOM's decomposition stage progressed in the same sequence. The longer turnover times of the light SOM fraction in comparison to the litter SOM fraction however may also have been influenced by: (1) a lower decomposability of root litter than aboveground litter, (2) less favorable conditions for decomposition in the mineral soil, or (3) residence of carbon in living roots considerably longer than the five years that we assumed. A considerable heterogeneity could have existed within SOM fractions of one site, as indicated by the high maximum coefficients of variation for mean turnover times corresponding to replicate $\Delta^{14}C$ analyses. Although one can argue whether two or three soil pits were sufficient to represent average turnover times, the high cost of the $\Delta^{14}C$ analyses limited the number of samples that could be analyzed.

The turnover times presented here were calculated assuming a constant level of annual carbon inputs to the SOM pools (i.e. constant aboveground litter and root litter inputs) and assuming a steady state of each SOM pool. Random variations in the carbon input levels may have occurred at our sites due to interannual variability in forest productivity. Moreover, shifts in the average annual carbon input level at our sites may have been caused by changes in forest management, increasing atmospheric CO_2 concentration, and atmospheric nitrogen deposition (Hyvönen et al. 2007). Land use changes around the time of the bomb peak cannot be excluded, given the mean tree age at some study sites (~ 50 years at sites Casteller, Toblino, Mattarello, and Brigolina B). The absence of a documented site history however hampered formulations of relevant non-constant input scenarios. Turnover times estimated with random variations in the mean annual carbon input differ only marginally from turnover times estimated with constant annual carbon inputs (Hsieh 1993). Turnover times estimated with a shift in the annual carbon input level however, can differ considerably from those estimated with an unchanged annual carbon input level. Thus the possibility of a shift in the annual carbon input level is a source of uncertainty. The larger the shift in the annual carbon input level the larger the difference between the different estimated turnover times will

be. Also the possibility of a systematic offset from the prescribed atmospheric $\Delta^{14}C$ values should be considered as a source of uncertainty. For SOM samples taken around 2000, in particular the relatively short estimated turnover times (roughly up to 100 years) are sensitive to such uncertainties (Bruun et al. 2005, S. Bruun, *personal communication*).

We assumed steady state of the SOM pools and modeled their decomposition based on first-order kinetics. Assuming steady state when in fact a soil is accumulating carbon can lead to an underestimation of turnover times. The range of $\Delta^{14}C$ values for which the difference between modeled turnover time at steady and at accumulation state is significant, depends on the starting point of the carbon accumulation. The earlier the starting point of SOM accumulation, the smaller the underestimation of the turnover time for a given $\Delta^{14}C$ value will be (Gaudinski et al. 2000). A conceptual SOM pool with first-order kinetics and constant annual carbon input level reaches 95 % of its steady state size after roughly three times its turnover time. Thus, the longer the estimated turnover time of a SOM pool the more likely it has not been accumulating carbon long enough to have reached steady state. Although mean tree ages at our study sites indicated that some forests were relatively young, we presume the soils were covered by vegetation and thus accumulating carbon long before establishment of the present forest. If carbon accumulation started after the last glaciation (i.e. roughly 10000 years ago) and only random variations in annual carbon inputs have occurred, sufficient time has passed for SOM pools to have reached their steady state size, given the maximum observed turnover time of almost 2000 years.

2.4.2 Temperature sensitivity

The turnover times of the litter SOM estimated in this study did not show a temperature sensitivity. Several studies however have shown a temperature sensitivity of the decomposition of litter SOM (Hanson et al. 2003, Reichstein et al. 2005b, Pare et al. 2006). The results found here for the litter SOM may have been influenced by uncertainties in the estimated turnover times, the occurrence of summer drought at some sites, differences in litter quality between sites associated with the many different dominating tree species, and the relatively small temperature range (from 4 to 12°C). The turnover times of the light as well as the heavy SOM fraction were found to be temperature sensitive. We did not find an indication that temperature sensitivities decreased with increasing temperature, because the van 't Hoff function fitted the data equally well as

the Arrhenius and Lloyd-Taylor functions. This result may be related to confounding effects of summer drought or the relatively small temperature range. Two other studies have used $\Delta^{14}C$ analyses to investigate the temperature sensitivity of SOM turnover. Townsend et al. (1995) observed a twofold change in the turnover times of an intermediate SOM pool which was within the range that we observed for the light SOM fraction. Trumbore et al. (1996) found a higher temperature sensitivity of a light SOM fraction than we did. They found no clear temperature sensitivity of the hydrolyzable part of the heavy SOM fraction, a result which seemed to be opposite to our findings.

In gradient studies many potentially influential factors can be correlated with each other and so complicate interpretation of results (Garten et al. 1999, Garten 2004). Therefore the temperature sensitivities found in this study need to be interpreted as apparent ones and not as the intrinsic temperature sensitivities (Davidson and Janssens 2006). Inverse correlations between soil water content and soil temperatures, which can have a confounding effect on temperature sensitivities, occur in several ecosystem types (Davidson et al. 2006). The positive correlation between summer soil water content and turnover times that was present here indicated that sites with lower turnover times, and thus higher mean annual soil temperatures, tended to have lower soil water contents during summer. This suggested the confounding effect of soil water content on the temperature sensitivity was probably also present in this study. In particular at the warmer sites, SOM turnover might have been limited by occasional drought. For some of the warmer sites (Casteller, Toblino, Mattarello, and Lagolo P) occurrence of (moderate) drought has been reported by Rodeghiero and Cescatti (2005). Given their correlation with temperature, soil acidity and clay content had confounding effects here on the temperature sensitivities. Unlike for soil water content, these confounding effects by soil acidity and clay content evidently do not have a general character. Therefore we also estimated temperature sensitivities with functions that accounted for the effects of soil acidity and clay content. These temperature sensitivities differed only slightly from those derived with the standard functions, suggesting that the confounding effects of soil acidity and clay content were limited.

Presence of two highly influential turnover times complicated the interpretation of our results. There were no indications for errors made on the measurements that corresponded to the two highly influential turnover times. From a statistical point of view however it is undesirable for single observations to have an exceptionally high influence, therefore repeating the regressions without the two highly influential

turnover times seemed appropriate. The equal temperature sensitivities of light and heavy SOM fractions that we found using all turnover times would be in agreement with results found in incubation experiments in which temperature sensitivities of two SOM fractions of different stabilities were compared (Fang et al. 2005, Reichstein et al. 2005b, Conen et al. 2006). In each of these incubation experiments a different technique was used to separate the different SOM fractions from each other. Thus the different labile SOM fractions in these experiments and also the one used in our study are not the same, and similarly this is the case for the stabilized SOM fractions. The higher temperature sensitivity of the heavy SOM fraction found after excluding two highly influential turnover times (of in total 82 turnover times) however agrees with theoretical work. Davidson and Janssens (2006) predicted that the temperature sensitivity of the reaction kinetics of SOM decomposition increases with increasing degree of SOM stability. Knorr et al. (2005) modeled SOM decomposition as observed in incubation experiment and also found that the temperature sensitivity increased with increasing stability of the conceptual SOM pools. The evidence presented in the latter study however was found to be rather weak (Reichstein et al. 2005a, Fang et al. 2006).

2.5 Conclusion

In our study the temperature sensitivities of intermediate and stabilized SOM fractions were estimated. The temperature sensitivity of a third labile SOM fraction could not be detected, which was related to limitations of the applied methodology. No evidence was found for decreasing temperature sensitivities of the turnover times of the intermediate and stabilized SOM fractions with increasing mean annual soil temperature.

With respect to climate change, our results suggested: (1) Largest absolute changes in the turnover times of intermediate and stabilized SOM fractions can be expected in areas with low mean annual soil temperatures. (2) A relative change in turnover times of the stabilized SOM fraction that can be as large as the relative change in turnover times of the intermediate SOM fraction and might be even larger. (3) A constant relative change in turnover times of intermediate and stabilized SOM fractions in the observed temperature range.

Two aspects may have influenced the results as observed here for the three SOM fractions and should be considered more thoroughly in future studies. First, SOM turnover times may considerably differ from our estimates if modeling assumptions, of leaf and needle longevities, annual carbon inputs, and steady-state SOM pools, were not

met. In particular if large shifts in the annual carbon input levels have taken place in the last 100 years. The advantages of modeling $\Delta^{14}C$ values of SOM can be optimally utilized in unmanaged forest or forests with a documented site history from which shifts in mean annual carbon input levels can be estimated. Second, environmental controls other than temperature may play an important role. A confounding effect of litter and soil water content on temperature sensitivities of SOM turnover is well known. Long-term measurements of litter and soil water content together with parameters from which one can infer turnover times might show to what extent SOM turnover is influenced by water content. In our study, soil acidity and clay content caused a confounding effect on the temperature sensitivities. Although their effects seemed to be limited, it nevertheless illustrates the importance of measuring potentially confounding factors and including functions that account for their effects on SOM turnover. Furthermore differences in quality of SOM that were not reflected by the nitrogen contents and the carbon to nitrogen ratios of the SOM may have been present at our sites. Insight in the effects of differences in SOM quality on turnover times may be obtained by the use of other indicators of SOM quality (e.g. soil microbial biomass or enzyme concentrations) and the use of additional fractionation techniques

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Appendix A

Tables A1.1 to A1.3

Three tables listing $\Delta^{14}C$ values and corresponding estimated turnover times of litter, light, and heavy SOM fractions.

Table A2

A table listing the pH values and estimated clay contents of the sites' soil layers.

Table A3

A table listing the estimated relative soil water content of the sites in summer.

3. Partitioning of annual soil respiration for forest ecosystems

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Abstract

Total soil respiration consists of respiration from roots, from root-associated organisms, and microbial respiration from soil organic matter (SOM) decomposition. Here we estimated SOM-derived soil respiration of 11 forest sites using previously published turnover times based on carbon-14 isotope values of SOM. The fraction of soil respiration derived from recently fixed carbon, including root respiration, was calculated by subtracting the SOM-derived component from total soil respiration. Our results suggest that on average total soil respiration was composed of following components: ~ 30 % from decomposition of litter layers; less than 10 % from belowground SOM; and the remaining ~ 60 % from the activity of roots, root-associated organisms, and the decomposition of plant litter that decomposes in less than one year. Our estimate of SOM-derived soil respiration was rather low compared with: (i) the sites' SOM-derived soil respiration presented in an earlier study using a regression of soil respiration, soil carbon stock, and root biomass data; and (ii) results from a meta-analysis of soil respiration data. Carbon-14 isotope analyses of SOM seem to be most suitable to estimate the respiration from homogenous SOM pools with carbon stocks that fluctuate little over the year.

Keywords: soil respiration partitioning; carbon-14 isotope; soil organic matter fractions; forest ecosystems

3.1 Introduction

Soil respiration releases carbon fixed by terrestrial ecosystems during photosynthesis back into the atmosphere. The total flux of soil respiration originates from different sources, which are living roots, mycorrhizal fungi, and microorganisms that decompose plant litter, rhizodeposits, and soil organic matter (SOM). Changes in rates of soil respiration, potentially could change the carbon balance of terrestrial ecosystems and thus act as a feedback mechanism to climate change (Trumbore 2006). Root and root-associated respiration are strongly linked with photosynthetic activity, whereas respiration resulting from the decomposition of SOM depends on the amount of SOM, its quality, and on the microbial activity in litter and mineral soil.

Given these different dependencies, it can be expected that the respiration derived from different carbon pools show different responses to changes in environmental conditions. For example, different responses of soil respiration components to changes in temperature and soil water potential have been observed (Rey et al. 2002, Lee et al. 2003, Lavigne et al. 2004, Heinemeyer et al. 2007, Moyano et al. 2007). Because of these different responses to changes in environmental conditions, partitioning of total soil respiration into contributions derived from one or more of the individual sources is important, and several methods have been developed for it (Baggs 2006, Kuzyakov 2006).

A common approach is to separate total soil respiration into SOM-derived soil respiration and root-derived soil respiration (the latter including root-associated respiration) (Bond-Lamberty et al. 2004, Subke et al. 2006). SOM-derived and root-derived respiration are also referred to as heterotrophic and autotrophic soil respiration, respectively. Although the approach above lumps together components produced by different sources, it is useful because it separates soil respiration into components resulting from two distinct processes. The respiration of recently fixed carbon depends strongly on photosynthetic activity. Whereas the respiration from SOM decomposition depends predominately on the activity of soil microorganisms (Högberg et al. 2006).

Carbon-14 isotope ($\Delta^{14}C$) analyses of litter and belowground SOM pools have been used to partition total soil respiration (Gaudinski et al. 2000). However $\Delta^{14}C$-based partitioning of soil respiration has not been applied as frequent as other partitioning

methods (Kuzyakov 2006, see Subke et al. 2006). After conversion of the $\Delta^{14}C$ values to turnover times with a model, soil respiration from SOM pools can be calculated as the ratio of their carbon stocks and turnover times. The use of $\Delta^{14}C$ analyses of SOM has some advantages: the method does not require disturbance or manipulation of the ecosystem, and the $\Delta^{14}C$ values reflect the long-term effect of litter accumulation and decomposition. The $\Delta^{14}C$-based estimates of SOM-derived respiration obtained in this way differ from other estimates of SOM-derived respiration in that the former does not include respiration from plant litter that is respired in less than one year after it has entered the litter or mineral soil. Litter decomposition rates estimated in litterbag studies (Silver and Miya 2001, Valachovic et al. 2004) suggests that between 20 and 80% of fresh litter can be lost within the first year of decomposition.

The aims of this study were (i) to determine decomposition and respiration fluxes from different SOM fractions based on carbon stocks and previously published $\Delta^{14}C$-based turnover times of the fractions; (ii) to use these SOM-derived respiration fluxes to partition previously published total soil respiration of the sites, and (iii) to discuss and evaluated this methodology.

3.2 Methods

3.2.1 Sites and Data

The study uses 11 forest sites in northern Italy located along an elevation gradient from 220 to 1740 meters. Seven sites are dominated by an evergreen tree species the remaining four sites by a deciduous species (see Table 2.1). Soil respiration at the sites was investigated in previous studies. Rodeghiero and Cescatti (2005) determined the sites total annual soil respiration based on soil respiration measurements (every 15 to 20 days during two years) and soil temperature frequency distributions (recorded every ten minutes). Total annual soil respiration at the sites ranged from 473 to 1079 $gC/m^2/yr$ (see Table 3.1 for all values). At the seven evergreen sites total annual soil respiration has been partitioned into root-derived (also referred to as autotrophic) and SOM-derived (also referred to as heterotrophic) respiration using regressions of soil respiration data against root biomass and soil carbon stocks (Rodeghiero and Cescatti 2006). Root-derived respiration was found to range between 16 to 58% of the total annual soil respiration (Table 3.1).

Table 3.1. Litterfall, total soil respiration, and partitioning of total soil respiration (only evergreen sites) as determined in previous studies.

Site (abbreviation	Litterfall (gC/ m2/ yr)	Total annual soil respiration† (gC/ m^2/ yr)	Estimated fraction of autotrophic soil respiration§ (%)
Casteller (CaH)	214 (26)	901	
Toblino (ToO)	515 (72)	1079	50.6
Mattarello (MaP)	328 (24)	670	16.3
Lagolo P (LaP)	188 (6)	647	39.9
Lagolo B (LaB)	233 (25)	594	
Brigolina B (BrB)	257 (31)	473	
Brigolina S (BrS)	275 (21)	575	52.4
Vaneze (VaS)	147 (17)	643	26.0
Lavarone (LaF)	254 (12)	772	46.5
Bondone (BoB)	177 (6)	829	
Renon (ReS)	115 (12)	1014	58.2

† (Rodeghiero and Cescatti 2005)
§ (Rodeghiero and Cescatti 2006)

3.2.2 Soil sampling and sample preparation

Litter layer samples were separated into fresh (L) and fermented plus humified (F+H) litter. The mineral soil was sampled in depth increments of 0-5, 5-10, 10-20, and 20-30 cm below the mineral soil surface. Litter samples were meticulously sorted in preparation for $\Delta^{14}C$ analysis. During coarse and fine sorting material other than those originating from leaves and needles, e.g. roots, twigs, and small pieces of wood, was removed. When samples were large, coarse sorting was done on a representative subsample. Fine sorting was always done on subsample of ~ 10 g. The fractions of mass removed from litter subsamples during coarse and fine sorting were used to calculate the minimum litter mass of the original sample. Using a separation of the soil sample in a heavy liquid (Trumbore and Zheng 1996), SOM in the mineral soil was separated into belowground litter (the so-called light fraction; organic matter not attached to the mineral soil) and stabilized SOM (the so-called heavy fraction; organic matter associated with the mineral soil). In general, the sum of the masses of the light and heavy SOM fractions was comparable to the total mass of the soil sample before fractionation. The number of $\Delta^{14}C$ analyses that could be made was limited due to the high costs. Therefore in most cases the soil samples of a site were pooled by layer prior to the density fractionation. For those soil samples that were not pooled, the recovery of carbon after density fractionation was found to be roughly 97%.

3.2.3 Carbon stocks of SOM fractions

The carbon stocks of the L and F+H litter layers were calculated as the product of carbon content (g carbon/g litter) and mean litter mass per area (g litter/m2). Minimum and

maximum litter carbon stocks were calculated using the masses of the sorted and unsorted litter samples, respectively (see paragraph above). The carbon stocks of light and heavy SOM fractions in a soil layer were calculated as the product of the fractions carbon content (g carbon/g SOM fraction), mass of the SOM fraction as compared to the mass of the bulk soil (g SOM fraction/g soil), the soil layer's bulk density (g soil/cm^3), volume occupied by the soil layer per square meter (cm^3/m^2), and a factor representing the soil layer's stone content. The latter was determined by Rodeghiero and Cescatti (2005). Carbon stocks of the soil pits are given in Tables B1 and B2 of Appendix B for the litter and mineral soil, respectively.

3.2.4 SOM turnover times

$\Delta^{14}C$ analyses of the SOM fractions have been used to estimate turnover times by applying a modelling approach (see Hakkenberg et al. 2008). For most litter and soil layers samples were pooled, and thus only one $\Delta^{14}C$ analysis was made for a SOM fraction per site per layer. In most cases errors in the turnover times are therefore not available. Only in a smaller number of cases two, three, or four $\Delta^{14}C$ analyses were made

Table 3.2. Estimated turnover times of the three SOM fractions based on their $\Delta^{14}C$ values (see Chapter 2). When multiple $\Delta^{14}C$ measurements were made, the average turnover time is given followed by the standard deviation and the number of observations in parentheses.

		Site (abbreviated)					
Layer	Fraction	CaH	ToO	MaP	LaP	LaB	BrB
L	Litter	1.8	1.8			3.5	1.8
F+H	Litter	4.1	8.6	3.6	6.9	9.2	6.7
0-5 cm	Light	53	45 (4; 2)	49 (13; 3)	27	49 (6; 2)	61
	Heavy	66	85 (53; 2)	78 (13; 3)	79	65 (1; 2)	116
5-10 cm	Light	79	47 (6; 2)	62 (16; 3)	39	83 (12; 2)	63
	Heavy	104	388 (31; 2)	100 (27; 3)	40	127 (8; 2)	121
10-20 cm	Light	106	57	76	38	103 (20; 2)	73
	Heavy	163	319 (89; 2)	184	157	279(44; 2)	256
20-30 cm	Light	118		115		98 (25; 2)	98
	Heavy	315		448		643 (129; 2)	574

Table 3.2 Extended.

		Site (abbreviated)				
Layer	Fraction	BrS	VaS	LaF	BoB	ReS
L	Litter	4.7	4.7	3.0 (0.9; 4)	1.9	3.0 (1.7; 4)
F+H	Litter	14.8	7.2	6.0 (0.6; 4)	7.5	7.4 (0.3; 4)
0-5 cm	Light	45 (17; 3)	64	50 (16; 4)	37	77 (30; 4)
	Heavy	81 (24; 3)	170	110 (37; 4)	70	176 (42; 4)
5-10 cm	Light	60 (21; 3)	97	69 (9; 4)	59	84 (20; 4)
	Heavy	145 (37; 3)	238	261 (122; 4)	95	207 (30; 4)
10-20 cm	Light	68	104	98 (15; 4)	60	264 (172; 4)
	Heavy	226	369	588 (435; 4)	112	861 (231; 4)
20-30 cm	Light	62	103	135 (81; 4)		797 (800; 4)
	Heavy	235	859	665 (373; 4)		1757 (136; 4)

per soil layer per SOM fraction. The turnover times of the different SOM fractions and soil layers are summarized in Table 3.2. When more than one $\Delta^{14}C$ analysis was made, a mean turnover time and a standard deviation are given. For calculations in the present study the turnover times corresponding to individual $\Delta^{14}C$ analyses were used (partly presented in Table 3.2, i.e. the turnover times without a standard deviation). All the individual $\Delta^{14}C$ analyses and turnover times are permanently available in the online archives of the Ecological Society of America (http://www.esapubs.org/archive-/appl/A018/003/).

3.2.5 SOM-derived soil respiration and partitioning of total soil respiration

The decomposition flux D of a SOM fraction in a soil layer was calculated as the carbon stock C (g C/m2) divided by turnover time τ (yr), similarly as described by Gaudinski et al. (2000). Decomposition fluxes of a SOM fraction f in layers 1 to n were summed up to calculated the fractions total decomposition flux D_f:

$$D_f = \frac{C_1}{\tau_1} + \ldots + \frac{C_n}{\tau_n} \qquad \text{Equation 3.1}$$

In case of the litter layers, minimum and maximum transfer fluxes were calculated using the minimum and maximum litter carbon stocks, respectively (see paragraph above). Material removed during litter sorting, like roots, twigs, and small pieces of wood, may be less easily decomposable than leave and needle litter, still they may have contributed to the litter respiration flux. The decomposition flux from the heavy SOM fraction was assumed to consist entirely of respiration. The decomposition fluxes from litter layers and light SOM fractions were considered to consist of both respiration and transfer to the heavy SOM fraction (see Figure 3.1).

The maximum transfer flux possible was assumed to be equal to the decomposition flux from the heavy SOM fraction, i.e. it was assumed that the size of the carbon stock of the heavy SOM fraction remained constant. For partitioning of total soil respiration, the transfer flux to the heavy SOM fraction was arbitrarily set to 50% of the maximum possible transfer and divided over the litter layers and light SOM fractions proportionally to the fractions' decomposition fluxes. The respiration flux R from the litter SOM fraction was calculated as its decomposition flux minus its transfer flux:

$$R_{litter} = D_{litter} - 0.5D_{heavy} \times \frac{D_{litter}}{D_{litter} + D_{light}}$$ Equation 3.2

The respiration flux for the light SOM fraction was calculated in a similar way as above for the litter SOM fraction. Concentrations of dissolved organic carbon in the subsoil have been found to be very low (van Hees et al. 2008). Therefore, the loss of carbon from the system through leaching of dissolved organic carbon was assumed to be negligible and not included in the analysis.

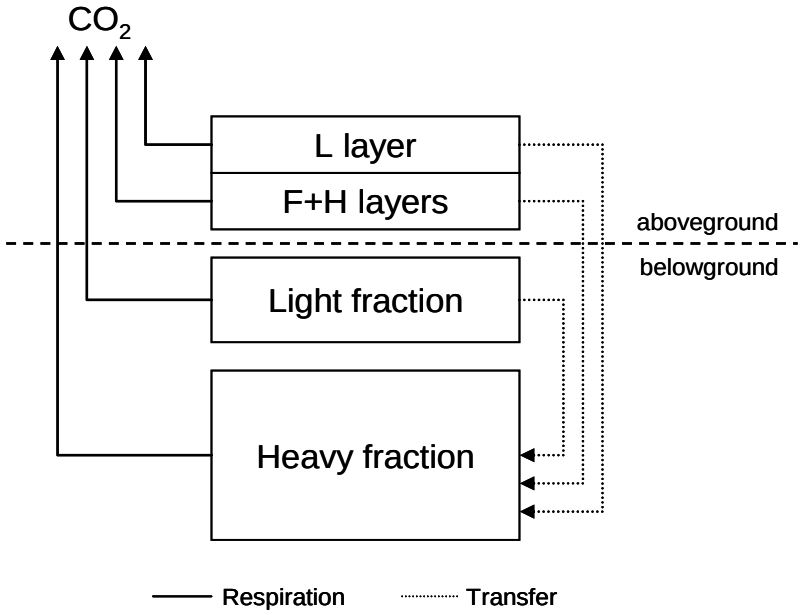

Figure 3.1. Schematic representation of the different SOM fractions with conceptual respiration and transfer fluxes for which values were estimated in this study.

The sum of the respiration fluxes from the three SOM fractions is referred to here as Δ^{14}C-based respiration. The difference between the sites' total soil respiration as determined by Rodeghiero and Cescatti (2005) and Δ^{14}C-based SOM-derived respiration consisted of soil respiration derived from recently fixed carbon. It is presumed that a large fraction of the respiration from recently fixed carbon was root and root-associated respiration. To estimate Δ^{14}C-based SOM-derived respiration a SOM fraction's carbon stock was used (Equation 3.1). However, in particular the size of fresh litter pools will show seasonal fluctuations over year. Thus, the Δ^{14}C-based SOM-derived respiration depends on the time of sampling. Given that sampling was done at the end of the summer, the aboveground litter stock probably had reached its minimum size. The fraction of aboveground litter that is respired at a site in one year was estimated from

the exponential decay of the site's annual litterfall (Table 3.1) and a decomposition rate equal to the inverse of the average turnover time of the L layer (Table 3.2).

3.2.6 Heterogeneity of the heavy SOM fraction

SOM fractions obtained with physical or chemical separation methods, like the heavy fraction, may consist of subfractions with different turnover times (Rasmussen et al. 2005, Mikutta et al. 2006). A brief sensitive analysis was made to investigate how the respiration from a SOM fraction with a turnover time of 200 years (roughly representing the heavy fraction in soil layer 5-10 cm) would change if its respiration is in fact produced from a younger and an older subfraction. Each subfraction represented half of the carbon stock of the total fraction. For ranges of $\Delta^{14}C$ values of the young and old subfraction turnover times were modelled as described by Hakkenberg et al. (2008). Subsequently respiration fluxes were calculated for the different turnover times of the two subfractions as described in Equation 3.1. Each specific combination of $\Delta^{14}C$ values of the two subfractions corresponded to a mean $\Delta^{14}C$ value of 32.5‰, which in turn corresponds to a turnover time of 200 years.

3.2.7 Role of site characteristics

The effects of mean annual temperature, annual precipitation, soil acidity (pH in soil-water suspension), and indices reflecting the ecosystems productivity (litterfall and fine root biomass) on the SOM fractions' carbon stocks and respiration fluxes were investigated by determining Pearson correlation coefficients. A Bonferroni correction was applied to account for testing of multiple hypotheses. After this correction a P value of 0.0083 was required for a correlation to be statistically significant at $P = 0.05$.

3.3 Results

3.3.1 Carbon stocks

On average 70% of the sites soil carbon stock was stored in the heavy SOM fraction. The remaining 30% was roughly equally distributed over the litter layers and light SOM fractions. The amount of carbon stored in the litter layers at site Brigolina S was considerably higher than that at the other sites (Figure 3.2). Within the litter, the amount of carbon stored in the F+H layers was larger than that stored in the L layer (Figure 3.3a; Appendix B; Table B1). Sites Brigolina S and Mattarello had thicker L layers than the other sites. Whereas most of the carbon in the light fraction was stored in the top of the mineral soil, the amount of carbon in the heavy fraction was more distributed over the soil profile (Figures 3.3b and 3.3c; Appendix B Table B2).

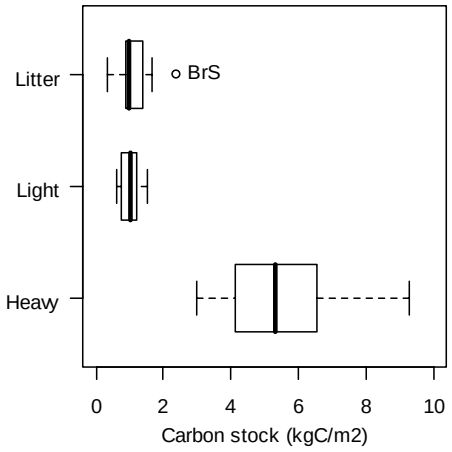

Figure 3.2. Observed ranges of total carbon stocks of three SOM fractions. Solid vertical line is the median, left and right sides of the boxes are approximately the first and third quartile, respectively, i.e. boxes represent the mid 50% of the observations. Horizontal lines extend up to 1.5 times the box size from the nearest box side; observations outside this range are shown as points with site abbreviation. Site abbreviation is as given in Table 3.1.

3.3.2 Decomposition fluxes

The total of the $\Delta^{14}C$-based decomposition fluxes of the sites ranged from 164 to 447 g C/m2/yr. By far the largest contribution (on average 81%) to the total $\Delta^{14}C$-based decomposition flux resulted from the litter layers (Figure 3.4a). Whereas the contributions of the different litter layers were comparable in size at some sites (Casteller, Lagolo B, Brigolina S, and Lavarone), at other sites the decomposition flux from litter was mainly derived from either the L layer (Brigolina B, Bondone) or the F+H

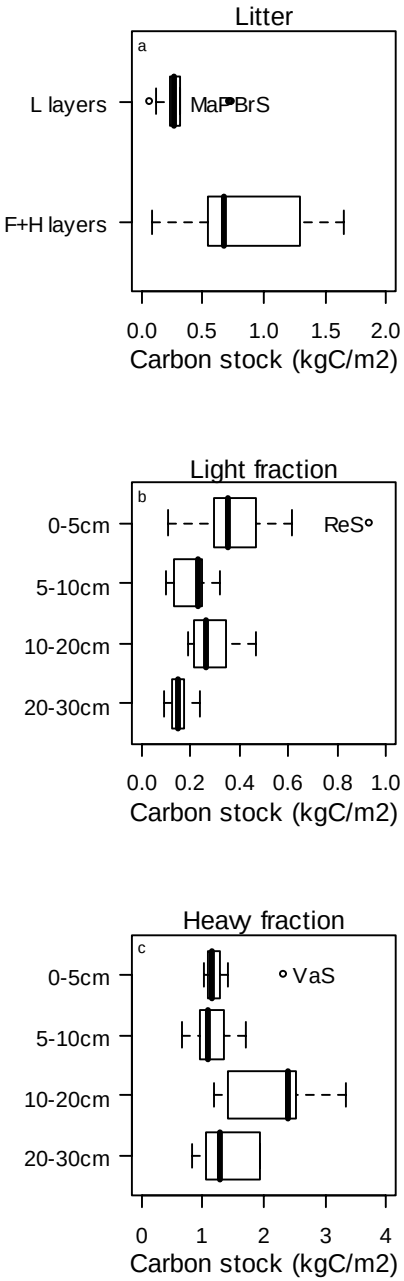

Figure 3.3. Observed ranges of (a) the distribution of litter SOM over two layers; (b)the distribution of light SOM over four soil layers; (c)the distribution of heavy SOM over four soil layer. Note the difference in volume occupied by the different layers. Explanation of the different elements in the figures is as in Figure 3.2.

layers (Vaneze, Renon). The error in the decomposition flux from the L layer-associated with the sorting of the litter (see section Methods) was for some sites +/- 50% or higher (Mattarello, Vaneze, Renon; Figure 3.4a). The error in the decomposition flux from the F+H layers due to sorting of the samples was smaller, on average +/- 11%. Much smaller contributions resulted from the decomposition of the light and heavy fractions

to the total decomposition flux. On average decomposition fluxes from the light and heavy fraction were 6 and 13% of the total SOM decomposition flux, respectively (Figure 3.4a).

3.3.3 Partitioning of total soil respiration

The $\Delta^{14}C$-based SOM-derived respiration accounted for 25 to 63% of the total annual soil respiration, with an average of 38% (Figure 3.4b). Decomposition fluxes from the litter and light fractions were presumed to consist of respiration and transfer to the heavy fraction (Figure 3.1). For the partitioning of total soil respiration it was arbitrarily assumed that the total transfer of carbon from the litter and light fraction to the heavy fraction was 50% of the respiration flux from the heavy fraction (see Methods). Given an average respiration flux from the heavy fraction that was equal to 5% of the total soil

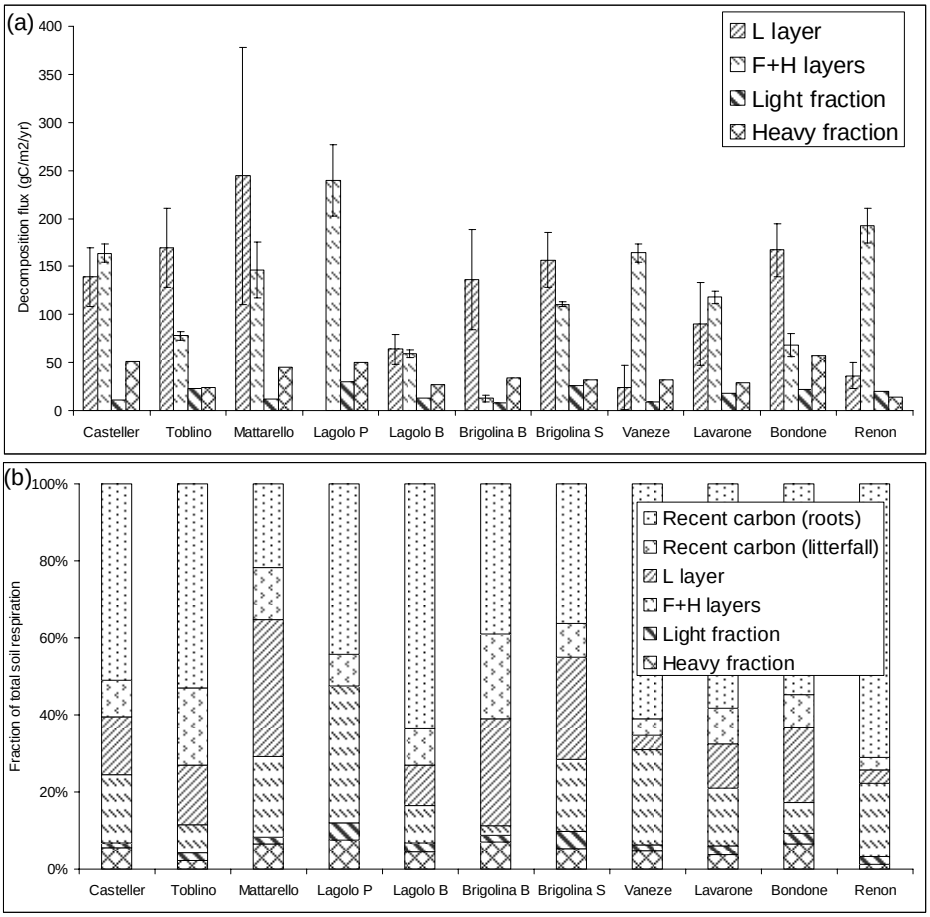

Figure 3.4 (a) Estimated annual carbon fluxes released by the decomposition of three SOM fractions. (b). Partitioning of total annual soil respiration into SOM-derived components and components derived from recently fixed carbon. The respiration from recently fixed carbon was subdivided into root-derived respiration and respiration that is produced from aboveground litter in the first year after litterfall. The SOM component was separated into the contributions of litter layers, light fraction and heavy fraction. With the latter two fractions obtained with a density fractionation of mineral soil.

respiration, the uncertainty in soil respiration partitioning associated with this assumption was rather small. The fraction of total soil respiration remaining after subtracting the total SOM-derived respiration was presumed to be respiration derived from recently fixed carbon (Figure 3.4b). Besides root respiration, respiration from recently fixed carbon also included respiration from the fraction litter that was respired within the first year after entering the litter or mineral soil compartment (see Methods). For the aboveground litter this flux was estimated to be in a range of 30 and 100 gC/m2/yr. Except for site Toblino, where, due to high litterfall (see Table 3.1), the estimate of this flux was much higher (217 gC/m2/yr). On average the contribution of aboveground litter to respiration from recently fixed carbon was estimated to be 11% of the total soil respiration, with the highest contributions found for sites Toblino and Brigolina B (~ 20%) and the lowest for sites Vaneze and Renon (< 5%). For individual sites, the annual litterfall and the sum of the respiration fluxes from the L and F+H layers did in most cases not balance (Figure 3.5). Overall however comparison of these two fluxes suggested that the sum of the respiration fluxes from L and F+H layers was only slightly lower than the annual litterfall, when site Toblino with its very high litterfall was excluded (Figure 3.5). The respiration from recently fixed carbon attributed to roots was obtained by subtracting the respiration estimated to be derived from litter within the first year after litterfall from the total respiration from recently fixed carbon. Which resulted in an average root-derived respiration of ~ 50% of the total soil respiration. Highest and lowest contributions of root-derived respiration were found for sites Mattarello (22%) and Renon (72%), respectively.

Our $\Delta^{14}C$-based estimates of SOM-derived respiration were 100 to 250 gC/m2/yr lower than the estimates determined for the evergreen sites by Rodeghiero and Cescatti (2006) with a partitioning method using regression analysis (Figure 3.6a). With the exception of site Brigolina S, for which the two estimates were roughly equal. Our $\Delta^{14}C$-based estimated of SOM-derived respiration were roughly between 100 and 300 gC/m2/yr lower than estimates of the sites' SOM-derived respiration calculated from the relationship determined by Subke et al. (2006) in a meta-analysis (Figure 3.6b). With the exception of sites Mattarello and Brigolina S for which the differences between the two estimates were relatively small.

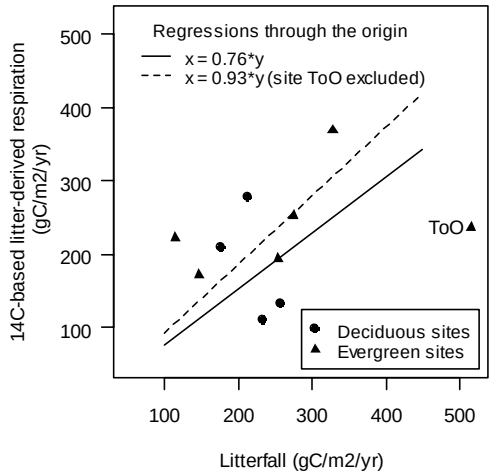

Figure 3.5. The $\Delta^{14}C$-based litter-derived respiration plotted against the annual litterfall at the sites. The order of magnitudes of both carbon fluxes are compared by a regression through the origin.

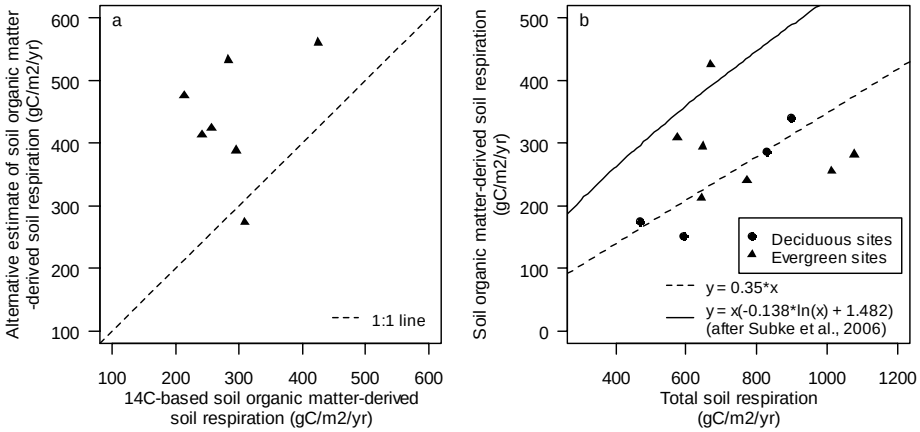

Figure 3.6 (a). SOM-derived soil respiration as determined by Rodeghiero and Cescatti (2006) with the regression technique" for the evergreen sites (y-axis) against SOM-derived soil respiration as estimated in this study ($\Delta^{14}C$-based; x-axis). (b) SOM-derived soil respiration as estimated in this study plotted against total annual soil respiration as determined by Rodeghiero and Cescatti (2005). The line is the relationship between the two plotted variables as observed in a meta-analysis by Subke at al. (2006).

3.3.4 Heterogeneity of the heavy SOM fraction

To investigate the possible effect of heterogeneity of the heavy SOM fraction on its decomposition flux, a conceptual SOM fraction with a turnover time of 200 years was divided in to a young and old subfraction. It was assumed that: (i) each of the subfractions represented half of the carbon stock of the total fraction; and (ii) the $\Delta^{14}C$ value of the total fraction was 32.5‰ (corresponding to a turnover time of 200 yr). Based on these assumptions the ranges in $\Delta^{14}C$ values and turnover times of the two subfractions were determined. The turnover times of the young and old subfraction

ranged from 25 to 200 yr and 200 to 1520 yr, respectively. Decomposition fluxes from each of the two subfractions were calculated and the sum was compared to the decomposition flux as calculated for the total undivided fraction (Figure 3.7). Results showed that the effect of considering two subfractions strongly depends on the turnover times, and thus the $\Delta^{14}C$ values, of the two subfractions. For turnover times of the young subfraction that are higher than 100 yr, the sum of the decomposition fluxes from the two subfractions may only be slightly higher than the respiration from the total undivided fraction. When the turnover time of the young subfraction decreases below 75 yr, the sum of the decomposition flux from the subfractions strongly increases and the sum of the decomposition fluxes from the two subfractions can become a factor two or three higher than the decomposition flux from the total undivided fraction (Figure 3.7).

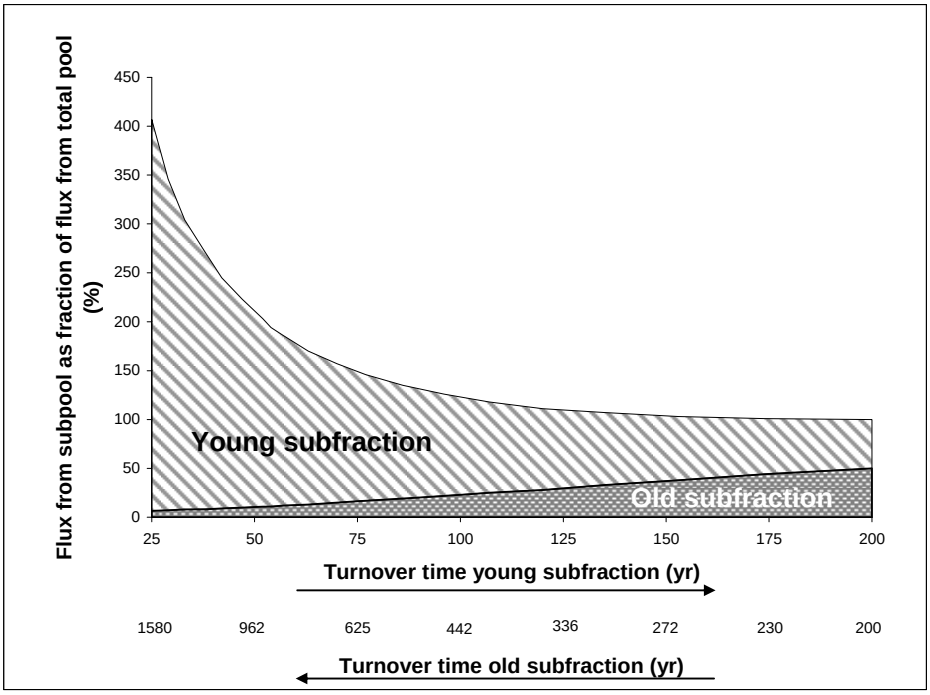

Figure 3.7. Possible underestimation of the respiration flux from a heavy SOM fraction with a turnover time of 200 years if the pool exists of a younger and an older subfraction. Each subfraction represents half of the carbon stock of the total fraction. When both subfractions have a turnover time of 200 yr the sum of their respiration equal to the respiration from the fraction when it is considered as a homogenous fraction.

3.3.5 Role of site characteristics

No indications were found for a strong influence of any of the investigated site characteristics (mean annual soil temperature, annual precipitation, soil acidity, litterfall,

fine root biomass, and the sum of the latter two) on either the carbon stored in a SOM fraction (Table 3.3) or the $\Delta^{14}C$-based respiration produced from SOM fractions (Table 3.4). (Recall that $\Delta^{14}C$-based respiration from SOM fractions are based on the carbon stock divided by turnover time.) A negative correlation occurred between the carbon stock of the light SOM fraction and soil acidity. Correlations between mean annual soil temperatures and $\Delta^{14}C$-based respiration fluxes from the light and heavy SOM fractions were not significant, although the turnover times of these fractions were found to have significant temperature sensitivities (Hakkenberg et al. 2008).

Table 3.3 Correlations of carbon stocks of different SOM pools with site characteristics. Correlation in bold was significant at $P < 0.05$ after a Bonferroni correction.

	Carbon stock of SOM pools				
	L layers	F+H layers	L+F+H layers	Light fraction	Heavy fraction
Temperature	0.39	-0.22	-0.09	-0.20	-0.34
Precipitation	-0.14	-0.10	-0.12	0.08	0.25
Soil acidity (pH in water)	0.15	-0.60	-0.52	**-0.81**	0.40
Litterfall	0.43	-0.32	-0.11	0.08	-0.36
Fine root biomass	-0.15	-0.05	-0.08	0.26	-0.11
Litterfall + fine root biomass	0.38	-0.42	-0.20	0.25	-0.48

Table 3.4. Correlations of $\Delta^{14}C$-based soil respiration fluxes from different SOM pools with site characteristics. No significant correlations ($P < 0.05$ after a Bonferroni correction) were observed.

	Soil respiration flux from SOM pools				
	L layer	F+H layers	L+F+H layers	Light fraction	Heavy fraction
Temperature	0.72	-0.06	0.46	0.11	0.44
Precipitation	-0.16	-0.14	-0.19	0.05	0.32
Soil acidity (pH in water)	0.46	-0.24	0.20	-0.56	0.72
Litterfall	0.63	-0.39	0.28	0.14	-0.14
Fine root biomass	-0.14	-0.19	-0.23	0.20	0.36
Litterfall + fine root biomass	0.64	-0.57	0.19	0.28	0.14

3.4 Discussion

3.4.1 Decomposition and respiration fluxes from the SOM fractions

Of the three investigated SOM fractions, the decomposition flux derived from the litter layers was by far the largest fraction of the total decomposition flux. The decomposition flux derived from belowground SOM, represented by the light and heavy SOM fractions, was small in comparison to the flux from the litter layers. The carbon stocks of the two belowground SOM fractions however were comparable (light fraction) or much larger (heavy fraction) than the total carbon stock of the litter layers. The low $\Delta^{14}C$-based decomposition fluxes from belowground SOM were thus explained by the much longer

turnover times of the light and heavy SOM fractions as compared to the litter layers. The $\Delta^{14}C$-based decomposition flux from the heavy fraction was larger than that from the light fraction, due to the much larger carbon stock of the former one. From the arbitrary assumption that the transfer from litter and light fraction to the heavy fraction was 50% of the decomposition flux from the heavy fraction, it followed that the difference between the total decomposition flux and the total SOM-derived respiration flux was rather small. That is, on average, this difference was 18 $gC/m^2/yr$ or 2.6% of the total soil respiration.

The decomposition fluxes were calculated by dividing carbon stocks by turnover times. In case of error propagation, the relative error in the decomposition flux would be the sum of the relative errors in carbon stock and turnover time. Given the spatial heterogeneity of soils, a considerable variation in both $\Delta^{14}C$ values and carbon stock is likely, and is also suggested by the standard deviations of the $\Delta^{14}C$ values as far as available (Table 3.2). Hence, a relative error in the decomposition fluxes of 50% or more is not unlikely at all. For the $\Delta^{14}C$ values and turnover times one value was available per site, per fraction, per layer in most cases. Also for the calculation of the carbon stock, a single value per site, per layer was often used for the amount of light and heavy fraction in a sample, because mineral soil samples were in many cased pooled by layer prior to density fractionation. Error propagation would have required a standard deviation calculated from at least e.g. five or six samples, and was not attempted here given the low and inconsistent number of observations.

The $\Delta^{14}C$-based decomposition fluxes of the different SOM fractions as estimated here, suggested that most of the annual carbon inputs to the SOM pool took place aboveground, and to a much smaller degree in the mineral soil. A comparable distribution of the annual carbon inputs to the SOM pool was suggested from a recent study using carbon-13 isotope labelling of tree leaves (Keel et al. 2006). There it was found that (i) on an annual basis only a small fraction (~10%) of carbon in fine roots (<1 mm) was replaced by recently fixed carbon and (ii) the isotopic signature of bulk soil SOM had not significantly changed after three and a half years. The results of Keel et al. (2006) suggested that annually only a small fraction of belowground SOM is respired and replaced by recently fixed carbon. However Keel et al. (2006) also suggest that mixing of the isotopic label with older carbon in the trees may have influenced their results (i.e. caused an underestimation of the allocation of carbon to roots).

Using a similar methodology as in this study, Gaudinski et al. (2000) found roughly comparable results as we did. They found that 41% of the total soil respiration was derived from SOM, and that 80% of this flux was from above- and belowground litter decomposition. Detailed comparison of our methodology with that of Gaudinski et al. (2000), suggested that we may have missed a fraction of SOM-derived respiration as a result of removing a small fraction of organic matter from our samples. That is, the removal of organic matter due to fine sieving (< 2 mm) of mineral soil samples and by removing roots from litter layer samples (see Hakkenberg et al. 2008). There was another difference between the fractionation scheme applied here as compared to that applied by Gaudinski et al. (2000). They separated root litter from both litter layers as well as from the light fraction, and estimated that a large fraction of $\Delta^{14}C$-based SOM-derived respiration was derived from this root litter pool. This result seems to be somewhat in contrast with the low contribution of the light fraction to $\Delta^{14}C$-based SOM-derived respiration that was found here. Due to methodological limitations Gaudinski et al. (2000) did not determined how respiration from root litter was divided over roots in litter layers and belowground root litter. They determined the total contribution of the root litter pool (i.e. roots in litter layers and light fraction together), which hampers the comparison with our results.

3.4.2 Partitioning of total soil respiration

A very large fraction of the total soil respiration (~ 90%) resulted from root respiration and the decomposition of fresh organic matter ($\Delta^{14}C$-based litter-derived respiration plus the respiration from recently fixed carbon). The decomposition of the intermediate (light fraction) and stabilized (heavy fraction) SOM fractions made only a small contribution (< 10%) to the total soil respiration. Our findings seem to be in agreement with what was stated by (Ryan and Law 2005), i.e. that current plant metabolism and the decomposition of recently produced organic material are the main contributors to total soil respiration.

The fraction of litter-derived respiration not included in the $\Delta^{14}C$-based litter-derived respiration may have been substantial (20% or more of the respiration of recently fixed carbon) at some sites, as estimated from an exponential decay function applied to the amount of litterfall in a single year. On the other hand the trend obtained from the comparison of the total $\Delta^{14}C$-based litter-derived respiration and the sites litterfall suggested that overall the litter-derived respiration and the litterfall

approximately balanced (result excluding site Toblino). This may indicate that the litter-derived respiration that was missing from the $\Delta^{14}C$-based estimate may be much smaller. For example because the input of litter at the evergreen sites takes place more gradually distributed over the whole year. It is however also possible that $\Delta^{14}C$-based litter-derived respiration was somewhat overestimated by using the mean litter carbon stock, which included 50% of the mass of roots, twigs and small pieces of wood. Similarly as aboveground, there is also pool of belowground fresh litter from roots. The relatively high turnover times of the light fraction (Table 3.2), suggest that this pool is not represented by the light SOM fraction. Estimates of root productivity and root turnover are associated with considerable uncertainty. Root turnover times may be between 2 and 5 years (Strand et al. 2008) and annual root productivities of forests are mostly within the range of 50 to 600 g/m^2 (Bernier and Robitaille 2004, Chen et al. 2004). Under the assumptions that (i) root productivity and the amount of root litter roughly balance annually and (ii) the carbon content of roots is 50%, an estimate of the respiration due to decomposition of fresh root litter within the first year after shedding, may lie in the rather wide range of 5 to 120 gC/m^2/yr.

3.4.3 Sources of uncertainty in $\Delta^{14}C$-based turnover times

Estimating turnover times of litter by fitting a model to measured $\Delta^{14}C$ values in some cases leads to two possible turnover times. Two possible turnover times occur for all samples with $\Delta^{14}C$ values higher than the (lagged) atmospheric $\Delta^{14}C$ in the year of sampling (and below the maximum $\Delta^{14}C$ value that can be modelled). Whereas the turnover times used here for the litter were the so-called short turnover times (see Hakkenberg et al. 2008), other authors have considered the long turnover times more plausible for some (Gaudinski et al. 2000) or all (Hahn et al. 2006) of the litter layers. Whereas this may point out strong differences in litter turnover times of different forest it may also show that choosing most plausible (based on additional data) or most realistic (based on expert knowledge) turnover times may be problematic. Short turnover times seem to be in better agreement with results (k values) from litterbag studies (Valachovic et al. 2004). When two possible turnover times occurred for the light fraction the long turnover times have been chosen as the more plausible ones. Motivation for this choice was the observation that the decomposition fluxes of the light fraction obtained with the long turnover times were in better agreement with the

presumed amount and distribution of belowground inputs. For more details on this issue we refer to Hakkenberg et al. (2008).

A brief sensitivity analysis showed that the correctness of the decomposition flux estimated for the large carbon stocks of the heavy fraction, depends on the degree of heterogeneity of this fraction. The example showed that within a certain range in turnover times, the effect of heterogeneity is limited. When the turnover time of the young subfraction decreases below a certain value the effect of heterogeneity on the decomposition flux strongly increases. This is because fluxes increase hyperbolically with decreasing turnover time (see Equitation 1). However for very short turnover times, the decomposition flux and thus the input required to balance the carbon stock become very high. Occurrence of such high belowground inputs seems unlikely. The actual degree of heterogeneity of the heavy fraction and the associated underestimation of the respiration fluxes could be investigated by further separation of this fraction prior to $\Delta^{14}C$ analysis. Also $\Delta^{14}C$-based respiration as obtained here may be verified by measuring $\Delta^{14}CO_2$ released from soils in-situ or in incubation experiments (see Gaudinski et al. 2000, Hahn and Buchmann 2004).

Another source of uncertainty associated with the use of $\Delta^{14}C$ analyses is the possibility that the actual atmospheric $\Delta^{14}C$ values differ from those of the atmospheric $\Delta^{14}C$ record that was used as input to the model. The relatively short turnover times of the litter layers will be most strongly affected by errors associated with such differences (Bruun et al. 2005).

3.4.4 Role of site characteristics

Temperature is a factor influencing total soil respiration (see e.g. Lloyd and Taylor 1994). Rodeghiero and Cescatti (2005) have shown that at our sites temperature explains 46% of the variability in the total soil respiration. The intersite variability in the respiration derived from the different SOM fractions as estimated here, were however not correlated with mean annual temperature and neither with any of the other included site characteristics. It is possible that the diversity of the sites (six different dominating tree species, conditions ranging from Mediterranean to subalpine) and the in comparison relatively low number of sites did not allow observation of temperature or other effects.

3.5 Conclusion

This study suggested that living roots and decomposition of litter are the main sources of soil respiration. Respiration derived from SOM that is an intermediate or advanced decomposition stage seemed to make only a marginal contribution to total soil respiration. The use of $\Delta^{14}C$ has the advantage that is does not require disturbance or manipulation of the ecosystem However, the $\Delta^{14}C$-based method as it was applied here: (i) seems to be less suitable for carbon stocks which sizes fluctuate considerable during the year; and (ii) may have resulted in an underestimation of the contribution of the stabilized SOM fraction to total soil respiration, if this fraction had a considerable heterogeneity. To assess the error in $\Delta^{14}C$-based respiration requires a sufficient number of replicate observations. Fractionating the stabilized SOM fraction into subfractions of different stabilities prior to $\Delta^{14}C$ analysis may further improve the method. Furthermore including $\Delta^{14}C$ analyses of soil respiration may be useful to verify respiration estimated obtained from $\Delta^{14}C$ values of SOM.

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Appendix B

Table B1

Carbon stocks of the organic layers

Table B2

Carbon stocks of the light and heavy SOM fractions

4. Soil respiration correlates with nitrogen content of decomposed litter layers

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Abstract

A changing terrestrial carbon balance through altering rates of soil respiration rates is a potentially important feedback mechanism to climate change. Knowing the controls on soil respiration helps to understand its response to changes in environmental conditions. The availability of nitrogen in the soil could influence soil respiration because it influences the decomposition of soil organic matter (SOM) as well as root respiration for nutrient uptake. Furthermore, productivity and therefore plant respiration increase with increasing availability of nitrogen. In this study we present a positive correlation between total annual soil respiration and the nitrogen content of decomposing litter for forest sites located along an elevation gradient. Previously determined soil respiration components (litter-derived and respiration from carbon recently fixed by plants) both seemed to increase with increasing nitrogen content of the decomposing litter, although these results were confounded by two apparent outliers. Our results suggest that (1) the activity of SOM decomposers and roots is for a large part located in and near the litter layers; (2) plants may maintain a high availability of nitrogen in the soil by producing litter with high nitrogen content; (3) canopy nitrogen content obtained from hyperspectral remote sensing data might be useful for upscaling of soil respiration to the landscape level, if higher availability of nitrogen in litter is also reflected in the canopy.

Key words
soil respiration; nitrogen; litter; litter quality; elevation gradient; Italian Alps.

4.1 Introduction

A large fraction of the carbon fixed by terrestrial ecosystems is released back into the atmosphere through soil respiration. On a global scale, this flux is estimated to be ~ 80 Pg C/yr (Raich et al. 2002). Changes in the terrestrial carbon balance (i.e. additional uptake or release of carbon as compared to a reference) are potential feedbacks to climate change. Therefore, understanding the controls on soil respiration, as well as modeling soil respiration is of importance. Temperature and soil moisture are main determinants on the temporal variation in soil respiration and their effects are also the ones most studied (Davidson et al. 2006, Reichstein and Beer 2008a). Among different sites however mean soil respiration rates sometimes do not increase with increasing temperature (e.g. Janssens et al. 2001, Rodeghiero and Cescatti 2005, e.g. Garten and Hanson 2006), or the effect of temperature is limited (Campbell and Law 2005). Even tough these studies reported clear temperature responses of the temporal variation in soil respiration rates of individual sites. Several studies have reported that variation in total soil respiration was related to gross or net primary productivity, spatially (Raich and Schlesinger 1992, Janssens et al. 2001, Hibbard et al. 2005) as well as temporarily (Moyano et al. 2007, Sampson et al. 2007). Productivity in turn is frequently limited by the amount of nitrogen available for plant growth (Vitousek et al. 2002). Thus, the availability of nitrogen in the soil could be a control on the mean soil respiration rate of ecosystems, given the link between productivity and soil respiration.

The importance of nitrogen for root metabolism and SOM decomposition has been shown in several studies. Zog et al. (1996) found that average root respiration was higher at sites with higher nitrogen availability in the top soil, including litter. Burton et al. (2000) showed that root longevity increased with increasing nitrogen mineralization rates. As explanation for the latter result it was suggested that roots may be maintained, and thus respire carbon, as long as trees benefit from their nutrient (e.g. nitrogen) uptake. Recently, Chapman et al. (2006) have suggested that nitrogen which is released from litter (either by leaching or mineralization) could provide a significant fraction of plant's total nitrogen requirement. Furthermore nitrogen or indices including nitrogen, like carbon-to-nitrogen (C:N) or lignin-to-nitrogen ratios, are considered to be indicators

of litter quality (Chapin et al. 2002). For fresh litter, a high nitrogen content indicates a high quality and high degradability. At a later stage of the litter decomposition process however, a high nitrogen content of litter may indicate the opposite because nitrogen is involved in the formation of recalcitrant compounds and suppresses the formation of specific decomposer enzymes (Berg 2000). It has been shown that higher availability of nitrogen in the soil results in higher nitrogen mineralization rates (Finzi et al. 1998, Fernandez et al. 2000, Ollinger et al. 2002) and higher litter respiration (Vesterdal 1998). The response of litter decomposition to nitrogen additions are variable (Hyvönen et al. 2007). With a meta-analysis, Knorr et al. (2005a) showed that the sign of the response to nitrogen additions may depend on several factors: the rate of nitrogen addition, the rate of atmospheric nitrogen deposition, as well as the quality of the litter. For central European forests, which receive a high atmospheric nitrogen deposition (Holland et al. 2005), it was shown that litter decomposition rates decreased with increasing litter nitrogen concentration (i.e. increasing C:N ratio; Michel and Matzner 2002). Nitrogen additions may also cause a decrease of root respiration (Bowden et al. 2004, Mo et al. 2008). The brief overview of studies given above suggests that the availability of nitrogen in the soil can be an indicator of both autotrophic and heterotrophic soil respiration rates. To our knowledge however relationships between total soil respiration and soil nitrogen on a landscape scale have not been reported.

In this study we report a positive correlation between mean annual soil respiration of forests sites and the nitrogen content of their decomposing litter. Tree species vary among the sites, with six different tree species occurring as the dominant species. Furthermore the sites are located along a mean annual temperature gradient of eight ^{o}C. We give possible explanations for the observed relationship and discuss the implications of our findings.

4.2 Methods

4.2.1 Sites

The 11 study sites are located in the southern Italian Alps, in the autonomous province of Trento. They are all forests, but their dominant tree species varies (Chapter 2; Table 2.1). Three sites are dominated by Beech (Lagolo B, Brigolina B, Bondone), three by Spruce (Brigolina S, Vaneze, Renon), two by Pine (Mattarello, Lagolo P). The three other sites are dominated by hop hornbeam (Casteller), Holm oak (Toblino), and silver fir (Lavarone). Mean annual temperature of the sites also varies (from ~ 4 to 12 ^{o}C), because

the sites are located along an elevation gradient from 220 to 1740 m above sea level. More site characteristics can be found in Rodeghiero and Cescatti (2005). Atmospheric nitrogen deposition in the region is relatively low (< 1 gN/m2/yr; Marchetti et al. 2002).

4.2.2 Soil respiration

Mean annual soil respiration of each site was determined by Rodeghiero and Cescatti (2005) based on soil respiration measurements (every 15 to 20 days during two years) and soil temperature frequency distributions (recorded every ten minutes). Mean annual soil respiration ranged from 475 to 1100 gC/m^2/yr, and was not correlated with mean annual temperature, litterfall, or annual wood increment (Figure 4.1; Rodeghiero and Cescatti 2005). The latter two were considered proxies for the sites productivity.

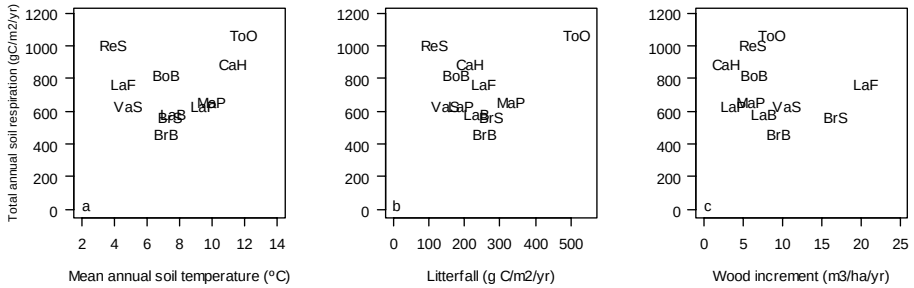

Figure 4.1: Total annual soil respiration of 11 forest sites plotted against (a) mean annual soil temperature, (b) annual litterfall, and (c) annual wood increment (a proxy for productivity).

4.2.3 Litter nitrogen content

Total nitrogen contents of the uppermost litter layer containing fresh litter (L layer) and of the two lower litter layers (fragmented (F) and humified (H) litter layers) containing decomposing litter, were measured in a CN-analyzer as reported previously (Hakkenberg et al. 2008). The number of soil pits sampled was two (sites Lavarone and Renon) or three (the other sites). In a few cases samples of the litter layers were only present from one pit (L layer: sites Mattarello, Lagolo B, and Vaneze; F+H layers: site Vaneze). The L layer was sampled separately at all sites, except at site Lagolo P were this layer was not present. The F and H layers were sampled, and subsequently analyzed together at most sites. At four sites (Brigolina S, Vaneze, Lavarone, and Renon) the F and H layers were sampled, and subsequently analyzed separately. For these four sites the nitrogen content of the F+H layers was calculated as the weighted average nitrogen content of the F and H layers. The weights for the averaging were the weights of the F

and H layers divided by the total weight of the F+H layers. Subsequently site mean nitrogen contents were calculated for L and F+H layers from the values of the different soils pits.

4.2.4 Statistical analysis

Linear regressions were applied to assess the effects of nitrogen and other parameters on total soil respiration and its components (SOM-derived respiration and respiration from recently fixed carbon). Whether slopes of the regressions were significantly different from zero was determined from P-values as derived from the t test. Regressions were made with R 2.6.2 (R Development Core Team 2008).

4.3 Results

Total annual soil respiration of the sites increased significantly with increasing nitrogen content of the F+H layers (p = 0.001, Figure 4.2b), but not with increasing nitrogen content of the L layer (Figure 4.2a). Nitrogen content of the F+H layers litter explained 70% of the variation in the total soil respiration.

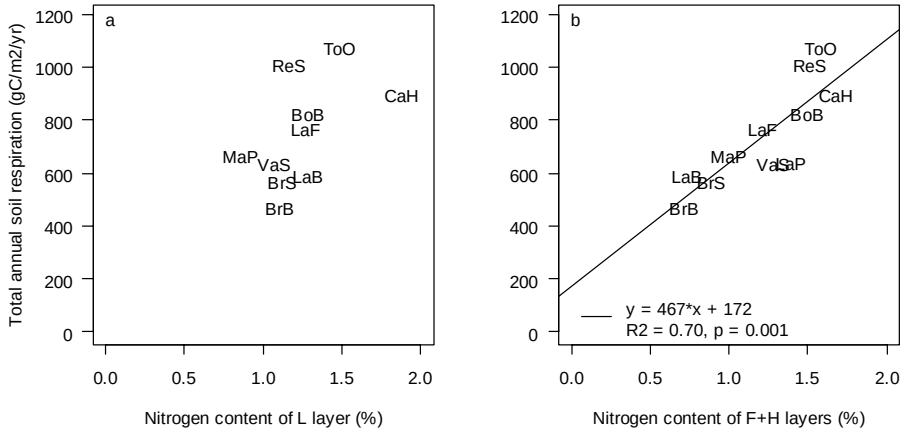

Figure 4.2: (a) Total soil respiration of 11 forest sites was not correlated with the nitrogen content of the fresh (L) litter, but (b) Total soil respiration increased significantly with increasing nitrogen content of the decomposing litter (F+H) layers.

Quality of the F+H layers litter, expressed as C:N ratio, was not significantly correlated with total annual soil respiration (Figure 4.3a). The nitrogen content of the F+H layers was only weakly related to the nitrogen content of the L layer (Figure 4.3b). The nitrogen content of the L layer however was probably more related to the nitrogen content of the canopy than the nitrogen content of the F+H layers was. Because the carbon and nitrogen contents of the F+H layers were correlated (Figure 4.4a), total soil respiration

was also correlated with carbon content (Figure 4.4b). However, a multiple regression of the total soil respiration against the nitrogen and carbon content of the F+H layers against showed that nitrogen content (P = 0.04) was a much more significant describing variable than the carbon content (P = 0.94). The fraction of variance explained by this

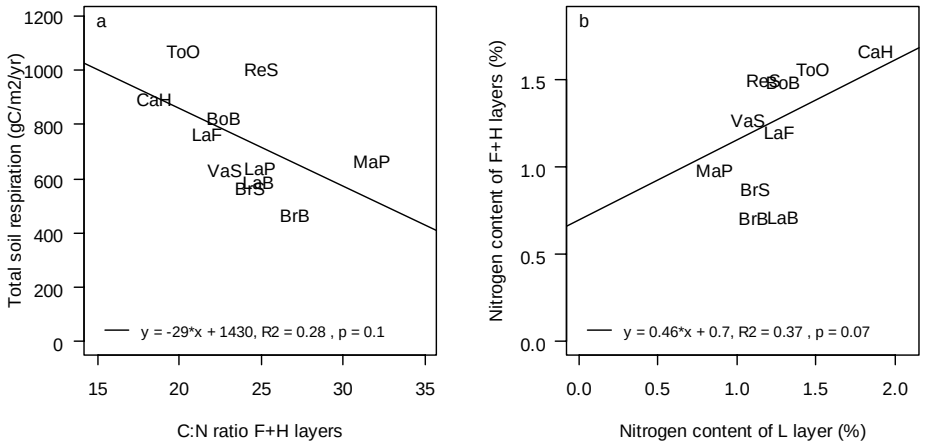

Figure 4.3: (a) Quality of the decomposing litter (F+H), expressed as carbon-to-nitrogen (C:N) ratio, was not correlated with total soil respiration. (b) The nitrogen content of the fresh (L) litter, which may have reflected the nitrogen content of the initial aboveground litter, was only weakly correlated with the nitrogen content of the F+H layers.

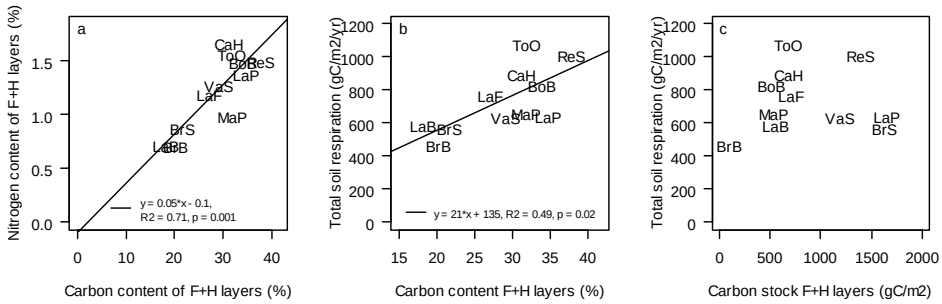

Figure 4.4: (a) Carbon and nitrogen contents of the decomposing (F+H) litter were correlated. Therefore (b and c) increases in total soil respiration and litter respiration were also observed with increasing carbon content of the litter layers. Carbon content explained however less of the variance in total soil respiration and litter-derived respiration than the nitrogen content did.

multiple regression model (70%) was similar as that of the regression model that had only nitrogen content as describing variable. Total soil respiration was not correlated with the carbon stock of the F+H layers (Figure 4.4c).

Previously determined components of total soil respiration i.e. litter-derived and respiration from recently fixed carbon (the latter including root respiration; see Hakkenberg et al. submitted) both tended to increase with increasing nitrogen content of the F+H layers (Figures 4.5a and 4.5b).However, SOM-derived respiration as estimated for Mattarello P and Brigolina S were exceptions to this trend. When plotted against the

nitrogen content of the F+H layers, the estimates of litter-derived respiration for these two sites appeared to very high (Figure 4.5a). These two sites had the highest litter carbon stocks of all sites (see Chapter 3; Figures 3.2 and 3.3a), which influenced the litter-derived respiration because it is based on the litter carbon stock divided by turnover time. When the two outliers were excluded, SOM-derived respiration and respiration from recently fixed carbon both increased significantly and near significantly, respectively, with increasing nitrogen content of the F+H layers.

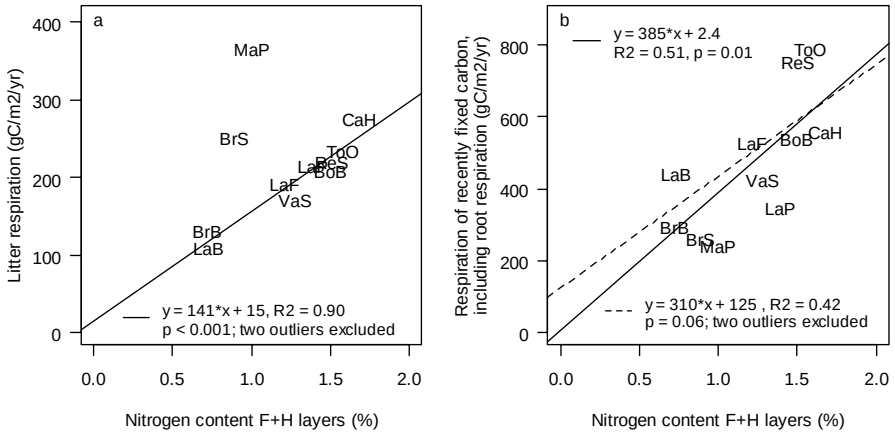

Figure 4.5: (a) Litter-derived soil respiration plotted against nitrogen content of the decomposing (F+H) litter. Litter-derived respiration, and total SOM-derived soil respiration, were previously estimated from carbon-14 isotopes analyses and carbon stocks of litter layers and belowground SOM fractions. The apparent outlier values for litter-derived respiration of sites Mattarello P and Brigolina resulted from the high litter carbon stocks of these sites. (b) Respiration from recently fixed carbon, including root respiration, showed a (near) significant increase with increasing nitrogen content of the F+H layers. Respiration from recently fixed carbon was estimated by subtracting previously estimated SOM-derived respiration from total soil respiration.

4.4 Discussion

4.4.1 Correlation of soil respiration and nitrogen content of litter

Mean annual soil respiration of 11 forest sites increased significantly with increasing nitrogen content of the F+H layers. When two outlier sites were excluded, previously estimated litter-derived and respiration from recently fixed carbon both showed significant and near significant increases respectively, with increasing nitrogen content of the F+H layers. However, unlike total soil respiration, the litter-derived respiration and respiration from recently fixed carbon may be biased as a result of the applied partitioning methodology (based on carbon-14 isotope analyses; see Hakkenberg et al. submitted). Several studies have shown a negative response of SOM-derived and root-

derived respiration to inorganic nitrogen additions (Agren et al. 2001; Bowden et al. 2004; Burton et al. 2004; Mo et al. 2008). Low nitrogen deposition in the region of our sites (< 1 gN/m2/yr; Marchetti et al. 2002) probably explains why at our sites total soil respiration, or one of its components, did not decrease with increasing litter nitrogen.

The correlation between carbon and nitrogen contents of the F+H layers suggested that the effect of nitrogen on total soil respiration could be a result of this correlation, or at least influenced by it. It seems however that the influence of the carbon content and carbon stock of the F+H layers was limited. First, a regression in which both the carbon and nitrogen contents of the F+H layers were included showed that nitrogen content was a much more significant describing variable of the total soil respiration than the carbon content. Second, total soil respiration was not correlated with the carbon stock of the F+H layers. Third, respiration from the F+H layers was estimated to be on average 16 % of total soil respiration (ranging from 2 to 34 %; Hakkenberg et al. submitted). If changes in the carbon content and carbon stock of the F+H layers were the main causes for the relationship as observed for total soil respiration and nitrogen content of the F+H layers, than the respiration from F+H layers must have been strongly underestimated previously. Alternatively, our result could suggest that the availability of nitrogen in litter itself was an important control on total soil respiration in these ecosystems, influencing both litter-derived and root-derived respiration. Below is discussed how litter nitrogen content can influence different components of total soil respiration.

4.4.2 Availability of nitrogen as indicator of litter quality

According to theory, litter with high nitrogen content is easier decomposable (Chapin et al. 2002; Chapter 7). In addition litter productivity can expected to be higher when nutrient availability is higher. The correlation coefficient reported previously for combined turnover times of L and F+H layers and their nitrogen content (see Chapter 2; Table 2.2) was near significant (P = 0.07). Thus, overall there was a tendency of increasing litter quality (lower turnover time) with increasing litter nitrogen content, which may have contributed to higher total soil respiration at sites with higher litter nitrogen. This seems a plausible explanation for our results. Aboveground productivity however, as reflected by litterfall, was not correlated with nitrogen content of the F+H layers. Furthermore, differences in litter quality as explanation for our results contrasts somewhat with the following two observations: (1) total soil respiration was not

correlated with the nitrogen content of the L layer, although this layer was probably more related to the initial quality of leaves and needles than the F+H layers. (2) total soil respiration was not correlated with the C:N ratio of the F+H layers. A significant amount of additional root and mycorrhizal litter input to the F+H layers as compared to the L layer litter may be a possible explanation for these contrasting observations. Root and mycorrhizal litter may have different C:N ratios than leaves and needle litter. Such quality differences in the F+H layers may cause that at some sites (Toblino, Mattarello, and Renon) the overall C:N ratio did not reflect the actual availability of nitrogen. Furthermore the lignin:N ratio may be a better indicator of litter quality (Scott and Binkley 1997), than the C:N ratio. The effect of the nitrogen content of F+H layers on litter-derived respiration was ambiguous. The two apparent outliers were the result of the higher litter stocks at these sites compared to the other sites. This resulted in high litter-derived respiration for these sites, because it is based on the ratio of litter carbon stock and litter turnover time. It might be possible that the litter stocks as determined for these sites were not representative, that is that they were overestimated. These two sites did not show higher litterfall than the other sites. For one of the two sites, Brigolina S, the high litter carbon stocks coincided with a relatively high turnover time of the decomposed litter (14.8 yr), which probably contributed to a higher litter accumulation. Results for the remaining nine sites suggested that nitrogen content of F+H layers was an important control on litter respiration.

Theoretically, a higher availability of nitrogen in the litter layers could also stimulate SOM decomposition in the mineral soil. Total soil respiration from mineral soil or from the upper five centimeter did however not increase with increasing availability of nitrogen in the F+H layers (result not shown).

4.4.3 Availability of nitrogen and root respiration

The uptake of nitrogen from the litter layers (and top of the mineral soil) by roots and mycorrhizae may have been higher at sites with a higher availability of nitrogen. This higher nitrogen uptake at these sites required a higher root and root-associated respiration. Zogg et al. (1996) found that root respiration was related to nitrogen availability in the topsoil (including litter) in sugar maple forests, in particular the spatial variability in root respiration was influenced by the nitrogen availability. In a review, Chapman et al. (2006) have suggested that a considerable fraction of plant's total nitrogen uptake consists of nitrogen released through mineralization and leaching in the

litter layers. In addition, Chapman et al. (2006) suggest that mycorrhizae, which are concentrated in the F+H layers and directly under it (Smith and Read 1997), enhance the uptake of nitrogen by plants.

Furthermore, a high nitrogen concentration in F+H layers may also have been an indirect indication of high photosynthetic activity and high productivity. Photosynthesis and productivity are known to be related to leaf nitrogen concentration (Field and Mooney 1986; Reich et al. 1999; Smith et al. 2002), and also to plant respiration, including root respiration (Amthor 1989; Ryan 1991). We do not know if nitrogen concentrations of canopy and F+H layers were correlated at our sites. In other studies however, it has been shown that nitrogen concentrations of different compartments of ecosystems can be correlated. Ollinger et al. (2002) showed that the nitrogen status of foliage and litter and upper soil were positively correlated. Newman and Hart (2006) showed that foliar nitrogen and leaf litter nitrogen were both correlated with fine root nitrogen concentration. Such results suggest that a high nitrogen concentration in one compartment indicates a high nitrogen status of an ecosystem in general. Thus, at our sites a high nitrogen concentration in F+H layer may also mean a high nitrogen concentration in canopy and, related to that, a higher root respiration.

4.4.4 Implications

Results presented here suggest that the availability of nitrogen in litter layers may serve as an indicator of mean annual soil respiration on the landscape-scale in areas with relatively low deposition of atmospheric nitrogen. Such a relationship might be applied for upscaling soil respiration fluxes and ecosystem carbon balances. Reichstein et al. (2003) showed that including leaf area index (LAI) as a measure of ecosystem productivity improved predictions of a temperature-precipitation based soil respiration model. Similarly this might be the case when soil nitrogen or canopy nitrogen is included. A link between soil respiration and nitrogen might be particularly useful when it can be observed for canopy nitrogen content. Canopy nitrogen can be determined from hyperspectral remote sensing data (Smith et al. 2002, Ollinger and Smith 2005). Such estimates of canopy nitrogen, combined with other spatially available data (e.g. mean temperature and LAI), could offer possibilities for upscaling of soil respiration data to a landscape-scale.

4.4.5 No species effect

No evidence was found which suggested the availability of nitrogen in the litter was related to tree species. Instead similar tree species occurred at the lower as well as at the higher end of the range in the nitrogen content of the F+H layers. The high number of tree species and the comparably low number of sites however may have prevented to observe a species effect.

4.5 Conclusion

This study showed that the availability of nitrogen can be an important control on total annual soil respiration. The good positive correlation between total annual soil respiration and nitrogen content of F+H litter layers that was found here, suggested that (1) a considerable fraction of the activity of decomposers, roots, mycorrhizae, and other root-associated organisms is concentrated in or near the litter layers; and (2) trees may support a high availability of nitrogen in the soil through the production of litter with a high nitrogen content; (3) Canopy nitrogen content derived from remote sensing data might be useful to scale up mean annual soil respiration to a landscape-level, if nitrogen content of litter and canopy are sufficiently correlated.

Acknowledgements

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Appendix C

Table C1. Data as plotted in Figures 4.1 to 4.5

5. Main findings and conclusions

5.1 Estimation of SOM turnover from $\Delta^{14}C$ analyses

Turnover times of SOM from 11 forest sites were estimated from $\Delta^{14}C$ values of different SOM fractions and soil layers. Turnover times of the litter layers (labile), light (intermediate), and heavy (stabilized) SOM fractions ranged from approximately 2–15, 25–150, and 50–900 years, respectively. Turnover times increased with increasing soil depth, a pattern which is typically observed. Estimation of the turnover times required assumption of constant annual carbon input and steady state SOM pools. To which extent these assumptions were met could not be verified. There were however indications that some sites have undergone land-use changes in the recent past. Alternative carbon input scenarios were not tested because documentation of the sites' management history, on which such scenarios need to be based, do not exist.

Estimating SOM turnover times from $\Delta^{14}C$ analyses can be best applied to unmanaged forest where the appropriateness of steady state and constant inputs is beyond doubt, or to forests with a documented management history from which changes in carbon inputs to the soil could be estimated.

5.2 Temperature sensitivity of SOM turnover times

A temperature response of the turnover times was found for the light and heavy SOM fractions, but not for the litter SOM fraction. A regression analysis showed that temperature sensitivities of the light and heavy SOM fractions were not significantly different. Two turnover times, from a total of 82, appeared to have an exceptionally high influence on the outcome of the regression. When these two turnover times were excluded from the analysis, the temperature sensitivity of the turnover times of the heavy SOM fraction was approximately twice as strong as that of the light SOM fraction. Two models describing a non-constant temperature sensitivity (i.e. decreasing with increasing temperature) did not fit the data better than a model with constant temperature sensitivity. Possible effects of soil acidity and soil clay content were included in the models. Their confounding effects on the temperature sensitivities seemed to be limited. At the warmer sites SOM turnover may occasionally have been influenced by summer drought. There was however no obvious drought effect on the turnover times of the light and heavy fractions, i.e. at higher temperatures the turnover

times did not show an obvious increase. Nor did regressions with the model that predicts the strongest decline in temperature sensitivity at higher temperatures (the Lloyd-Taylor function) result in better fits.

A temperature sensitivity of the turnover times of the labile fraction could not be detected in this study. This may have been the result of a confounding effect of summer drought occurring at the warmer sites or of differences in the quality of the labile SOM fractions among sites, e.g. as a result of six different dominating tree species. Temperature sensitivity of the heavy SOM fraction was at least equal to that of the light fraction, and possible twice as high. Since the fitted models are exponential, results suggest that largest absolute changes in SOM turnover as a result of warming may take place in relatively cold areas (e.g. alpine and boreal forests). No evidence was found for a non-constant (i.e. decreasing with increasing temperature) temperature sensitivity of the light and heavy SOM fractions. This may however been related to the relatively short mean annual temperature range (from 4^{o} to 12^{o}C).

5.3 Δ^{14}C-based partitioning of soil respiration

Respiration derived from the three SOM fractions was calculated by combining their Δ^{14}C-based turnover times and carbon stocks. Litter was found to be the main source of SOM-derived respiration, with an average respiration flux of 218 gC/m^2/yr. Average contributions of the light and heavy SOM fractions to soil respiration were much lower with 16 and 36 gC/m^2/yr, respectively. On average respiration derived from the litter, light and heavy SOM fractions accounted for ~30, ~2, and ~5% of the sites total soil respiration, respectively. The remaining ~63% of total soil respiration was derived from roots, root-associated organisms, and very labile litter which decomposes in less than one year. Δ^{14}C-based SOM-derived respiration as estimated here was relatively low as compared to two alternative estimates taken from published studies and which are based on (1) regressions of the sites' soil respiration against total carbon stocks and fine root biomass and (2) on a meta-analysis of results from soil respiration partitioning studies.

Roots, root-associated organisms, and aboveground litter decomposition were found to be the dominant sources of soil respiration. Estimation of SOM-derived respiration from Δ^{14}C analyses may however be less suitable for: (i) SOM fractions like aboveground litter which carbon stocks fluctuate considerably during the year because, depending on the time of sampling, the carbon respired in the current year or a fraction

of it is not included in the carbon stock, and thus not included in the $\Delta^{14}C$-based respiration; or for (ii) SOM fractions that are very heterogeneous because this may result in an underestimation of this fraction's respiration flux.

5.4 Soil respiration and nitrogen content of decomposed litter

The nitrogen content of the decomposed litter layers was found to be an important control on total annual soil respiration. The relationship explained 70% of the variation in the mean annual soil respiration rates of the 11 forest sites. The $\Delta^{14}C$-based litter respiration and the corresponding estimates of root-derived respiration (i.e. the two main components of total soil respiration; see above) both tended to increase with increasing litter nitrogen. The importance of nitrogen on litter decomposition, total soil respiration, root respiration, and ecosystem productivity has been demonstrated in many other studies. The sign of the effect of nitrogen availability may however depend on whether and how much nitrogen is added to the ecosystem.

These results suggested that much of the biological activity in the soil is located in or near the decomposed litter layers. Roots, microorganisms associated with roots, and SOM decomposers all take up the nitrogen that is available in the decomposed litter. Furthermore, results suggested that plants are able to influence the nitrogen availability through the quality of their litter. A similar relationship might exist between total soil respiration and canopy nitrogen. Canopy nitrogen content obtained from hyperspectral remote sensing data might therefore be useful to estimates of soil respiration on the landscape level, or help further improve estimated based on e.g. temperature and leaf area index.

5.5 Outlook

Carbon-14 isotope analyses of different SOM fractions are a useful tool to estimate turnover times of different SOM fractions. Combining different SOM fractionation techniques, as well as their further development, may improve the understanding of differences in SOM turnover in the soil profile.

In this study the temperature sensitivity of the heavy SOM fraction was at least equal to that of the light fraction, and possibly twice as high. To quantify the temperature sensitivities of SOM fractions in different ecosystems requires more effort. Whether temperature sensitivity of SOM turnover is constant or decreasing with increasing temperature requires studies along extensive temperature gradients.

SOM-derived respiration based on $\Delta^{14}C$ provides an indication of the order of magnitude of the different components of soil respiration. However, the method is not able to separate root respiration and respiration derived from the decomposition of very labile SOM. Combining the $\Delta^{14}C$-based method with methods that are able to capture the seasonal dynamics in soil respiration components may improve partitioning of soil respiration. Furthermore, the $\Delta^{14}C$-based partitioning method may be influenced by heterogeneity of the isolated SOM fractions. Comparison of $\Delta^{14}CO_2$ of soil respiration in incubation experiments can help to evaluate the $\Delta^{14}C$-based method, and it may provide indications about the homogeneity of isolated SOM fractions.

Results obtained here suggest soil nitrogen availability can drive both root as well as soil microbial activity. Other studies on the other hand show that effects of nitrogen additions are variable but that such additions may also slow down SOM turnover and negatively affect root respiration. Increasing nitrogen depositions therefore have the potential to change the carbon balance of forests in different directions. Studying soil carbon and nitrogen dynamics together may improve the understanding of the role of nitrogen for soil carbon turnover. In addition, further research should clarify to which extent nitrogen concentrations in litter and canopies are linked. If a good or reasonable correlation between the two parameters is found than canopy nitrogen concentrations derived from remotely sensed data may be used to estimate soil respiration on a landscape scale.

6. Appendices

Appendix A

Table A1.1. $\Delta^{14}C$ values of fresh (L), fragmented (F), and humified (H) litter samples and their corresponding estimated turnover times. Replicate measurements were only performed for sites Lavarone and Renon.

Site no.	Site name	Layer(s)	Pooled sample	Pit number(s)			Replicate	$\Delta^{14}C$ (‰) in 2000	error $\Delta^{14}C$ (‰)	SOM turnover time (years)
1	Casteller	L	Yes	1	2	3		90.2	3.1	1.8
2	Toblino	L	Yes	1	2	3		100.9	2.9	1.8
3	Mattarello	L	No		2			94.7	3.9	n.a.
5	Lagolo B	L	No		2			99.8	3.0	3.5
6	Brigolina B	L	Yes	1	2	3		90.2	2.9	1.8
7	Brigolina S	L	Yes	1	2	3		135.2	3.0	4.7
8	Vaneze	L	No	1				144.0	4.5	4.7
9	Lavarone	L	No	2			A	127.8	3.2	3.1
9	Lavarone	L	No	2			B	139.6	5.2	4.3
9	Lavarone	L	No		6		A	121.9	3.2	2.4
9	Lavarone	L	No		6		B	119.2	5.1	2.0
10	Bondone	L	Yes	1	2	3		90.4	3.3	1.9
11	Renon	L	No	4			A	124.5	3.0	1.8
11	Renon	L	No	4			B	119.8	5.2	1.1
11	Renon	L	No		15		A	126.3	3.0	3.8
11	Renon	L	No		15		B	142.7	5.3	5.4
1	Casteller	F+H	Yes	1	2	3		103.6	3.4	4.1
2	Toblino	F+H	Yes	1	2	3		160.5	3.0	8.6
3	Mattarello	F+H	Yes	1	2	3		111.9	3.1	3.6
4	Lagolo P	F+H	No	1				150.5	3.8	6.9
5	Lagolo B	F+H	Yes		2	3		149.7	3.2	9.2
6	Brigolina B	F+H	Yes	1	2	3		126.5	3.5	6.7
7	Brigolina S	F+H						†		14.8
8	Vaneze	F+H						†		7.2
9	Lavarone	F+H		2			A	†		6.6
9	Lavarone	F+H		2			B	†		6.2
9	Lavarone	F+H			6		A	†		6.3
9	Lavarone	F+H			6		B	†		5.1
10	Bondone	F+H	Yes	1	2	3		133.8	2.9	7.5
11	Renon	F+H		4			A	†		7.7
11	Renon	F+H		4			B	†		7.5
11	Renon	F+H			15		A	†		6.8
11	Renon	F+H			15		B	†		7.4
7	Brigolina S	F	Yes	1	2	3		196.6	3.7	‡
8	Vaneze	F	Yes	1	2	3		169.0	2.9	‡
9	Lavarone	F	No	2			A	154.5	3.3	‡
9	Lavarone	F	No	2			B	157.7	5.3	‡
9	Lavarone	F	No		6		A	146.3	3.3	‡
9	Lavarone	F	No		6		B	135.3	6.5	‡
11	Renon	F	No	4			A	167.4	3.3	‡

Site no.	Site name	Layer(s)	Pooled sample	Pit number(s)	Replicate	$\Delta^{14}C$ (‰) in 2000	error $\Delta^{14}C$ (‰)	SOM turnover time (years)
11	Renon	F	No	4	B	153.5	5.3	‡
11	Renon	F	No	15	A	144.5	4.4	‡
11	Renon	F	No	15	B	143.5	6.2	‡
7	Brigolina S	H	Yes	1 2 3		227.4	3.0	||
8	Vaneze	H	No	1		181.8	3.4	||
9	Lavarone	H	No	2	A	182.2	4.2	||
9	Lavarone	H	No	2	B	165.7	6.8	||
9	Lavarone	H	No	6	A	173.6	3.4	||
9	Lavarone	H	No	6	B	158.1	5.3	||
11	Renon	H	No	4	A	204.1	3.9	||
11	Renon	H	No	4	B	210.3	5.6	||
11	Renon	H	No	15	A	160.9	4.1	||
11	Renon	H	No	15	B	168.4	5.4	||

n.a. = Not available because the model could not be fitted to this $\Delta^{14}C$ value.
† The turnover time in this row was determined from a weighted average $\Delta^{14}C$ value of the corresponding F and H layers, as described in the paper.
‡ A turnover time was determined from a weighted $\Delta^{14}C$ value of this layer and the $\Delta^{14}C$ values of the corresponding H layer.
|| A turnover time was determined from a weighted $\Delta^{14}C$ value of this layer and the $\Delta^{14}C$ values of the corresponding F layer.

Table A1.2. $\Delta^{14}C$ values of the light SOM fraction samples (density ≤ 1.6 g/cm^3) of mineral soil samples from four soil layers and their corresponding estimated turnover times. Replicate measurements were only performed for sites Lavarone and Renon.

Site no.	Site name	Layer	Pooled sample	Pit number(s)	Replicate	$\Delta^{14}C$ (‰) in 2000	error $\Delta^{14}C$ (‰)	SOM turnover time (years)
1	Casteller	0-5 cm	Yes	1 2 3		150.0	7.0	53.4
2	Toblino	0-5 cm	Yes	1 2		162.3	3.0	47.2
2	Toblino	0-5 cm	No	3		178.9	2.9	39.6
3	Mattarello	0-5 cm	No	1		157.2	3.2	49.6
3	Mattarello	0-5 cm	No	2		132.0	2.9	63.9
3	Mattarello	0-5 cm	No	3		195.4	3.8	32.6
4	Lagolo P	0-5 cm	Yes	1 2 3		209.0	3.0	26.6
5	Lagolo B	0-5 cm	Yes	1 2		150.2	4.1	53.3
5	Lagolo B	0-5 cm	No	3		177.6	1.6	40.2
6	Brigolina B	0-5 cm	Yes	1 2 3		136.6	2.7	61.0
7	Brigolina S	0-5 cm	No	1		174.6	3.8	41.5
7	Brigolina S	0-5 cm	No	2		126.3	2.8	67.6
7	Brigolina S	0-5 cm	No	3		207.4	2.8	27.3
8	Vaneze	0-5 cm	Yes	1 2 3		132.1	2.8	63.8
9	Lavarone	0-5 cm	No	2	A	187.4	5.3	36.0
9	Lavarone	0-5 cm	No	2	B	193.4	6.6	33.4
9	Lavarone	0-5 cm	No	6	A	125.7	5.6	68.0
9	Lavarone	0-5 cm	No	6	B	130.9	5.0	64.5
10	Bondone	0-5 cm	Yes	1 2 3		184.2	3.4	37.3
11	Renon	0-5 cm	No	4	A	68.0	5.1	126.9

Site no.	Site name	Layer	Pooled sample	Pit number(s)			Replicate	$\Delta^{14}C$ (‰) in 2000	error $\Delta^{14}C$ (‰)	SOM turnover time (years)
11	Renon	0-5 cm	No	4			B	158.6	3.3	49.0
11	Renon	0-5 cm	No		15		A	117.1	6.9	74.2
11	Renon	0-5 cm	No		15		B	145.0	6.9	56.1
1	Casteller	5-10 cm	Yes	1	2	3		111.3	3.0	78.7
2	Toblino	5-10 cm	Yes	1	2			173.1	3.1	42.1
2	Toblino	5-10 cm	No			3		146.0	2.9	55.5
3	Mattarello	5-10 cm	No	1				169.0	3.1	44.0
3	Mattarello	5-10 cm	No		2			105.4	2.9	83.7
3	Mattarello	5-10 cm	No			3		140.7	3.0	58.5
4	Lagolo P	5-10 cm	Yes	1	2	3		180.7	3.4	38.8
5	Lagolo B	5-10 cm	Yes	1	2			97.3	1.9	91.1
5	Lagolo B	5-10 cm	No			3		129.5	2.6	65.5
6	Brigolina B	5-10 cm	Yes	1	2	3		133.8	2.9	62.7
7	Brigolina S	5-10 cm	No	1				147.9	2.9	54.5
7	Brigolina S	5-10 cm	No		2			100.0	2.7	88.5
7	Brigolina S	5-10 cm	No			3		184.3	2.3	37.2
8	Vaneze	5-10 cm	Yes	1	2	3		91.5	3.6	97.1
9	Lavarone	5-10 cm	No	2			A	112.4	6.6	77.8
9	Lavarone	5-10 cm	No	2			B	132.0	5.8	63.8
9	Lavarone	5-10 cm	No		6		A	141.4	7.0	58.1
9	Lavarone	5-10 cm	No		6		B	111.9	5.3	78.2
10	Bondone	5-10 cm	Yes	1	2	3		140.6	2.8	58.6
11	Renon	5-10 cm	No	4			A	154.0	5.1	51.3
11	Renon	5-10 cm	No	4			B	104.8	4.9	84.2
11	Renon	5-10 cm	No		15		A	94.3	4.9	94.1
11	Renon	5-10 cm	No		15		B	83.8	5.0	105.6
1	Casteller	10-20 cm	Yes	1		3		83.6	3.2	106.0
2	Toblino	10-20 cm	Yes	1	2			232.9	2.8	n.a.
2	Toblino	10-20 cm	No			3		143.5	2.9	56.9
3	Mattarello	10-20 cm	Yes	1	2	3		114.6	3.2	76.0
4	Lagolo P	10-20 cm	Yes	1	2	3		182.9	4.4	37.9
5	Lagolo B	10-20 cm	Yes	1	2			74.8	3.1	117.2
5	Lagolo B	10-20 cm	No			3		116.9	3.7	74.3
6	Brigolina B	10-20 cm	Yes	1	2	3		118.0	2.8	73.5
7	Brigolina S	10-20 cm	Yes	1	2			125.8	1.8	67.9
8	Vaneze	10-20 cm	Yes	1	2	3		85.3	2.8	103.9
9	Lavarone	10-20 cm	No	2			A	84.5	5.2	104.8
9	Lavarone	10-20 cm	No	2			B	74.1	5.4	118.1
9	Lavarone	10-20 cm	No		6		A	99.7	6.8	88.8
9	Lavarone	10-20 cm	No		6		B	110.6	5.0	79.3
10	Bondone	10-20 cm	Yes	1	2	3		138.8	3.3	59.7
11	Renon	10-20 cm	No	4			A	210.5	6.4	25.8
11	Renon	10-20 cm	No	4			B	219.9	6.8	n.a.
11	Renon	10-20 cm	No		15		A	-4.7	5.2	338.8
11	Renon	10-20 cm	No		15		B	-21.5	4.5	428.1
1	Casteller	20-30 cm	Yes	1		3		74.5	2.7	117.6
3	Mattarello	20-30 cm	Yes	1	2	3		76.4	2.6	115.0
5	Lagolo B	20-30 cm	Yes	1	2			75.8	3.2	115.8

Site no.	Site name	Layer	Pooled sample	Pit number(s)	Replicate	$\Delta^{14}C$ (‰) in 2000	error $\Delta^{14}C$ (‰)	SOM turnover time (years)
5	Lagolo B	20-30 cm	No	3		134.4	3.2	62.3
6	Brigolina B	20-30 cm	Yes	1 2 3		90.7	3.7	97.9
7	Brigolina S	20-30 cm	Yes	1 2 3		135.2	2.8	61.9
8	Vaneze	20-30 cm	Yes	1 2 3		85.9	3.2	103.2
9	Lavarone	20-30 cm	No	2	A	140.4	5.1	58.7
9	Lavarone	20-30 cm	No	2	B	153.0	6.9	51.8
9	Lavarone	20-30 cm	No	6	A	33.0	4.6	198.7
9	Lavarone	20-30 cm	No	6	B	22.0	4.6	231.2
11	Renon	20-30 cm	No	4	A	100.8	5.7	87.9
11	Renon	20-30 cm	No	4	B	104.7	6.6	84.3
11	Renon	20-30 cm	No	15	A	-94.5	4.3	989.1
11	Renon	20-30 cm	No	15	B	-190.8	5.4	2027.4

n.a. = Not available because the model could not be fitted to this $\Delta^{14}C$ value.

Table A1.3. $\Delta^{14}C$ values of the heavy SOM fraction samples (density > 1.6 g/cm^3) of mineral soil samples from four soil layers and their corresponding estimated turnover times. Replicate measurements were only performed for sites Lavarone and Renon.

Site no.	Site name	Soil layer	Pooled sample	Pit number(s)	Replicate	$\Delta^{14}C$ (‰) in 2000	error $\Delta^{14}C$ (‰)	Lime correction	Fraction of organic carbon (X)	Lime corrected $\Delta^{14}C$ (‰) in 2000	SOM turnover time (years)
1	Casteller	0-5 cm	Yes	1 2 3		128.6	2.8	No			66.0
2	Toblino	0-5 cm	Yes	1 2		162.6	2.8	No			47.0
2	Toblino	0-5 cm	No	3		49.4	2.7	No			159.8
3	Mattarello	0-5 cm	No	1		-23.0	2.1	Yes	0.86	136.0	61.3
3	Mattarello	0-5 cm	No	2		78.4	2.9	Yes	0.97	111.7	78.3
3	Mattarello	0-5 cm	No	3		-58.1	2.6	Yes	0.86	95.3	93.2
4	Lagolo P	0-5 cm	Yes	1 2 3		111.3	3.5	No			78.7
5	Lagolo B	0-5 cm	Yes	1 2		130.9	2.7	No			64.6
5	Lagolo B	0-5 cm	No	3		128.0	2.7	No			66.4
6	Brigolina B	0-5 cm	Yes	1 2 3		75.9	2.8	No			115.7
7	Brigolina S	0-5 cm	No	1		143.6	2.9	No			56.9
7	Brigolina S	0-5 cm	No	2		62.4	2.3	Yes	0.98	84.1	105.3
7	Brigolina S	0-5 cm	No	3		189.5	2.9	Yes	0.92	292.9	n.a.
8	Vaneze	0-5 cm	Yes	1 2 3		44.5	2.8	No			170.2
9	Lavarone	0-5 cm	No	2	A	114.5	2.8	No			76.2
9	Lavarone	0-5 cm	No	2	B	120.5	2.6	No			71.6
9	Lavarone	0-5 cm	No	6	A	59.0	3.4	No			141.5
9	Lavarone	0-5 cm	No	6	B	42.5	2.7	Yes	0.99	53.0	152.6
10	Bondone	0-5 cm	Yes	1 2 3		122.8	2.8	No			70.0
11	Renon	0-5 cm	No	4	A	32.4	2.8	No			200.3
11	Renon	0-5 cm	No	4	B	24.7	2.8	No			222.9
11	Renon	0-5 cm	No	15	A	44.2	3.3	No			171.0
11	Renon	0-5 cm	No	15	B	79.1	4.7	No			111.4
1	Casteller	5-10 cm	Yes	1 2 3		20.4	4.6	Yes	0.94	85.5	103.7
2	Toblino	5-10 cm	Yes	1 2		-18.2	2.6	No			409.4

Site no.	Site name	Soil layer	Pooled sample	Pit number(s)			Replicate	$\Delta^{14}C$ (‰) in 2000	error $\Delta^{14}C$ (‰)	Lime correction	Fraction of organic carbon (*X*)	Lime corrected $\Delta^{14}C$ (‰) in 2000	SOM turnover time (years)
2	Toblino	5-10 cm	No			3		-5.9	3.1	No			344.4
3	Mattarello	5-10 cm	No	1				2.1	3.4	Yes	0.89	126.0	67.8
3	Mattarello	5-10 cm	No		2			37.1	2.8	Yes	0.95	91.7	96.8
3	Mattarello	5-10 cm	No			3		-117.6	2.7	Yes	0.83	63.1	134.5
4	Lagolo P	5-10 cm	Yes	1	2	3		131.9	3.9	Yes	0.96	179.1	39.5
5	Lagolo B	5-10 cm	Yes	1	2			64.4	2.7	No			132.4
5	Lagolo B	5-10 cm	No			3		75.6	2.8	No			116.0
6	Brigolina B	5-10 cm	Yes	1	2	3		72.0	2.8	No			121.1
7	Brigolina S	5-10 cm	No	1				82.0	3.0	No			107.8
7	Brigolina S	5-10 cm	No		2			39.7	3.1	No			181.5
7	Brigolina S	5-10 cm	No			3		206.1	3.0	Yes	0.91	325.4	n.a.
8	Vaneze	5-10 cm	Yes	1	2	3		20.0	3.2	No			238.0
9	Lavarone	5-10 cm	No	2			A	62.7	3.0	No			135.2
9	Lavarone	5-10 cm	No	2			B	57.4	3.1	No			144.4
9	Lavarone	5-10 cm	No		6		A	-14.6	2.4	No			389.5
9	Lavarone	5-10 cm	No		6		B	-12.1	2.8	No			376.2
10	Bondone	5-10 cm	Yes	1	2	3		93.1	2.8	No			95.4
11	Renon	5-10 cm	No	4			A	34.3	4.8	No			195.2
11	Renon	5-10 cm	No	4			B	47.6	4.8	No			163.5
11	Renon	5-10 cm	No		15		A	22.4	3.3	No			230.0
11	Renon	5-10 cm	No		15		B	19.9	5.1	No			238.3
1	Casteller	10-20 cm	Yes	1		3		-98.8	3.9	Yes	0.86	48.0	162.8
2	Toblino	10-20 cm	Yes	1	2			14.8	3.2	No			256.3
2	Toblino	10-20 cm	No			3		-24.4	2.7	No			445.5
3	Mattarello	10-20 cm	Yes	1	2	3		-106.9	3.0	Yes	0.86	38.5	184.4
4	Lagolo P	10-20 cm	Yes	1	2	3		50.7	2.1	No			157.1
5	Lagolo B	10-20 cm	Yes	1	2			1.5	2.6	No			310.0
5	Lagolo B	10-20 cm	No			3		26.6	2.7	No			216.9
6	Brigolina B	10-20 cm	Yes	1	2	3		14.9	2.8	No			255.8
7	Brigolina S	10-20 cm	Yes	1	2			23.8	2.1	No			225.8
8	Vaneze	10-20 cm	Yes	1	2	3		-10.8	3.2	No			369.0
9	Lavarone	10-20 cm	No	2			A	8.9	2.5	No			278.9
9	Lavarone	10-20 cm	No	2			B	18.4	2.5	No			243.4
9	Lavarone	10-20 cm	No		6		A	-34.4	2.4	No			508.4
9	Lavarone	10-20 cm	No		6		B	-128.5	1.9	No			1321.2
10	Bondone	10-20 cm	Yes	1	2	3		78.4	3.4	No			112.4
11	Renon	10-20 cm	No	4			A	-110.5	2.7	No			1141.1
11	Renon	10-20 cm	No	4			B	-99.5	2.6	No			1035.9
11	Renon	10-20 cm	No		15		A	-53.1	3.4	No			641.4
11	Renon	10-20 cm	No		15		B	-50.8	4.4	No			623.8
1	Casteller	20-30 cm	Yes	1		3		-219.8	5.9	Yes	0.78	0.3	315.3
3	Mattarello	20-30 cm	Yes	1	2	3		-258.9	2.6	Yes	0.76	-24.8	448.0
5	Lagolo B	20-30 cm	Yes	1	2			-65.0	2.6	No			733.8
5	Lagolo B	20-30 cm	No			3		-26.9	2.6	No			460.7
6	Brigolina B	20-30 cm	Yes	1	2	3		-44.0	3.5	No			574.4
7	Brigolina S	20-30 cm	Yes	1	2	3		20.9	2.7	No			235.2

Site no.	Site name	Soil layer	Pooled sample	Pit number(s)	Replicate	$\Delta^{14}C$ (‰) in 2000	error $\Delta^{14}C$ (‰)	Lime correction	Fraction of organic carbon (*X*)	Lime corrected $\Delta^{14}C$ (‰) in 2000	SOM turnover time (years)
8	Vaneze	20-30 cm	Yes	1 2 3		-79.9	3.5	No			859.0
9	Lavarone	20-30 cm	No	2	A	-9.2	2.5	No			361.0
9	Lavarone	20-30 cm	No	2	B	-21.0	3.7	No			425.1
9	Lavarone	20-30 cm	No	6	A	-126.0	2.2	No			1295.8
9	Lavarone	20-30 cm	No	6	B	-44.3	2.7	No			576.5
11	Renon	20-30 cm	No	4	A	-183.7	3.0	No			1940.5
11	Renon	20-30 cm	No	4	B	-174.8	2.9	No			1833.2
11	Renon	20-30 cm	No	15	A	-157.6	2.7	No			1634.9
11	Renon	20-30 cm	No	15	B	-156.1	4.0	No			1618.1

n.a. = Not available because the model could not be fitted to this $\Delta^{14}C$ value.

Table A2 listing the pH values and estimated clay contents of the sites' soil layers. The pH values are averaged values of the three pits (two pits in case of sites Lavarone and Renon)

Site no.	Site name	Soil layer	pH	Clay content (%)‡
1	Casteller	0-5 cm	6.7	34.3
2	Toblino	0-5 cm	6.1	48.1
3	Mattarello	0-5 cm	7.3	26.2
4	Lagolo P	0-5 cm	6.3	37.4
5	Lagolo B	0-5 cm	5.8	27.4
6	Brigolina B	0-5 cm	6.8	39.2
7	Brigolina S	0-5 cm	5.0	15.6
8	Vaneze	0-5 cm	6.0	19.9
9	Lavarone	0-5 cm	4.9	25.3
10	Bondone	0-5 cm	6.9	38.0
11	Renon	0-5 cm	4.1	10.0
1	Casteller	5-10 cm	7.2	36.5
2	Toblino	5-10 cm	5.9	40.5
3	Mattarello	5-10 cm	7.4	33.4
4	Lagolo P	5-10 cm	6.3	37.4
5	Lagolo B	5-10 cm	5.8	15.6
6	Brigolina B	5-10 cm	6.9	39.2
7	Brigolina S	5-10 cm	5.1	44.5
8	Vaneze	5-10 cm	6.4	26.4
9	Lavarone	5-10 cm	4.9	34.2
10	Bondone	5-10 cm	7.0	38.0
11	Renon	5-10 cm	4.5	10.6
1	Casteller	10-20 cm	7.4	36.5
2	Toblino	10-20 cm	6.3	27.0
3	Mattarello	10-20 cm	7.5	38.2
4	Lagolo P	10-20 cm	6.4	35.6
5	Lagolo B	10-20 cm	6.7	16.6
6	Brigolina B	10-20 cm	6.9	40.2
7	Brigolina S	10-20 cm	5.4	44.1

Site no.	Site name	Soil layer	pH	Clay content (%)‡
8	Vaneze	10-20 cm	6.6	36.7
9	Lavarone	10-20 cm	5.5	22.0
10	Bondone	10-20 cm	7.1	45.7
11	Renon	10-20 cm	5.1	11.1
1	Casteller	20-30 cm	7.5	36.5
2	Toblino	20-30 cm	†	27.0
3	Mattarello	20-30 cm	7.6	38.2
4	Lagolo P	20-30 cm	†	24.9
5	Lagolo B	20-30 cm	7.5	29.7
6	Brigolina B	20-30 cm	6.9	41.2
7	Brigolina S	20-30 cm	5.5	43.1
8	Vaneze	20-30 cm	7.4	37.7
9	Lavarone	20-30 cm	6.1	12.0
10	Bondone	20-30 cm	†	47.6
11	Renon	20-30 cm	5.3	11.1

† Soil layer was not sampled.
‡Clay contents are values as presented by Rodeghiero (2003) or where necessary calculated from those values.

Table A3 listing the estimated relative soil water content of the sites in summer of 2001, calculated from the measurements of Rodeghiero and Cescatti (2005).

Site no.	Site name	Relative soil water content
1	Casteller	0.49
2	Toblino	0.39
3	Mattarello	0.33
4	Lagolo P	0.28
5	Lagolo B	0.37
6	Brigolina B	0.56
7	Brigolina S	0.38
8	Vaneze	0.48
9	Lavarone	0.40
10	Bondone	0.37
11	Renon	0.59

Appendix B

Table B1. Carbon stocks of the organic layers. Minimum and maximum carbon stocks refer to sorted and unsorted litter samples, as described in the paper.

Site no.	Site name	Layer(s)	Pit number	Carbon stock (gC/m²)		
				Maximum	Minimum	Average
1	Casteller	L	1	231	93	162
1	Casteller	L	2	494	380	437
1	Casteller	L	3	210	126	168
2	Toblino	L	1	303	135	219
2	Toblino	L	2	408	265	336
2	Toblino	L	3	443	307	375
3	Mattarello	L	1	1476	454	965
3	Mattarello	L	2	1118	318	718
3	Mattarello	L	3	721	195	458
5	Lagolo B	L	1	383	202	292
5	Lagolo B	L	2	284	219	251
5	Lagolo B	L	3	169	89	129
6	Brigolina B	L	1	268	153	210
6	Brigolina B	L	2	452	152	302
6	Brigolina B	L	3	319	160	240
7	Brigolina S	L	1	455	388	421
7	Brigolina S	L	2	853	566	710
7	Brigolina S	L	3	1300	848	1074
8	Vaneze	L	1	663	10	337
9	Lavarone	L	2	682	222	452
9	Lavarone	L	2	687	224	455
9	Lavarone	L	6	165	69	117
9	Lavarone	L	6	169	70	120
10	Bondone	L	1	328	236	282
10	Bondone	L	2	461	318	389
10	Bondone	L	3	304	229	266
11	Renon	L	4	110	41	76
11	Renon	L	4	108	40	74
11	Renon	L	15	81	67	74
11	Renon	L	15	81	67	74
1	Casteller	F+H	1	201	158	179
1	Casteller	F+H	2	160	143	151
1	Casteller	F+H	3	1759	1590	1675
2	Toblino	F+H	1	280	214	247
2	Toblino	F+H	2	669	615	642
2	Toblino	F+H	3	1180	1067	1124
3	Mattarello	F+H	1	1492	1016	1254
3	Mattarello	F+H	2	186	127	157
3	Mattarello	F+H	3	203	114	158
4	Lagolo P	F+H	1	1392	1193	1292
4	Lagolo P	F+H	2	2686	1800	2243
4	Lagolo P	F+H	3	1614	1185	1400
5	Lagolo B	F+H	1	577	510	544
5	Lagolo B	F+H	2	514	478	496
5	Lagolo B	F+H	3	666	545	605
6	Brigolina B	F+H	1	98	57	77

Site no.	Site name	Layer(s)	Pit number	Carbon stock (gC/m²)		
				Maximum	Minimum	Average
6	Brigolina B	F+H	2	106	48	77
6	Brigolina B	F+H	3	113	86	99
7	Brigolina S	F+H	1	487	467	477
7	Brigolina S	F+H	2	2311	2180	2246
7	Brigolina S	F+H	3	2231	2154	2192
8	Vaneze	F+H	1	3183	2862	3022
8	Vaneze	F+H	2	414	340	377
8	Vaneze	F+H	3	159	127	143
9	Lavarone	F+H	2	695	583	639
9	Lavarone	F+H	2	701	588	645
9	Lavarone	F+H	6	783	734	758
9	Lavarone	F+H	6	790	741	765
10	Bondone	F+H	1	722	502	612
10	Bondone	F+H	2	528	400	464
10	Bondone	F+H	3	556	354	455
11	Renon	F+H	4	979	771	875
11	Renon	F+H	4	980	772	876
11	Renon	F+H	15	2065	1747	1906
11	Renon	F+H	15	2068	1749	1908

Table B2. Carbon stocks of the light and heavy fraction. Sample treatment indicates whether the sample was pooled (P) prior to density fractionation and if so with the samples from which other pits (the later in parenthesis) or if it was processed as a single (S) sample.

Site no.	Site name	Pit	Layer	Sample treatment	Replicate§	Carbon stock (gC/m²)	
						Heavy fraction	Light fraction
1	Casteller	1	0-5 cm	P (1,2,3)		387	1427
1	Casteller	2	0-5 cm	P (1,2,3)		411	1516
1	Casteller	3	0-5 cm	P (1,2,3)		270	995
2	Toblino	1	0-5 cm	P (1,2)		844	1278
2	Toblino	2	0-5 cm	P (1,2)		703	1064
2	Toblino	3	0-5 cm	S		282	751
3	Mattarello	1	0-5 cm	S		198	984
3	Mattarello	2	0-5 cm	S		234	1414
3	Mattarello	3	0-5 cm	S		264	1209
4	Lagolo P	1	0-5 cm	P (1,2,3)		404	1316
4	Lagolo P	2	0-5 cm	P (1,2,3)		360	1173
4	Lagolo P	3	0-5 cm	P (1,2,3)		286	933
5	Lagolo B	1	0-5 cm	P (1,2)		386	1095
5	Lagolo B	2	0-5 cm	P (1,2)		318	905
5	Lagolo B	3	0-5 cm	S		305	1046
6	Brigolina B	1	0-5 cm	P (1,2,3)		104	1053
6	Brigolina B	2	0-5 cm	P (1,2,3)		103	1046
6	Brigolina B	3	0-5 cm	P (1,2,3)		122	1234
7	Brigolina S	1	0-5 cm	S		223	1046
7	Brigolina S	2	0-5 cm	S		825	916
7	Brigolina S	3	0-5 cm	S		569	1316
8	Vaneze	1	0-5 cm	P (1,2,3)		256	2392

Site no.	Site name	Pit	Layer	Sample treatment	Replicate§	Carbon stock (gC/m²)	
						Heavy fraction	Light fraction
8	Vaneze	2	0-5 cm	P (1,2,3)		209	1952
8	Vaneze	3	0-5 cm	P (1,2,3)		280	2625
9	Lavarone	2	0-5 cm	S	A	540	1316
9	Lavarone	2	0-5 cm	S	B	693	1401
9	Lavarone	6	0-5 cm	S	A	130	1128
9	Lavarone	6	0-5 cm	S	B	161	1210
10	Bondone	1	0-5 cm	P (1,2,3)		380	1365
10	Bondone	2	0-5 cm	P (1,2,3)		393	1412
10	Bondone	3	0-5 cm	P (1,2,3)		392	1409
11	Renon	4	0-5 cm	S	A	907	1178
11	Renon	4	0-5 cm	S	B	722	1214
11	Renon	15	0-5 cm	S	A	1380	553
11	Renon	15	0-5 cm	S	B	720	1299
1	Casteller	1	5-10 cm	P (1,2,3)		114	1055
1	Casteller	2	5-10 cm	P (1,2,3)		137	1267
1	Casteller	3	5-10 cm	P (1,2,3)		153	1415
2	Toblino	1	5-10 cm	P (1,2)		263	732
2	Toblino	2	5-10 cm	P (1,2)		262	729
2	Toblino	3	5-10 cm	S		209	848
3	Mattarello	1	5-10 cm	S		175	1038
3	Mattarello	2	5-10 cm	S		96	746
3	Mattarello	3	5-10 cm	S		106	982
4	Lagolo P	1	5-10 cm	P (1,2,3)		239	924
4	Lagolo P	2	5-10 cm	P (1,2,3)		276	1064
4	Lagolo P	3	5-10 cm	P (1,2,3)		223	860
5	Lagolo B	1	5-10 cm	P (1,2)		184	822
5	Lagolo B	2	5-10 cm	P (1,2)		122	546
5	Lagolo B	3	5-10 cm	S		162	595
6	Brigolina B	1	5-10 cm	P (1,2,3)		100	1397
6	Brigolina B	2	5-10 cm	P (1,2,3)		96	1350
6	Brigolina B	3	5-10 cm	P (1,2,3)		106	1484
7	Brigolina S	1	5-10 cm	S		142	859
7	Brigolina S	2	5-10 cm	S		466	1022
7	Brigolina S	3	5-10 cm	S		355	1383
8	Vaneze	1	5-10 cm	P (1,2,3)		146	1953
8	Vaneze	2	5-10 cm	P (1,2,3)		80	1073
8	Vaneze	3	5-10 cm	P (1,2,3)		156	2089
9	Lavarone	2	5-10 cm	S	A	325	1702
9	Lavarone	2	5-10 cm	S	B	319	1849
9	Lavarone	6	5-10 cm	S	A	128	865
9	Lavarone	6	5-10 cm	S	B	146	923
10	Bondone	1	5-10 cm	P (1,2,3)		271	1423
10	Bondone	2	5-10 cm	P (1,2,3)		272	1431
10	Bondone	3	5-10 cm	P (1,2,3)		210	1107
11	Renon	4	5-10 cm	S	A	218	882
11	Renon	4	5-10 cm	S	B	185	984
11	Renon	15	5-10 cm	S	A	305	1003
11	Renon	15	5-10 cm	S	B	303	1039
1	Casteller	1	10-20 cm	P (1,3)		163	2123

Site no.	Site name	Pit	Layer	Sample treatment	Replicate§	Carbon stock (gC/m²)	
						Heavy fraction	Light fraction
1	Casteller	3	10-20 cm	P (1,3)		208	2721
2	Toblino	1	10-20 cm	P (1,2)		601	1210
2	Toblino	2	10-20 cm	P (1,2)		466	939
2	Toblino	3	10-20 cm	S		269	1421
3	Mattarello	1	10-20 cm	P (1,2,3)		267	3101
3	Mattarello	2	10-20 cm	P (1,2,3)		280	3251
3	Mattarello	3	10-20 cm	P (1,2,3)		165	1913
4	Lagolo P	1	10-20 cm	P (1,2,3)		424	1910
4	Lagolo P	2	10-20 cm	P (1,2,3)		426	1918
4	Lagolo P	3	10-20 cm	P (1,2,3)		350	1575
5	Lagolo B	1	10-20 cm	P (1,2)		300	1604
5	Lagolo B	2	10-20 cm	P (1,2)		243	1301
5	Lagolo B	3	10-20 cm	S		239	1262
6	Brigolina B	1	10-20 cm	P (1,2,3)		202	2391
6	Brigolina B	2	10-20 cm	P (1,2,3)		226	2665
6	Brigolina B	3	10-20 cm	P (1,2,3)		193	2277
7	Brigolina S	1	10-20 cm	P (1,2)		197	1262
7	Brigolina S	2	10-20 cm	P (1,2)		250	1600
8	Vaneze	1	10-20 cm	P (1,2,3)		265	3250
8	Vaneze	2	10-20 cm	P (1,2,3)		257	3152
8	Vaneze	3	10-20 cm	P (1,2,3)		296	3632
9	Lavarone	2	10-20 cm	S	A	311	2954
9	Lavarone	2	10-20 cm	S	B	371	2722
9	Lavarone	6	10-20 cm	S	A	207	1972
9	Lavarone	6	10-20 cm	S	B	273	1916
10	Bondone	1	10-20 cm	P (1,2,3)		405	2242
10	Bondone	2	10-20 cm	P (1,2,3)		513	2838
10	Bondone	3	10-20 cm	P (1,2,3)		484	2678
11	Renon	4	10-20 cm	S	A	179	1421
11	Renon	4	10-20 cm	S	B	185	1541
11	Renon	15	10-20 cm	S	A	177	1113
11	Renon	15	10-20 cm	S	B	209	1564
1	Casteller	1	20-30 cm	P (1,3)		128	1883
1	Casteller	3	20-30 cm	P (1,3)		57	837
3	Mattarello	1	20-30 cm	P (1,2,3)		143	1853
3	Mattarello	2	20-30 cm	P (1,2,3)		179	2323
3	Mattarello	3	20-30 cm	P (1,2,3)		121	1571
5	Lagolo B	1	20-30 cm	P (1,2)		125	815
5	Lagolo B	2	20-30 cm	P (1,2)		158	1025
5	Lagolo B	3	20-30 cm	S		169	673
6	Brigolina B	1	20-30 cm	P (1,2,3)		191	1910
6	Brigolina B	2	20-30 cm	P (1,2,3)		211	2108
6	Brigolina B	3	20-30 cm	P (1,2,3)		181	1806
7	Brigolina S	1	20-30 cm	P (1,2,3)		230	1165
7	Brigolina S	2	20-30 cm	P (1,2,3)		227	1148
7	Brigolina S	3	20-30 cm	P (1,2,3)		244	1236
8	Vaneze	1	20-30 cm	P (1,2,3)		172	2913
8	Vaneze	2	20-30 cm	P (1,2,3)		134	2274
8	Vaneze	3	20-30 cm	P (1,2,3)		36	612

Site no.	Site name	Pit	Layer	Sample treatment	Replicate§	Carbon stock (gC/m^2)	
						Heavy fraction	Light fraction
9	Lavarone	2	20-30 cm	S	A	158	925
9	Lavarone	2	20-30 cm	S	B	143	930
9	Lavarone	6	20-30 cm	S	A	134	1491
9	Lavarone	6	20-30 cm	S	B	156	1405
11	Renon	4	20-30 cm	S	A	329	1116
11	Renon	4	20-30 cm	S	B	97	975
11	Renon	15	20-30 cm	S	A	72	753
11	Renon	15	20-30 cm	S	B	57	734

§ Replicate density fractionations were only made for sites Lavarone and Renon

Appendix C

Table C1. Data as plotted in Figures 4.1 to 4.5

Site (abbreviation)	Mean annual soil tempe-rature (°C)	Annual wood increment ($m^3/ha/yr$)	Annual litterfall ($gC/m^2/yr$)	Respiration ($gC/m^2/yr$)		
				Total	L+F+H layers	Recently fixed carbon
Casteller (CaH)	11.2	2.7	214	900.7	278.2	561.4
Toblino (ToO)	11.9	8.7	515	1078.5	236.4	795.7
Mattarello (MaP)	9.9	5.9	328	669.8	368.6	244.9
Lagolo P (LaP)	9.4	3.6	188	647.1	217.6	352.3
Lagolo B (LaB)	7.6	7.5	233	594.1	111.0	444.2
Brigolina B (BrB)	7.2	9.4	257	473	132.5	299.0
Brigolina S (BrS)	7.4	16.7	275	575.2	252.9	266.3
Vaneze (VaS)	4.8	10.6	147	643.3	172.5	430.5
Lavarone (LaF)	4.5	20.5	254	772	194.3	531.3
Bondone (BoB)	7.2	6.3	177	828.8	209.3	542.7
Renon (ReS)	3.9	6.2	115	1014.2	222.4	758.4

Table C.1. Extended

Site	L layer	F+H layers			
	Nitrogen content (%)	Nitrogen content (%)	Carbon content (%)	C:N ratio	Carbon stock (gC/m^2)
CaH	1.88	1.68	31.2	18.5	668.4
ToO	1.48	1.58	31.9	20.3	671.0
MaP	0.86	1.00	31.7	31.7	523.0
LaP		1.39	34.6	25.0	1645.0
LaB	1.29	0.73	18.2	24.9	548.2
BrB	1.11	0.72	20.2	27.1	84.5
BrS	1.12	0.89	21.8	24.3	1638.4
VaS	1.07	1.28	29.1	22.8	1180.8
LaF	1.27	1.21	27.0	21.7	701.8
BoB	1.29	1.50	34.0	22.8	510.5
ReS	1.17	1.51	37.9	25.0	1391.3

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