

Soil C:N stoichiometry controls carbon sink partitioning between above-ground tree biomass and soil organic matter in high fertility forests

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The release of organic compounds from roots is a key process influencing soil carbon (C) dynamics and nutrient availability in terrestrial ecosystems. Through this process, plants stimulate microbial activity and soil organic matter (SOM) mineralization thus releasing nitrogen (N) that sustains gross and net primary production (*GPP* and *NPP*, respectively). Root inputs also contribute to SOM formation. In this study, we quantified the annual net root-derived C input to soil (*Net-C_{root}*) across six high fertility forests using an in-growth core isotope technique. On the basis of *Net-C_{root}*, wood and coarse root biomass changes, and eddy covariance data, we quantified net belowground C sequestration. Belowground C accumulation and *GPP* were inversely related to soil C:N, but not to climate or stand age. Soil C content and C:N were also related to soil texture. At these high fertility sites, biomass growth did not change with soil C:N; however, biomass growth-to-*GPP* ratio significantly increased with increasing soil C:N. This was true for both our six forest sites and for another 23 high fertility sites selected at a global scale. We suggest that, at high fertility sites, plant N demand interacts with soil C:N stoichiometry and microbial activity, resulting in higher allocation of C to above ground tree biomass with increasing soil C:N ratio. When C:N is high, microbes have a low C use efficiency, respire more of the fresh C inputs by roots and prime SOM decomposition, thereby increasing N availability for tree uptake. Soil C sequestration would therefore decrease, whereas the extra N released during SOM decomposition can promote tree growth and ecosystem C sink allocation in aboveground biomass. Conversely, C is sequestered in soil when low soil C:N promotes microbial C use efficiency and new SOM formation and stabilization on clay particles.

Keywords: Net Root-derived Carbon, Ingrowth Cores, Soil C:N, Carbon Sequestration, Carbon Partitioning, Isotopes

Introduction

Forest ecosystems worldwide are currently acting as carbon (C) sinks (Pan et al. 2011). Several factors may, however, influence the magnitude and direction of the net C balance, including recovery from historical land use (e.g., abandoned agricultural land reverting to forested land), increases in atmospheric CO₂ concentration and nitrogen (N) deposition, and climate change (Schimel et al. 2001, Thomas et al. 2010). Nonetheless, while much research has been done to understand the controls on net ecosystem C balance (Valentini et al. 2000, Rustad et al. 2001, Reichstein et al. 2007a), we know little about the controls on C sink partitioning between plant biomass and soil organic matter (SOM) pools. Soils may store C for long

periods of time (Lal 2005), accumulating on average three times the C in terrestrial vegetation (Post et al. 1982). On the other hand, more N is required per unit of C stored in soil as compared to plant biomass (Yang & Luo 2011). Hence, while an allocation to SOM may increase C sequestration in the long term, a preferential allocation to plant biomass is a more nutrient-efficient C sequestration process in the shorter term.

Studying ecosystem C sink partitioning is challenging due to the difficulties associated with quantifying the different ecosystem fluxes. Especially complex is the assessment of rapid and small changes in SOM which are linked to the balance between microbial respiration and plant inputs, including both litter and root-derived C (Schrumpf et al.

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2011). Thus, belowground C allocation and subsequent C dynamics are still far from being accurately quantified and understood (Phillips et al. 2011, Vicca et al. 2012). Root C inputs have been shown to influence soil

C sequestration, but both the magnitude and direction of this root effect are variable (Karlen & Cambardella 1996, Parton et al. 1996, Cardon et al. 2001, Rasse et al. 2005, Dijkstra & Cheng 2007).

A robust definition of net ecosystem production (*NEP*) should be based on a full ecosystem mass balance (Randerson et al. 2002), which accounts for both plant and soil sinks. When it is flux-based, *NEP* is defined as the difference between ecosystem-level gross photosynthetic gain of C (gross primary production, *GPP*) and ecosystem respiratory losses (*R_{eco}*). Alternatively, *NEP* (g C m⁻² y⁻¹) can be expressed as (Campbell et al. 2004 - eqn. 1):

$$NEP = \Delta C_{biomass} + \Delta C_{soil}$$

In deciduous forest ecosystems, $\Delta C_{biomass}$ is the annual change in plant biomass (wood, branches, coarse roots), and ΔC_{soil} is the annual net change in soil organic C (SOC) stock. In this equation, litterfall and fine root turnover are considered as soil C input and therefore contributing to the ΔC_{soil} (see eqn. 2).

Net ecosystem productivity can be directly determined using eddy covariance techniques starting from net ecosystem exchange (*NEE* = -*NEP* - Baldocchi 2003, Aubinet et al. 2012). Plant biomass changes are usually estimated *via* a combination of repeated inventories and allometric relationships (Clark et al. 2001). On the other hand, direct SOC determination methods are generally unable to quantify ΔC_{soil} in the short term (Schrumpp et al. 2011), and, at annual timescales, alternative methods are required to estimate soil C changes.

Considering that the dissolved organic C (DOC) is typically negligible, representing around 1% of forest *NPP* (Luyssaert et al. 2010), ΔC_{soil} can also be written as (eqn. 2):

$$\Delta C_{soil} = Input_{soil} - Output_{soil} \\ = Input_{litter} + Input_{root} - R_{C-rhizosphere} - Rh$$

where *Input_{litter}* is the above-ground litterfall (*i.e.*, leaves, branches, wood, etc.), *Input_{roots}* is the root-derived C input (*i.e.*, exudates, root slashing and turnover), *R_{C-rhizosphere}* is the rhizosphere respiration of root-derived C, and *Rh* is the heterotrophic respiration. Litter input is conventionally measured by litter traps, while wood input is measured using repeated sampling (Harmon & Sexton 1996), and rhizosphere and heterotrophic respiration can be estimated by a variety of methods (*e.g.*, trenching, girdling, isotopes), as reviewed by Subke et al. (2006) and Kuzyakov (2006). The largest challenge is estimating gross root inputs. However, methods exist to estimate net annual root-derived C input (*Net-C_{root}*), which is the difference between *Input_{roots}* and *R_{C-rhizosphere}* (eqn. 3):

$$NetC_{root} = Input_{roots} - R_{C-rhizosphere}$$

Different tracer methods have been used to date to estimate *Net-C_{root}*, such as pulse labeling, continuous labeling, and ¹³C natural abundance (Kuzyakov & Domanski 2000). The latter uses the difference in the stable C isotope composition of native SOM and new plant-derived organic matter to quantify *Net-C_{root}*. When natural isotope abundances do not allow the use of this approach, distinct C isotope signatures in the soil organic C (SOC) pool and plant-derived organic matter can be obtained in manipulation experiments, by growing C₃ plants (^{δ¹³C} of approximately -27‰) in soil with organic matter derived from C₄ plants (^{δ¹³C} of approximately -12‰) or *vice versa*. This approach has been successfully applied in pot (Ineson et al. 1995, Vicca et al. 2010) and field studies (Hoosbeek et al. 2004, Cotrufo et al. 2011) and was used in this investigation.

Net-C_{root}, combined with aboveground inputs to the soil (litter and dead wood), also provides interesting information about soil C dynamics. For soils at steady-state ($\Delta C_{soil}=0$), the sum of *Net-C_{root}* and aboveground inputs is the amount of C that replaces SOC decomposition, thus becoming a measure for SOC turnover. For soils which are net C sinks ($\Delta C_{soil}>0$), this sum exceeds SOC mineralization and a fraction of it enlarges the SOC pool, thus leading to soil C sequestration. In this context, for soils which are net C sinks, the ratio between ΔC_{soil} and *Net-C_{root}* + aboveground inputs indicates the fate of C input: the higher the ratio, the larger the contribution of fresh C to soil C sequestration. The opposite is true for soils that are net C sources ($\Delta C_{soil}<0$).

Root C input rates vary considerably depending on tree species, mycorrhizal associations and environmental factors (Lynch & Whipps 1990), with values of up to 40% of net assimilated C being reported (Van Veen et al. 1991). According to the microbial efficiency-mineral stabilization (MEMS) framework (Cotrufo et al. 2013), the fraction of *Net-C_{root}* inputs sequestered in the soil depends on the efficiency of decomposers to convert C into bio-products as compared to the amount of C lost as CO₂ (Six et al. 2006) and on soil matrix interactions (Sollins et al. 1996, Kleber et al. 2007). Soil organic matter mineralization is driven by both substrate stoichiometry and microbial demand for resources (Melillo et al. 1982, Hessen et al. 2004): when N is limiting, microbes use labile substrate to mineralize recalcitrant SOM (Moorhead & Sinsabaugh 2006, Craine et al. 2007). Root exudates can thus prime SOM decomposition (Lohnis 1926, Bingeman et al. 1953, Fontaine et al. 2004). Clearly, root-derived soil C inputs can either stimulate soil C sequestration or, conversely, induce pri-

ming with consequent losses of stabilized SOM but likely enhancements in N availability, which in turn can stimulate plant growth. The key factors determining the direction (and magnitude) of this effect are, however, not yet clear. Understanding the fate of root-derived C, and its effects on N dynamics and ecosystem C sequestration, is relevant from an ecological perspective and is also an urgent challenge to address, particularly in the context of global changes such as atmospheric CO₂ increase and N deposition.

The aims of the present study were: (1) to obtain an estimate of *Net-C_{root}* in six different forest ecosystems; (2) to partition *NEP* into aboveground tree biomass production and soil C sinks; and (3) to investigate the controls of this partitioning. Specifically, we tested the hypothesis that soil C:N stoichiometry controls ecosystem C uptake (*GPP*) and sink partitioning (*ANPP* vs. soil C) across forest ecosystems. To verify if our hypothesis could be generalized to other forests, we tested it on several world forest sites for which *ANPP*, *GPP* and soil C:N data were available in the literature.

Materials and methods

Study sites

Six forests were considered in the present study. Three sites were in central Italy, two sites in northern Italy, and one in Croatia. All sites were equipped with an eddy covariance tower for mass, momentum and energy ecosystem exchange measurements and can be classified as high fertility sites, according to key soil properties (Vicca et al. 2012 - see also Appendix 1). Site characteristics and flux data are reported in Tab. 1, while a brief description for each site is given below.

Roccarespampani (42° 24' N, 11° 55' E - Claus & George 2005, Tedeschi et al. 2006) is a Turkey oak (*Quercus cerris* L.) coppice forest at about 235 m a.s.l. in central Italy. Mean annual temperature is 14 °C and mean annual rainfall is 755 mm. Soil is sandy clay Luvisol (which is typically nutrient rich), derived from sedimentary material of volcanic origin and marine deposits, and is moderately acid (pH=5.7), with a total depth > 100 cm (Rey et al. 2002). Cation exchange capacity (CEC) is high, ranging between 19 and 42 meq 100g⁻¹ in the different soil layers (Tedeschi et al. 2006). The forest has been managed as a "coppice with standards" over the last 200 years, with a rotation cycle varying between 15 and 20 years. Two stands were selected: a 6-year-old coppice (RO1) and a 15-year-old coppice (RO2).

Lecceto (LE - 43° 18' N, 11° 16' E) is a Holm oak (*Quercus ilex* L.) coppice with a rotation period of 18-20 years at about 300 m a.s.l. in central Italy. Holm oak represents

Tab. 1 - General characteristics for the six forest sites used in this study. (ΔC_{wood}): change in aboveground wood biomass; (ΔC_{roots}): change in coarse root biomass; (NEP): net ecosystem production; (NEE): net ecosystem exchange; (GPP): gross primary production; (R_{eco}): ecosystem respiration; (RO1): Roccarespampani site 1; (RO2): Roccarespampani site 2; (LE): Lecceto; (JA): Jastrebarsko; (LM): La Mandria; (CO): = Collelongo. (a): N wet deposition in 1990 were derived for all sites using published gridded maps with $0.5^\circ \times 0.5^\circ$ resolution derived from interpolated (krieged) ground data (available at <http://www.daac.ornl.gov>). Total wet depositions ($\text{kg N ha}^{-1} \text{y}^{-1}$) were then computed as the sum of aqueous NO_3^- and NH_4^+ fields, which were available. (b): For Collelongo, the reported number refers to direct measurements available for the period 2002-2009 (Flechard et al. 2011).

Group	Parameters	RO1	RO2	LE	JA	LM	CO
Vegetation characteristics	Main species	Turkey oak	Turkey oak	Holm oak	Pedunculate oak	Pedunculate oak - Hornbeam	Beech
	Management	coppice with standards	coppice with standards	coppice with standards	high forest	high forest	coppice converted to high forest since 1950
	Mean stand age in 2006-2007 (years)	6 (approx. 70 standards ha^{-1} of 20-40 years-old present)	15 (approx. 70 standards ha^{-1} of 20-40 years-old present)	15	35	80	110
	Aboveground biomass (kg C m^{-2})	1.9	4.5	5.0	6.3	7.8	13.7
	Wet N deposition ¹ ($\text{kg N ha}^{-1} \text{y}^{-1}$) ^a	10.0	10.0	8.6	11.2	9.4	10.8 ^b
Soil characteristics	Soil type	Volcanic Luvisol	Volcanic Luvisol	Xerocept	Luvic Stagnosol	Typic Fragiudalf	Humic Alisols
	Bulk density (0-15 cm, g cm^{-3})	1.29	1.29	1.20	0.77	1.09	0.58
	Bulk density (15-30 cm, g cm^{-3})	1.25	1.25	1.20	1.11	1.27	0.66
	Soil C stock 0-30 cm (kg C m^{-2})	8.6	7.4	27.4	7.7	7.4	14.7
	Soil N stock 0-30 cm (kg N m^{-2})	0.8	0.5	1.3	0.7	0.3	0.9
	C:N	10	14	22	11	24	16
	Sand (%)	52	52	40	18	6	6
	Silt (%)	12	12	35	28	80	50
	Clay (%)	35	35	25	54	14	44
	Carbon fluxes	GPP ($\text{g C m}^{-2} \text{yr}^{-1}$)	1577	1356	901	1633	754
Reco ($\text{g C m}^{-2} \text{yr}^{-1}$)		1060	810	368	1049	183	722
ΔC_{wood} ($\text{g C m}^{-2} \text{yr}^{-1}$)		161	315	334	325	360	363
Root:shoot ratio		0.30 (Mokany et al. 2006)	0.30 (Mokany et al. 2006)	0.30 (Mokany et al. 2006)	0.30 (Mokany et al. 2006)	0.30 (Mokany et al. 2006)	0.28 (assessed at the site)
ΔC_{roots} ($\text{g C m}^{-2} \text{yr}^{-1}$)		48	95	100	98	108	102
$\Delta C_{\text{biomass}} = \Delta C_{\text{wood}} + \Delta C_{\text{roots}}$ ($\text{g C m}^{-2} \text{yr}^{-1}$)		209	410	435	423	468	464
Litterfall ($\text{g C m}^{-2} \text{yr}^{-1}$)		47	123	107	203	223	245
NEP (= $-NEE$) ($\text{g C m}^{-2} \text{yr}^{-1}$)		517	545	533	584	571	535

81% of the total tree canopy; others species include *Arbutus unedo* L., *Juniperus communis* L., *Quercus pubescens* L., *Phillyrea latifolia* L., *Fraxinus ornus* L. Mean annual temperature is 13.5 °C and annual average rainfall is 780 mm.

Jastrebarsko (JA - 45° 37' N, 15° 41' E; Marjanovic et al. 2010, 2011) is a 35-year-old forest in Croatia dominated by pedunculate oak (*Quercus robur* L.) with 19% of black alder (*Alnus glutinosa* Haernt.), 14% hornbeam (*Carpinus betulus* L.) and 9% of narrow-leaved ash (*Fraxinus angustifolia* L.). Mean annual temperature is 10.4 °C

with mean monthly temperatures of -0.2 °C and 20.7 °C in January and July, respectively. Average annual precipitation is 900 mm year⁻¹, of which around 500 mm falls during the active vegetation period (April-September). Soil is a Luvic Stagnosol with a depth > 100 cm and an acidic pH (4.9) in the upper mineral layer (0-20 cm) that linearly increases to neutral pH at depths > 100 cm. At the beginning of the growing season, the soil drains and water content soon drops below water holding capacity (46% v/v) allowing enough oxygen supply for root growth and substantially increasing nutrient availa-

bility in these soils, where nutrient availability can be constrained by high water levels.

La Mandria (LM - 45° 09' N, 7° 34' E) is an 80-year-old pedunculate oak-hornbeam forest (*Quercus robur* L. and *Carpinus betulus* L.) in northern Italy. Mean annual temperature at the site is 11.6 °C and annual precipitation is 1030 mm. Soil is Typic Fragiudalf with adequate moisture content throughout the year, neutral pH and good CEC (ranging from 17 to 11 meq 100 g⁻¹ at soil surface and Bh horizons, respectively).

Collelongo (CO - 41° 52' N, 13° 38' E; Valentini et al. 1996, Scartazza et al. 2004)

is an 110-years-old pure beech (*Fagus sylvatica* L.) forest in northern Italy that has been part of the network of Long Term Ecological Research sites (LTER Italy) since 2006. Mean annual temperature at the site is 7.1 °C and mean annual rainfall is 1188 mm. The soil is a Humic Alisol with volcanic ash also present. Both CEC and N content are high in the different soil layers, ranging from 14.8 to 23.3 meq 100g⁻¹ and from 4 to 7.3 mg N g⁻¹, respectively (Persson et al. 2000). Wet N deposition rates in the period 2002-2009 averaged 10.8 kg N ha⁻¹ yr⁻¹ (Flechar et al. 2011)

Net root-derived C input to soil

Net-C_{root} was quantified using the in-growth core isotope technique, following Cotrufo et al. (2011). A soil depleted in ¹³C (δ¹³C = -17.22‰) was collected from the USDA-ARS Central Plains Experimental Range located in NE Colorado, USA (40° 49' N, 104° 46' W). The soil is classified as a Zigweid soil series (Fine-loamy, mixed, superactive, mesic Ustic Haplocambid), with a pH of 7.4, N content of 1.37 g kg⁻¹, and P content of 0.5 g kg⁻¹ (Cotrufo et al. 2011). At this site, plant cover is approximately 75% C₄ grasses, and for brevity we call henceforth this soil as "C₄ soil". Soil was air-dried prior to being sealed and boxed for shipment to Italy. Upon arrival, the C₄ soil was ground and sieved to 2 mm and well mixed to make a homogeneous soil pool, before using it for in-growth cores and chemical (C% and δ¹³C) analyses as described below.

At each forest site, six cores, made of a 2 mm mesh net (thus allowing the penetration of fine roots) with a diameter of 4 cm and a height of 30 cm, were placed randomly within the eddy covariance tower footprint in October 2006 (2008 for Jastrebarsko) and filled with the C₄ soil to a bulk density similar to the average bulk density for the site. At the top of each core the net was closed to avoid above-ground litter input. Cores were sampled a year later, and the soil from each core was separated into 0-15 cm and 15-30 cm depth layers, except for Jastrebarsko, where the entire 0-30 cm core was considered.

All soil samples were sieved to 2 mm, and root samples carefully removed and washed with deionized water. Root samples were pooled by site and depth, and each samples analyzed in triplicates. Both soil and root samples were oven-dried at 70 °C, pulverized and analyzed for %C and δ¹³C by an elemental analyzer (Flash EA 1112 NC, CE Instrument, Wigan, UK) connected to an Isotope Ratio Mass Spectrometer (IRMS, Delta Plus, Thermo-Finnigan, Bremen, Germany). Prior to C analyses, soil samples were treated with HCl to eliminate carbonates (Harris et al. 2001). The measured δ¹³C values were used to calculate the proportion of new C (*f_{new}*, i.e., the *Net-C_{root}*), by using a mass ba-

lance equation (Del Galdo et al. 2003, Cotrufo et al. 2011 - eqn. 4):

$$f_{new} = \frac{\delta_{soil} - \delta_{old}}{\delta_{veg} - \delta_{old}}$$

where δ_{soil} is δ¹³C of the organic matter of the C₄ soil collected from each core after one year of field incubation, δ_{old} is the δ¹³C of the organic matter of the C₄ soil measured before incubation, and δ_{veg} is the δ¹³C of the roots averaged by site and depth. The average δ_{veg} value across all our sites was -28.11±0.29‰, while variation (standard deviation) within a site was between 0.15 and 0.57‰ at RO1 and RO2, respectively. Knowing the *f* values for the new C, the soil organic C concentrations (%C), soil depth (D, m), and soil bulk density (σ, kg m⁻³), *Net-C_{root}* amounts (g m⁻²) were computed for all soil samples as follows (eqn. 5):

$$C = f \cdot \%C \cdot \sigma \cdot D$$

Estimates of *Net-C_{root}* using this method (Cotrufo et al. 2011) rely on the assumptions that: (1) root inputs are the same inside and outside the in-growth bags and are independent of the C₄ soil properties; and (2) that there is no isotopic fractionation during the decomposition of the native SOM or formation of the new SOM from the root tissues. New studies applying this method should test those assumptions, since some fractionation could occur (Hobbie et al. 2004).

Ecosystem fluxes and primary production

Eddy covariance flux data from all five Italian sites were analyzed for the years 2006-2007 (Tab. 1). Data of net ecosystem exchange (*NEE*), gross primary production (*GPP*) and ecosystem respiration (*R_{eco}*) at monthly time steps were downloaded from the central Fluxnet database (<http://gaia.agraria.unitus.it/database/>). Specifically, we used the *NEE* gap-filled data using the Artificial Neural Network method (*NEE_ANN* from level 4 dataset - Papale et al. 2006). *R_{eco}* was computed according to the short-term temperature response of night-time fluxes (Reichstein et al. 2005) and *GPP* values were derived as sum of the absolute values of *NEE_ANN* and *R_{eco}*. At sites where data for the years 2006 or 2007 were incomplete even after gap-filling because of missing weather data, data for 2008 were also included in the analysis for the calculation of annual means. As for the Jastrebarsko site, 2009 eddy flux data were derived from Marjanovic et al. (2010).

Mean annual temperature (MAT), mean annual precipitation (MAP), and soil C stocks (0-30 cm), as well as changes in wood biomass (stem and branches - Δ*C_{wood}*), were derived from ancillary data files available at

the central database, updated to 2006-2007 when necessary, or using specific yield tables available at the site (e.g., Jastrebarsko). All data were checked, if necessary updated and completed by site Principal Investigators, who are co-authors of the present study. Changes in root biomass (Δ*C_{roots}*) were derived from Δ*C_{wood}* using root-to-shoot ratios reported by Mokany et al. (2006) or using site-specific relationships as in the case of Collelongo and do not include fine root productivity.

ANPP was calculated as the sum between Δ*C_{biomass}* and *NPP_{leaves}* (foliar net primary production). The latter corresponds to litterfall in the case of broadleaved forests, and was directly measured at the site (i.e., Rocca, Jastrebarsko, Collelongo) or assessed from *NPP_{wood}* using biomass expansion factors derived at nearby sites with similar species composition and structure (i.e., La Mandria). In the case of Lecceto, where the dominant species is evergreen (Holm oak), we assumed that the system was at steady state and thus litterfall = *NPP_{leaves}*. Then the *ANPP*:*GPP* ratio was calculated.

World forest sites data

In order to test if the relationship between *ANPP*:*GPP* and soil C:N, observed across our study sites, was generalizable across forest ecosystems, we searched published datasets (Litton et al. 2007, Luyssaert et al. 2007, Vicca et al. 2012) for forest sites that provided the data suitable to our analyses. Twenty-three additional sites were found including *ANPP* and *GPP* data, as well as soil C:N (determined for a depth up to 45 cm) were found (Tab. 2). Fertility classification followed Vicca et al. (2012). More details are given in Appendix 1.

Data analysis

At each site the annual change in net soil C (Δ*C_{soil}* - g C m⁻² y⁻¹) was calculated starting from eddy covariance *NEE* data and measured changes in aboveground wood biomass (Δ*C_{wood}*) and coarse roots (Δ*C_{roots}*) by re-arranging eqn. 1 (eqn. 6):

$$\begin{aligned} \Delta C_{soil} &= -NEE - \Delta C_{wood} - \Delta C_{roots} \\ &= NEP - \Delta C_{biomass} \end{aligned}$$

Statistical analyses were performed using the package SIGMA PLOT® 11.0 (Systat® Software, San José, CA, USA). Data were tested for normal distributions, using the Shapiro-Wilk's test, and homogeneity of variance, and log transformed when necessary. To assess differences in *Net-C_{root}* among sites, a one way analysis of variance (one-way ANOVA) was used. Significant treatment (site) effects (P<0.05) were further explored via a treatment (site) comparison using the Least-Squares means test with Tukey's adjustment for multiple comparisons. For sites

where data for 0-15 and 15-30 cm depths were available, a two-way ANOVA with site and depth as fixed factors was also performed.

A correlation analysis between all available variables was performed using the Spearman's rank method through a correlation matrix in STATA10® (StataCorp®, College Station, TX, USA). For variables that were correlated with $p < 0.10$, linear models were fitted to measured data.

Results

Net root-derived C input to soil

Total $Net-C_{root}$ in the top 30 cm soil layer ranged between 420 g C m⁻² year⁻¹ at Collelongo and 818 g C m⁻² year⁻¹ at Jastrebarco (Fig. 1). Mean annual $Net-C_{root}$ across sites was 606 ± 164 g C m⁻² year⁻¹ (mean ± stan-

dard deviation). A significant difference in total $Net-C_{root}$ (0-30 cm) was detected among sites (ANOVA, $p = 0.007$). In particular, *post-hoc* Tukey's tests showed a significant difference between Jastrebarco and Collelongo ($p = 0.013$) and Lecceto and Collelongo ($p = 0.041$ - Fig. 1). For sites where data for 0-15 and 15-30 cm depths were available (*i.e.*, all sites except Jastrebarco), the two-way ANOVA applied showed significant differences among sites ($p = 0.004$), between depths ($p = 0.024$) and for site × depth interaction ($p = 0.035$). No differences among sites were detected at 0-15 cm depth (Tukey's test: $p > 0.05$), while $Net-C_{root}$ at 15-30 cm in Lecceto was significantly different from Rocca1 ($p = 0.002$), Collelongo ($p = 0.003$) and Rocca2 ($p = 0.021$). Climate (*i.e.*, MAT, MAP, soil water content) did not explain significant variability in $Net-C_{root}$

among the different sites (see Tab. S1 in Appendix 1). Moreover, total $Net-C_{root}$ was not significantly correlated to soil C:N.

Ecosystem C sink partitioning

All six sites were net C sinks with similar *NEP* values (average *NEP* was 547 ± 25 g C m⁻² year⁻¹) but with large differences in annual *GPP* (Tab. 1). They actively sequestered C both aboveground and in the soil: ΔC_{wood} represented between 10 and 48% of annual *GPP* (RO1 and LM, respectively), $ANPP$ ($=\Delta C_{wood} + \text{litterfall}$) was between 13 and 77% (RO1 and LM, respectively) and ΔC_{soil} was positive for all sites representing between 6 and 20% of annual *GPP* (CO and RO1, respectively).

In accordance with our hypothesis, *GPP* and ΔC_{soil} were correlated to soil C:N ($p = 0.0048$ and $p = 0.07$, respectively - Tab. S1

Tab. 2 - Studies used to validate the relationship between $ANPP:GPP$ and soil C:N across gradients of forest stands and environmental conditions. Nutrient availability was assessed according to Vicca et al. (2012), when possible. (n.a.): not available. (1): Ryan et al. (2004), Binkley et al. (2004); (2) Gholz et al. (1986), Gholz & Fisher (1982), Gholz et al. (1985); (3) Gower et al. (1997), Ryan et al. (1997), Online BOREAS dataset. Site: "NSA-OJP-9OJP1"; (4) Malhi et al. (1999), Marland et al. (2004); (5) Malhi et al. (1999), Luizao et al. (2004); (6) Chambers et al. (2004), Luizao et al. (2004); (7) Harris et al. (1975), Marland et al. (2004); (8) Kinerson et al. (1977); (9) Woodwell & Botkin (1970); $ANPP = NPP/1.3$; Marland et al. (2004); (10) Kutsch et al. (2001); (11) Dilly et al. (2000); (12) Sun et al. (2004); (13) Malhi et al. (2009); (14) Kelliher et al. (2004); (15) Kelliher et al. (2004); (16) Malhi et al. (2009); (17) Present study; $ANPP = \Delta C_{wood} + \text{litterfall}$.

Forest type and location	Management or treatment	Nutrient availability	<i>ANPP</i>	<i>GPP</i>	<i>ANPP</i> : <i>GPP</i>	Depth (cm)	Soil C:N
<i>Eucalyptus saligna</i> plantation, Pepeekeo, HI ¹	2 yr, 1x1 m	high	1427	5057	0.28	0-45	16
	6 yr, 1x1 m	high	480	2369	0.20	0-45	15
	2 yr, 3x3 m	high	1456	4413	0.33	0-45	16
	6 yr, 3x3 m	high	828	2930	0.28	0-45	15
<i>Pinus radiata</i> plantation, Canberra, Australia ¹	20 yr C	medium	599	2415	0.25	0-30	19
<i>Pinus elliotii</i> plantation, Bradford, FL ²	7-9 yr	low	199	1407	0.14	0-15	12
<i>Picea mariana</i> , N-BOREAS ³	150 yr	low	132	563	0.23	n.a.	13
<i>Pinus banksiana</i> , N-BOREAS ³	63 yr	low	115	677	0.17	n.a.	15
Oak-Hickory, Oak Ridge, TN ⁴	55 yr	low	510	1329	0.38	0-20	16
Tropical forest, Manaus Brazil ⁵	Old growth	low	870	2620	0.33	0-10	14
Tropical forest, Manaus Brazil ⁶	Old growth terra firme	low	650	2860	0.23	0-10	12
Liriodendron, Oak Ridge, TN ⁷	50 yr	n.a.	352	2162	0.16	0-20	14
<i>Pinus taeda</i> , Oak Ridge, TN ⁸	16 yr	n.a.	1490	4124	0.36	0-20	15
<i>Pinus-Quercus</i> , Oak Ridge, TN ⁹	43 yr	n.a.	462	1280	0.36	0-20	14
Bornhoved Alder ¹⁰	Temperate Humid-Broadleaved	low	589	2420	0.24	0-30	18
Bornhoved Beech ¹¹	Temperate Humid-Broadleaved	medium	601	1324	0.45	0-5	15
Cascade Head (1) ¹²	Temperate Humid-Needle-leaved	high	569	1400	0.41	0-30	21
Cascade Head (1A) ¹²	Temperate Humid-Broadleaved	high	640	1558	0.41	0-30	20
Caxiuanã ¹³	Tropical Humid-Broadleaved	low	869	3630	0.24	0-30	13
Jacaranda/K34 ¹³	Tropical Humid-Broadleaved	low	796	3040	0.26	0-30	17
Metolius ¹⁴	Temperate Semi-arid-Needle-leaved	medium	183	1143	0.16	0-30	20
Metolius young ¹⁵	Temperate Semi-arid-Needle-leaved	medium	104	724	0.14	0-30	21
Tapajos 67 ¹⁶	Tropical Humid-Broadleaved	low	1400	3141	0.45	0-30	15
Rocca 1 ¹⁷	Mediterranean Turkey oak	high	208	1577	0.13	0-30	10
Rocca 2 ¹⁷	Mediterranean Turkey oak	high	438	1356	0.32	0-30	14
Lecceto ¹⁷	Mediterranean Holm oak	high	441	901	0.49	0-30	22
Jastrebarco ¹⁷	Mediterranean Pedunculate oak	high	528	1633	0.32	0-30	11
La Mandria ¹⁷	Mediterranean Pedunculate oak - Hornbeam	high	583	754	0.77	0-30	24
Collelongo ¹⁷	Mediterranean mountain beech	high	608	1258	0.48	0-30	16

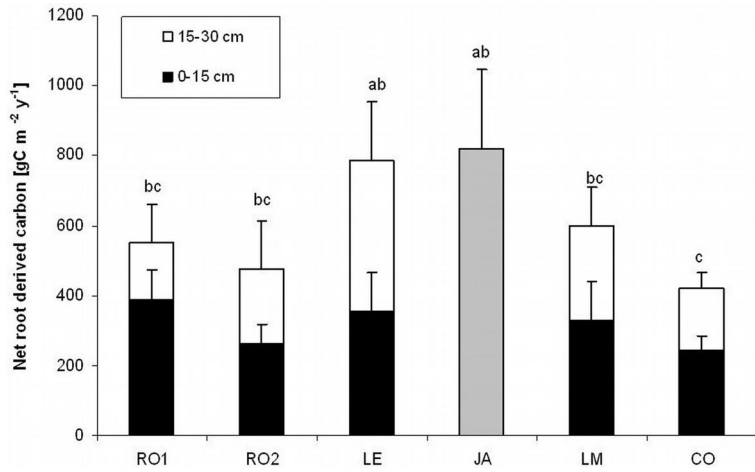


Fig. 1 - Net annual root-derived carbon input ($Net-C_{root}$) to soils (0-15 and 15-30 cm) quantified using isotope-labelled (e.g., C_4) soil in-growth cores at the six study sites. Vertical bars indicate standard deviation. Different letters indicate significant difference in total $Net-C_{root}$ at $p < 0.05$. For site labels, see Tab. 1. As for the Jastrebarsko site (JA), only total net derived carbon is reported (grey bar).

in Appendix 1) and decreased linearly as soil C:N increased (Fig. 2). Moreover, GPP was linearly and inversely related to soil clay content ($p = 0.05$) but, similarly to ΔC_{soil} , it was not correlated with either MAT, MAP or stand age. ΔC_{wood} was weakly related with soil C:N ($p = 0.07$), while ΔC_{wood} -to- GPP ratio (Fig. 3.a) and $ANPP$ -to- GPP ratio significantly increased with soil C:N ($p < 0.0001$ and $p = 0.005$, respectively - Tab. S1 in Ap-

pendix 1). In contrast to GPP , Spearman's correlation analysis revealed a significant relationship between ΔC_{wood} and both MAT and MAP ($p = 0.05$ and $p = 0.008$, respectively - Tab. S1 in Appendix 1). Similarly, $ANPP$ was significantly correlated with MAT and MAP ($p = 0.001$ and $p = 0.0003$, respectively). Finally, the fate of root C input appeared to depend on soil C:N stoichiometry, with proportionally more $Net-C_{root}$ be-

ing allocated to C sequestration with decreasing soil C:N (ΔC_{soil} vs. $Net-C_{root}$ $p = 0.07$) and soil C:N was able to explain 40% of the variation in the ratio of ΔC_{soil} to $Net-C_{root} +$ litterfall (Fig. 3.b).

World forest sites

The positive relationship between $ANPP$ -to- GPP ratio and soil C:N found across our six study sites was confirmed also when in-

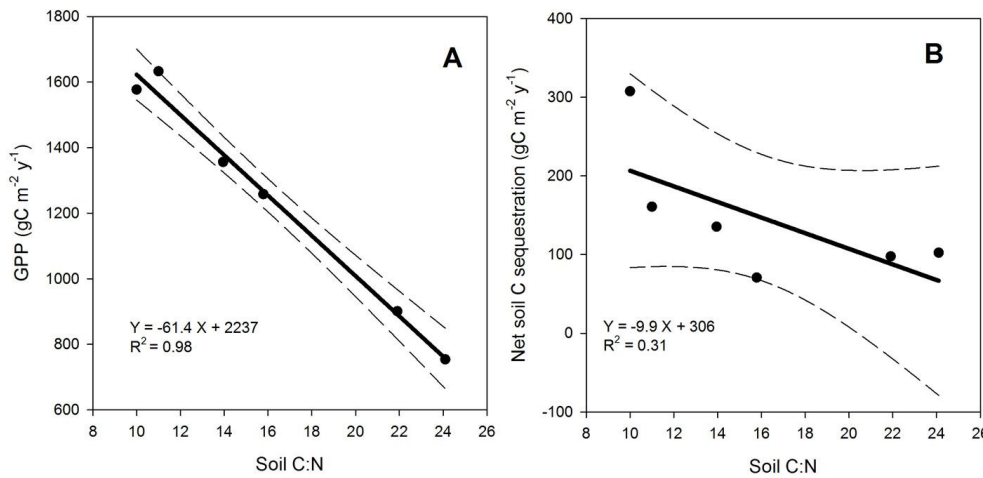


Fig. 2 - Relationships between soil C:N stoichiometry and gross primary productivity (GPP - panel A) or net soil C sequestration (panel B) as related to soil C:N ratio. Dashed lines represent 95% confidence interval; the reported R^2 is the adjusted R^2 .

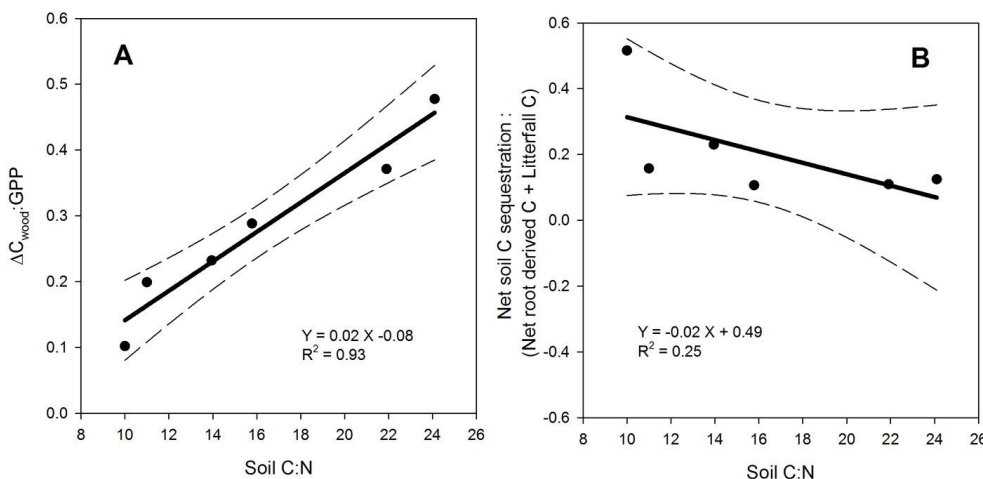


Fig. 3 - Relationships between soil C:N stoichiometry and ΔC_{wood} -to- GPP ratio (panel A), or ΔC_{soil} : ($Net-C_{root} +$ litterfall) ratio (panel B). Dashed lines represent 95% confidence interval; the reported R^2 is the adjusted R^2 .

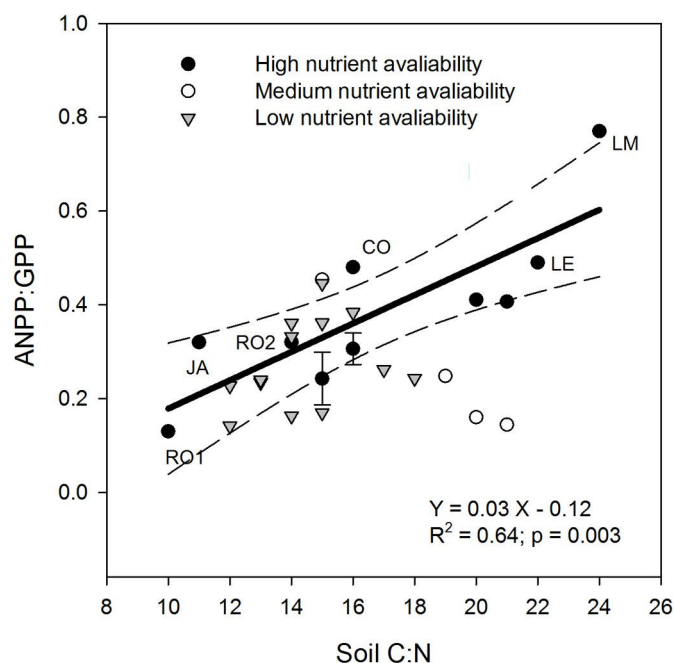


Fig. 4 - Relationships between soil C:N stoichiometry and the $ANPP:GPP$ ratio at forest sites with different fertility levels. For the complete list of sites see Tab. 2. Dashed lines represent 95% confidence intervals. The six sites considered in the present study are labeled as reported in Tab. 1. *Eucalyptus saligna* plantations (Tab. 2) have been averaged by stand age and vertical bars indicate standard deviation. The reported R^2 is the adjusted R^2 .

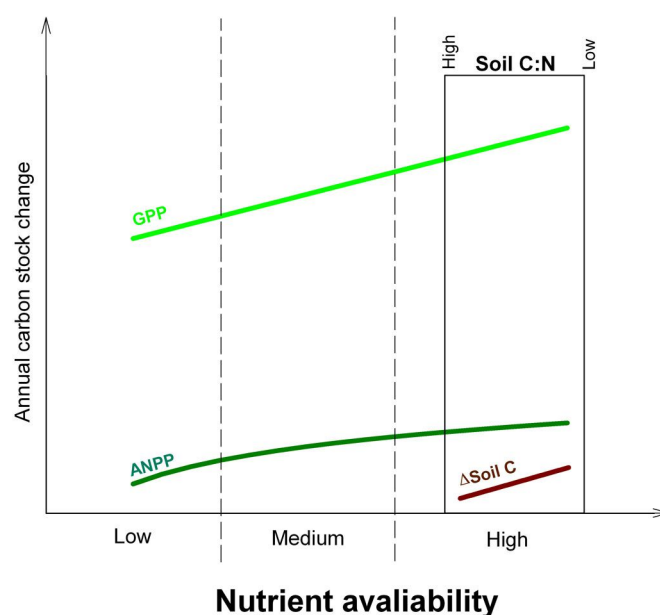


Fig. 5 - Schematic representation of the proposed dynamics of gross (GPP) and aboveground net primary production ($ANPP$) with changes in nutrient availability. At high fertility sites (such as the sites considered in the present paper), GPP , $ANPP$ and soil C sequestration (ΔC) changes are controlled by soil C:N stoichiometry. At low soil C:N ratio, C sink allocation shifts from NPP to soil C sequestration.

cluding additional fertile forests from different regions (Tab. 2). In particular, a positive relationship was found between $ANPP:GPP$ and soil C:N for high fertility (*sensu* Vicca et al. 2012) sites (adjusted- $R^2 = 0.64$; $p = 0.03$; Fig. 4). Conversely, no significant relationship was detected for low and medium fertility sites.

Discussion and conclusions

To our knowledge, this study is the first to quantify $Net-C_{root}$ in a range of forest ecosystems. The measurement of $Net-C_{root}$ *in situ* is difficult, thus measured values are lacking and modeled estimates cannot be validated. However, the in-growth core isotope technique has already been shown to allow detection of changes in $Net-C_{root}$ in CO_2 and climate manipulation experiments (Hoosbeek et al. 2004, Cotrufo et al. 2011), even though it does suffer from several caveats related to the use of an exogenous soil and high spatial variability. Steingrobe et al. (2000) reviewed the in-growth core method for measuring gross root growth: a first shortcoming associated with this method is achieving the soil conditions inside the bag similar to the bulk soil. Moreover, soil texture has also been shown to significantly influence rhizodeposition rates (Scandellari et al. 2010), although it is difficult to determine whether soil texture influenced rhizodeposition rates in our study.

Our estimates of $Net-C_{root}$ using the in-growth core isotope technique were on average $606 \text{ g C m}^{-2} \text{ y}^{-1}$, which is higher than values reported by Cotrufo et al. (2011) for a *Arbutus unedo* L. coppice in dry Mediterranean conditions, but lower than values reported by Hoosbeek et al. (2004) for an irrigated and fertilized poplar plantation in central Italy. A possible overestimation of $Net-C_{root}$ can be also related to the fact that a certain amount of fine root fragments could have passed through the 2 mm sieve. Such an amount is a function of root integrity as affected by plant age and sample processing. Being aware of this possible overestimation and of the above-mentioned limitations associated with the in-growth core isotope technique, in this study we used $Net-C_{root}$ estimates solely as an indicator of differences in the effect of root-derived C on SOC sequestration through the calculation of the ratio $\Delta C_{soil} : (\text{Net root-derived C} + \text{litterfall C})$.

Many factors have been suggested to affect soil C sequestration, including the characteristics of input material, soil texture and mineralogy, climatic factors, and soil nutrient status (Galantini et al. 1992, Andr n & K tterer 1997, Janssens et al. 2010). We found that the proportion of root C input resulting in C sequestration at these high fertility sites was related to soil C:N ratio, and soil C sequestration was greater at low C:N (Fig. 2b) therefore confirming our hypothesis. Recen-

tly, Manzoni et al. (2012) suggested a C-to-nutrient stoichiometric control on microbial C use efficiency (CUE), which would increase with increasing nutrient availability. The importance of CUE as a determinant of the fate of plant inputs to soils has also been recognized by other recent studies (Schimel & Schaeffer 2012, Cotrufo et al. 2013) and some models have suggested that low nutrient availability, particularly N, might limit soil C storage through mechanisms that are still not completely understood (Rastetter et al. 1997, Hungate et al. 2003). Recently, Kirkby et al. (2013) hypothesized that the sequestration of C-rich crop residue material into SOM could be improved only by adding supplementary nutrients, as the more stable SOM fraction has more N, P and S per unit of C than the plant material input due to microbial reprocessing. Thus, the increase in soil C sequestration at lower soil C:N values observed in this study may be explained by a higher microbial CUE of root C inputs.

Soil C:N exerted a strong control on GPP across our six forests and GPP increased with decreasing soil C:N (Fig. 2a). This relationship is based on six forest sites and we cannot exclude the possibility that other factors influenced this relation. At the ecosystem scale, variation in global plant productivity across ecosystems has often been related to environmental factors (Field et al. 1995, Reichstein et al. 2007b), but also to

nutrient availability (Vicca et al. 2012). In this context, Zha et al. (2013) reported a strong positive relationship between *GPP* or *NPP* and total soil N. Across our sites, ΔC_{wood} and *ANPP* increased slightly, but not significantly with increasing soil C:N, and showed significant relations with MAT, MAP and stand age, thus confirming previous studies (Curtis et al. 2002, Hsu et al. 2012, Robinson et al. 2012, He et al. 2012). How such different behavior between *GPP* and ΔC_{wood} or *ANPP* with respect to soil C:N could be explained? We suggest that this result is due to the lower demand for N by woody tissues (which comprise the largest fraction of the tree and are characterized by very high C:N) as compared to green leaves (which control *GPP*, and have much lower C:N than woody tissues). As a result of these variations in both *GPP* and *ANPP*, the ratio between *ANPP* and *GPP* varied substantially among our six forest sites.

Following the distinct patterns of *ANPP* and *GPP* versus soil C:N, the *ANPP*-to-*GPP* ratio significantly increased with increasing soil C:N (Fig. 2a). At first sight, this seems to contradict the current understanding that partitioning of photosynthates into above-ground biomass increases with increasing nutrient availability across a wide range of forests (Vicca et al. 2012). However, all six forest sites had high nutrient availability but, at those sites where soil N presumably exceeded tree demand for wood growth (*i.e.*, sites with low C:N), root C inputs were probably responsible for the higher net soil C sequestration. We speculate that the link between soil C:N stoichiometry and microbial activity controls C sequestration below-ground, as well as for the increase in *ANPP*-to-*GPP* ratio with increasing soil C:N across the high fertility forests in our dataset. At soil C:N below 15, CUE is expected to be high, and more of the fresh C input is used for microbial products, resulting in the net formation of new SOM. Conversely, when C:N is high, microbes have a low C use efficiency and therefore they respire more of the fresh C inputs and prime SOM decomposition (Fontaine et al. 2004), which increases N availability and supports a higher allocation of fixed C (*GPP*) to *ANPP*. Our observations of increasing *ANPP*-to-*GPP* ratio, and the tendency for a decrease in soil C sequestration with increasing soil C:N (Fig. 2b), support this hypothesis.

In order to further test this hypothesis, we analyzed a larger dataset. Also in this case, *ANPP*-to-*GPP* ratios were quite variable (average *ANPP*:*GPP* = 0.28 with SD = 0.10; Tab. 2) and our analysis confirmed the relationship between *ANPP*-to-*GPP* ratio and soil C:N at sites with high fertility (Fig. 4). At sites where overall nutrient availability was low, this relationship did not hold. Variation in partitioning of *GPP* to *ANPP* at

these sites is probably driven by the need for plants to invest in the nutrient acquiring system (*i.e.*, roots and root symbionts - Vicca et al. 2012). When nutrient availability is limited, belowground input by plants may be the dominant control of microbial activity and SOM mineralization (Hamilton & Frank 2001, Wardle et al. 2004, De Deyn et al. 2008, De Graaff et al. 2010), thereby influencing mineral nutrient availability for plant uptake. Our speculation is also consistent with other recent findings. At the Duke Free Air CO₂ Enrichment (FACE) experiment, the increase in the belowground C flux stimulated microbial activity, accelerated SOM decomposition, and stimulated tree uptake of N bound to this SOM, sustaining *ANPP* (Drake et al. 2011, 2013, Phillips et al. 2012). Yin et al. (2013) found that an increase in the release of root exudates into the soil was an important physiological mechanism to sustain growth responses of plants to experimental warming.

At our study sites, soil C:N stoichiometry appeared to be weakly controlled by the soil clay content ($p = 0.15$ - Tab. S1 in Appendix 1), decreasing with increasing %clay in soil. This is consistent with our knowledge of soil primary organo-mineral particles, which describes clay-associated SOM as the fraction with the highest microbial contribution and lowest C:N ratio (Christensen 1992, Grandy & Neff 2008).

In conclusion, our results suggest that a specific site property, such as soil texture, could drive soil C:N stoichiometry which in turn would control ecosystem C uptake and partitioning within forests of high nutrient availability. While *GPP* strongly and linearly increased with increasing soil N, above-ground tree biomass demand for N appeared to saturate, possibly because of the higher C:N of wood *vs.* green leaves, and, at high nutrient availability, *NPP* became limited by other environmental factors. When this occurs, more C is sequestered by soil (Fig. 5), where the high N availability promotes CUE efficiency and new SOM formation.

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Supplementary Material

Appendix 1

Box S1 - Nutrient classification.

Tab. S1 - Spearman correlation matrix for the six Mediterranean forests considered in the study.

Link: [Alberti_1196@suppl001.pdf](#)