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Forest soils in France are sequestering substantial amounts of carbon

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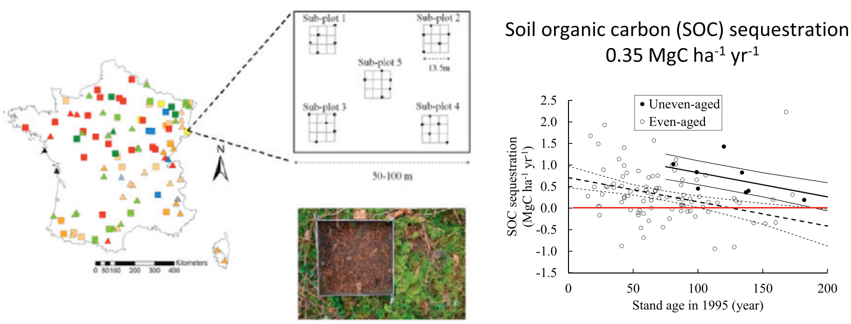
HIGHLIGHTS

- We evaluated whether French forest soils are sources or sinks of carbon?
- Soils were resampled after 15 years in the 102 French forest monitoring plots.
- Forest soils across France have accumulated 0.35 MgC ha^{-1} yr^{-1} between 1993 and 2012.
- Soil carbon sequestration declined with tree age and was affected by stand structure.
- Forest management has the potential to influence this carbon sink.

GRAPHICAL ABSTRACT



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ABSTRACT

The aim of this study was to assess whether French forest soils are sources or sinks of carbon and to quantify changes in soil organic carbon (SOC) stocks over time by resampling soil in long-term forest monitoring plots. Within each plot, and for each survey, soils were sampled at five points selected in five subplots and divided into layers. Composite samples were produced for each layer and subplot, then analysed for mass, bulk density and SOC. Linear mixed models were used to estimate SOC changes over 15 years between two soil surveys carried out in 102 plots in France. A factor analysis and a budget approach were also used to identify which factors and processes were primarily responsible for SOC dynamics. Forest soils throughout France substantially accumulated SOC (+0.35 MgC ha^{-1} yr^{-1}) between 1993 and 2012. The SOC sequestration rate declined with stand age and was affected by stand structure. Uneven-aged stands sequestered more SOC than did even-aged stands ($p < 0.001$). For the forest floor, the SOC sequestration rate estimated by the budget approach was in agreement with that based on stock comparison. This increasing SOC stock in the forest floor can be explained by recent changes in certain factors affecting litter decomposition (climate and litter quality). For the mineral soil, the budget approach was unable to replicate the observed SOC sequestration rate, probably because SOC stocks were not yet at equilibrium with litter inputs at the beginning of the monitoring period (contrary to our steady-state assumption). This explanation is also supported by the fact that the SOC sequestration rate decreased with stand age. As the SOC sequestration rate declines with stand age and is higher in uneven-aged stands, forest management has the potential to influence this carbon sink.

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1. Introduction

On a global scale, undisturbed terrestrial ecosystems accumulated carbon (C) at a rate of 2.5 PgC yr^{-1} during the period 2002–2011, which offset about 30% of the carbon emitted into the atmosphere from fossil fuel consumption (Ciais et al., 2013). The majority of this C was sequestered in temperate and boreal forests (Pan et al., 2011) and about 30% of the C currently accumulating in these forests is stored in the soils (Janssens et al., 2003), which contain almost as much C as the atmosphere (787 vs 829 PgC; Dixon et al., 1994; Ciais et al., 2013). In recognition of their importance, estimates of soil organic carbon (SOC) changes arising from Land Use, Land Use Change and Forestry (LULUCF) must be reported under the United Nations Framework Convention on Climate Change (UNFCCC) and the Kyoto Protocol.

Most large-scale studies on C sequestration have concluded that forest soils act as a C sink in Europe, but large – and probably underestimated – uncertainties are associated with current estimates of the SOC sequestration rate (Liski et al., 2002; Mol-Dijkstra et al., 2009; Luyssaert et al., 2010). At large scales, changes in SOC are generally evaluated with simple SOC models, which estimate the main C fluxes based on commonly available data and empirical relationships (Liski et al., 2002; Mol-Dijkstra et al., 2009; Luyssaert et al., 2010). To estimate the uncertainty associated with predicted changes in SOC, one must account for the uncertainties of each C flux arising from various sources of errors (inaccuracy of input data, overly simplified modelling concepts, uncertainty of model parameters and unexplained variability), not all of which are taken into account or accurately quantifiable. This leads to an underestimation of the overall uncertainty. Alternatively, soil monitoring provides direct measurements of the SOC sequestration rate and though uncertainty estimates from this approach are also large due to the spatial heterogeneity of SOC, it can be accurately quantified.

For Europe, a first forest soil condition inventory was conducted between 1985 and 1996 on the level I plots of the International Cooperative Programme on Forests (ICP Forests) launched under the UNECE Convention on Long Range Transboundary Air Pollution (Vanmechelen et al., 1997) and a second soil inventory was carried out between 2006 and 2008 within the "BioSoil Demonstration project" (De Vos and Cools, 2011). One of the objectives of the second survey was to assess temporal changes in soil properties, but methodological difficulties appeared when researchers tried to detect changes in SOC stocks: (i) real or apparent changes in plot position occurred between survey dates, (ii) methods of sampling and chemical analysis varied among countries and between the two soil surveys (iii) and were poorly-documented for the first soil survey (Hiederer et al., 2011). As a result, SOC dynamics remain difficult to assess at European level. At the national scale, SOC change can only be evaluated in countries where resampling occurred on the same plots with exactly the same methods of soil sampling and chemical analysis. SOC dynamics have been assessed at site level in several studies (e.g. Poeplau et al., 2011; Barcena et al., 2014); but as far as we know, only two papers with repeated sampling to a sufficient soil depth have reported SOC changes at the national scale. These two studies delivered contrasting results: Bellamy et al. (2005) reported SOC losses from soils in coniferous and deciduous woodlands across England and Wales, while Grüneberg et al. (2014) reported an accumulation of SOC in forest soils in Germany.

The ecological processes responsible for SOC sequestration in forests remain poorly understood. SOC sequestration may occur because the litter production rate increases faster than the heterotrophic respiration rate in response to environmental changes (Magnani et al., 2007; Bond-Lamberty and Thomson, 2010). SOC sequestration in forests can also result from changes in land use, for example, when old coppices were converted into high forests or conifer plantations were established on abandoned farmlands during the last century (Luyssaert et al., 2010). In addition, the abandonment of the formerly widespread practices of litter raking and coppicing (a silvicultural system based on tree regeneration from cut stumps) is probably leading to a recovery in above- and below-ground carbon pools, especially in plantations of productive tree species such as Norway spruce and Douglas fir (Ciais et al., 2008; Rautiainen et al., 2010). More recently, management practices have moved toward the conversion of monocultures into uneven-aged mixed stands to improve forest resilience and ecosystem service provision while ensuring sustainable wood production. Although rarely studied to date, such conversions may enhance SOC sequestration in forests (Vesterdal et al., 2013).

To estimate the carbon sequestration rate in French forest soils, we quantified changes in SOC stocks based on data from two soil surveys carried out in the French forest monitoring plots (RENECOFOR) which are part of the level II network of ICP Forests. Identical sampling designs and analytical methods were used for both surveys. In addition, many environmental variables were regularly assessed on the monitoring plots, thereby allowing us to test which factors most influence SOC dynamics. Among all the available environmental variables, we preselected those which could potentially influence the key mechanisms driving SOC sequestration in forest soils (litter production and decomposition, SOC stabilization in mineral soil, difference between current and steady-state SOC stocks).

To evaluate whether recent environmental changes or preexisting imbalance between litter production and decomposition were primarily responsible for SOC sequestration patterns, we applied a simplified budget approach assuming that SOC stocks were at steady state at the beginning of the monitoring period. Above- and below-ground litter production and decomposition rates, as well as their recent temporal changes, were measured or modelled.

2. Materials and methods

2.1. Sampling design

Soil sampling was carried out in the French level II forest monitoring plots (RENECOFOR) in 1993–1995 and in 2007–2012. The 102 plots are distributed throughout France and comprise a wide range of ecological conditions (Fig. 1 and Appendix 1). Within the central zone of each 0.5 ha plot, sampling was carried out on five 13.5 m × 13.5 m subplots. Four of the subplots were located near the corners of the main plot and the fifth subplot was in the centre (Fig. 2). In each subplot, five sampling points were selected from the 16 intersections of a systematic grid (4.5 × 4.5 m) so as to have good spatial distribution and to avoid disturbed areas (logging residues, skidder tracks) and proximity to living trees. At each sampling point, the forest floor was collected by horizon and the underlying mineral soil was sampled by fixed-depth layers down to 40 cm depth. While this depth is not sufficient to have a complete picture of SOC stocks in forests, SOC changes can be detected since they mainly occur in the upper soil horizons (Jandl et al., 2014). For a given layer, all samples from a same subplot were pooled into one composite sample for analysis. Exactly the same protocol was followed for both soil surveys, except that the subplots were moved by 1.5 m in a fixed direction for re-sampling, in order to avoid soil that might have been disturbed by the previous sampling. For a given plot, the soil was sampled during the same season, and usually the same month, for both surveys. In addition, at the same time as the first soil survey, two soil pits were excavated and described on each plot, in order to characterize the soil horizons down to 1 m depth (Brêthes and Ulrich, 1997).

2.2. Soil collection and pre-treatment

At each sampling point within a 30 cm × 30 cm frame, the three humus layers (Ol, Of and Oh) of the forest floor were collected separately (see the picture of the graphical abstract). Ol is the upper humus layer, made of un- or slightly-decomposed litter. If present, Of lies under

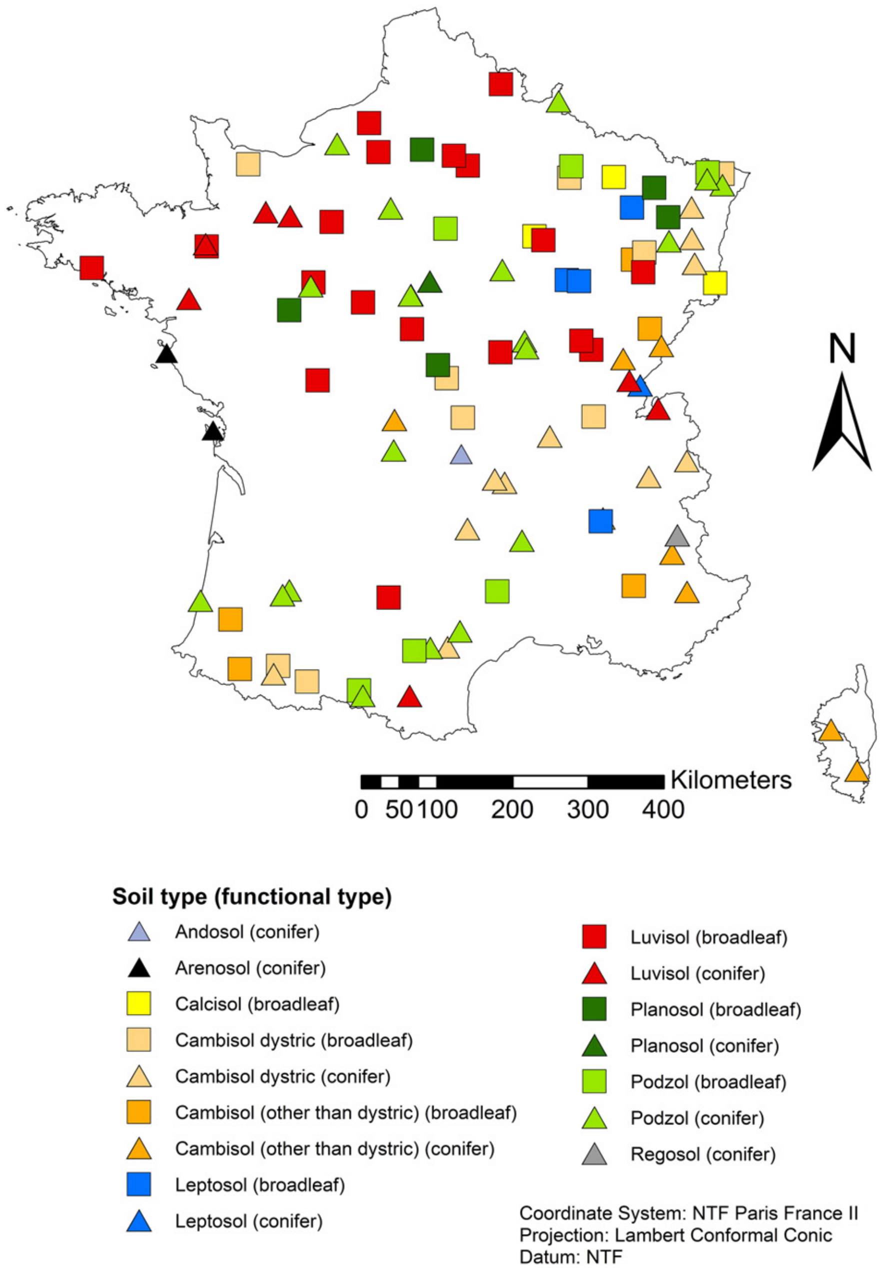

Fig. 1. Spatial distribution of the French forest monitoring plots according to soil (FAO) and functional type.

Ol and is composed of fragmented debris mixed with humic substances. If present, Oh lies under Of and is mainly composed of fine humic substances possibly mixed with a small proportion of fragmented debris. Three underlying mineral soil layers based on soil depth (0–10 cm, 10–20 cm, 20–40 cm) were also sampled by digging a small pit, layer by layer, over an approximately 50 cm × 50 cm area. For each mineral layer, an undisturbed soil sample was taken with a Kopecky cylinder (250 cm^3, h = 5 cm, Ø = 8 cm) to measure bulk density, and then the remaining soil – i.e. over the whole height of the layer and the whole area of the pit – was removed onto a large plastic sheet, homogenized and then sampled for chemical analyses. When sampling for bulk density, the 5 cm-high Kopecky cylinder was entirely pressed down with an open ring holder, from the top of the layer for the 0–10 cm and 10–20 cm layers or at mid-height for the 20–40 cm layer. The cylinder was then carefully removed and any soil extending beyond either of its two ends was trimmed away with a knife. In the first soil survey, two additional layers (40–80 cm, 80–100 cm) were sampled from the soil pits, also for both bulk density and chemical measurements. The sampling of these layers was not repeated during the second campaign to limit financial costs and because no substantial changes were expected at those depths (Jandl et al., 2014).

All the samples for chemical analysis were oven-dried at 35 °C for 24 h. For the forest floor samples, sub-samples were oven-dried at 105 °C until constant weight was obtained to determine their water content and convert their fresh mass into dry mass. All mineral soil samples were passed through a 2-mm sieve and those for fine-earth bulk density measurements were oven-dried at 105 °C before being weighed.

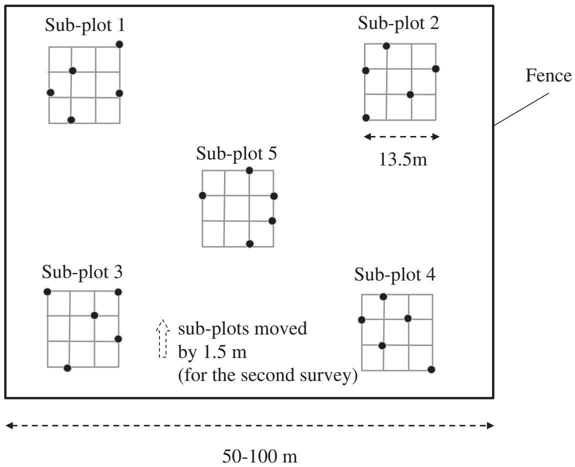

Fig. 2. Schematic representation of the soil sampling design.

2.3. Determining organic carbon content and calculating stocks

The organic carbon content of the soil samples was determined (i) by dry combustion (after subtraction of the carbonate content) for the forest floor and for the 0–10 cm mineral layer (analysed with a Carlo Erba NA 1500 for the first survey and a Thermo Flash 2000 for the second survey) and (ii) by the Anne method for the 10–20 and 20–40 cm layers (Anne, 1945; NF ISO 14235). This variant of the Walkley and Black (1934) consists of oxidising organic carbon by excess $K_2Cr_2O_7$ in an acidic medium (H_2SO_4) at 30 °C. The organic carbon concentration is then derived from the colorimetric determination of reduced Cr^{3+} ions. According to the comparison of methods carried out during the first soil survey (Ponette et al., 1997), the Anne method slightly underestimates organic carbon content (by 5%) compared to dry combustion.

For both soil campaigns, the carbon stock of each forest floor layer was obtained by multiplying its organic carbon content by its dry mass expressed per surface area unit. The carbon stocks of the mineral layers were evaluated based on their organic carbon content, their thickness, their fine-earth bulk density measured during the first soil campaign and the fraction of coarse fragments that could not be accounted for by the cylinder technique for bulk density determination.

$$SOC\ stock = SOC\ cont{\cdot}BD{\cdot}THK{\cdot}(1-F){\cdot}\frac{1}{100} \quad (1)$$

with SOC stock in MgC ha^{-1}, SOC cont in mg g^{-1}, BD (bulk density) in g cm^{-3}, THK (soil layer thickness) in cm and F (volumetric stoniness) in $m^3\ m^{-3}$.

The volumetric stoniness was determined by visual inspection of the soil pits. Even if this technique is less precise than the excavation method (which provides the gravimetric stone content), this should not have affected our estimates of the SOC sequestration rate since stoniness and fine-earth bulk density were supposed to be constant between the two soil surveys. Bulk density was assumed to be constant to avoid introducing a bias in the SOC sequestration rate estimates since the bulk density measurements of the two soil surveys were not strictly comparable due to a change in the sieving technique (manual for the first soil survey and mechanical for the second). However, for a subset of soil samples (260) covering the diversity of soil types and the different soil layers, the sieving was done mechanically for both soil surveys: this enabled us to verify that no significant change in bulk density occurred (1.031 and 1.027 g cm^{-3} at the first and second survey, respectively; p value of the paired *t*-test = 0.71).

2.4. Environmental factors

Based on the data available for the French level II plots, a series of environmental variables were preselected for their potential influence on key mechanisms driving the SOC sequestration rate in forest soils:

(i) Litter production depends on stand productivity and is affected by:
- climate (*climate type*, *precipitation*, *mean air temperature*) which varies with location (*Lambert II Etendu X and Y coordinate*) and *altitude*, and can be modified locally by *landscape position*, *orientation* and *slope*,
- soil properties determining water and nutrient availability (*soil type*, *soil depth*, *maximum extractable water reserve*, *C/N ratio of the forest floor and of the mineral soil*, *base saturation*, *pH*$_{H2O}$),
- atmospheric deposition (*N bulk deposition in 1993–1998*),
- stand characteristics (*functional type* determined based on the dominant tree species: broadleaf *vs* conifer, stand age in 1995, mean basal area, stand structure defined based on tree size distribution),
- harvesting intensity and natural disturbances (*basal area removed by thinning and storm damage in % of stems*).

(ii) Litter decomposition is influenced by
- climate and soil properties (*same factors as above +hydromorphy*),
- litter quality which depends on *functional type* and on soil properties,
- micro-climatic conditions which are determined by stand characteristics and may be temporarily affected by *cutting intensity* or *storm damage*;

(iii) SOC stabilization depends on soil constituents (*clay content*, *Al oxy-hydroxide content*, *Fe oxy-hydroxide content*) and SOC distribution within the soil profile (*proportion of SOC in the forest floor*)

(iv) Current SOC stocks compared to steady-state SOC stocks (*total SOC stock at the first survey*, *time since afforestation*, *land use change and regeneration type*: *artificial* vs *natural*)

Except for the meteorological data from MétéoFrance, all the selected environmental variables were regularly assessed in the French level II forest monitoring plots according to the ICP Forests harmonized protocols available at http://icp-forests.net/page/icp-forests-manual. More information on these factors is provided in Appendix 2.

2.5. Estimating SOC sequestration rate based on C fluxes

The four C fluxes affecting the SOC sequestration rate in forests (i.e. above- and below-ground litter production and decomposition) were measured or modelled at the beginning (1994) and the middle (2002) of the monitoring period. SOC stocks were assumed to have reached a steady state at the onset of the monitoring period. We considered the middle of the monitoring period in order to obtain average fluxes representative of the whole period, assuming linear changes over time. The method developed for estimating these fluxes is explained in details below and described schematically in Appendix 3.

To estimate the SOC budget in 1994, the above-ground litter production was derived from litterfall data collected four times per year in 10 traps (0.5 m^2) per plot placed systematically on a 20 m × 20 m grid. The collected samples were air-dried and sorted into leaves, branches and fruit for the dominant tree species while the remaining litter of all other tree species was combined. All the litter components were weighed and sub-samples were oven-dried at 105 °C for 24 h in order to determine water content and convert fresh mass into dry mass. Considering that fine root litter production represents about one third of the carbon allocated to roots (Nadelhoffer and Raich, 1992), below-ground litter production was estimated based on the Raich and Nadelhoffer (1989) relationship linking total root carbon allocation to litterfall (both expressed in gC m^{-2} yr^{-1}):

$$\textit{Fine root litter production} = 0.333\cdot(1.92\ \textit{Litterfall} + 130) \qquad (2)$$

Given our steady-state assumption, the C fluxes associated to above-ground and below-ground litter decomposition were obtained directly from the corresponding litter production fluxes.

To estimate the SOC budget in 2002, we evaluated the extent to which litter production and decomposition could have changed during the monitoring period. Based on trend analyses of litterfall data collected from all the plots between 1994 and 2008, we estimated the temporal changes in above-ground litter production and derived the corresponding changes in below-ground litter production following Eq. (2). As no litter decomposition data were available for the monitoring plots, we calculated Jenny's decomposition coefficient (k') by taking the ratio between litter input and SOC stock at the first soil survey for the above-ground and below-ground compartments (assuming a steady-state, Jenny et al., 1949). We then converted k' into the exponential decay coefficient (k) according to Olson (1963). To estimate how temporal changes in climate could have affected this decay rate (k), we used the climate deposition index (CDI), a function of air temperature, precipitation and potential evapotranspiration (Adair et al., 2008) and assessed its temporal change based on meteorological data (1992–2009 period) obtained from meteorological stations located near the plots. In addition, we used empirical decomposition models to estimate how changes in initial litter chemical composition (nutrient concentrations) could have affected the decay rate (k), as follows:

Above-ground litter (Jacob et al., 2010):

$$k = -2.177 + 0.381\ N\ (mg/g) \qquad (3)$$

Below-ground litter (Silver and Miya, 2001):

$$\ln(k) = 3.79 + 0.74\ \ln Ca\ (mg/g) - 1.22\ \ln(C/N) \qquad (4)$$

Changes in initial litter chemical composition were derived from litter chemistry data and time series in foliar chemistry collected on each plot between 1994 and 2008 (Jonard et al., 2009), assuming that the relative changes in litter chemistry were similar to those in the foliage. We considered the estimated changes in decay rates to be multiplicative and used them to adapt the initial Jenny coefficient which, in turn, allowed us to estimate the above- and below-ground litter decomposition fluxes (Appendix 3).

2.6. Statistical analyses

For each layer, we estimated the SOC sequestration rate by dividing the SOC stock difference by the time elapsed between the two soil surveys. We then used a linear mixed model to evaluate the SOC sequestration rate for each soil layer and for all layers combined and accounted for inter-plot variability by introducing a random factor:

$$\textit{SOC sequestration} = a + \textit{plot}\left(0, \sigma^2_{plot}\right) + \varepsilon\left(0, \sigma^2_{\varepsilon}\right) \qquad (5)$$

where a is a parameter estimating the SOC sequestration rate (MgC ha^{-1} yr^{-1}), *plot* is a normally distributed random variable N $(0, \sigma^2_{plot})$ accounting for inter-plot variability and ε is the residual term, the values of which are approximately normal N $(0, \sigma^2_{\varepsilon})$. Checking the skewness and kurtosis of residuals confirmed normality.

In order to determine which factors most influenced SOC dynamics, we applied a stepwise forward selection procedure based on Schwarz Bayesian Information Criterion (SBC) to the plot-averaged SOC sequestration data. Next, we adjusted a linear mixed model and took heteroscedasticity into account by controlling for the covariance structure of the residuals. The *p*-values for parameters and effects were not adjusted for the fact that the terms in the model have been selected and so are generally liberal.

Finally, we used linear mixed models to analyse temporal trends in above-ground litterfall rate, climate decomposition index (CDI) and foliar concentrations, while considering various random factors (plot, year and month). *Year* was considered to be a numerical variable for the fixed effect and a categorical variable for the random effect.

$$\textit{Litterfall} = a + b\cdot\textit{year} + \textit{plot}\left(0, \sigma^2_{plot}\right) + \textit{year}\left(0, \sigma^2_{year}\right) + \varepsilon\left(0, \sigma^2_{\varepsilon}\right) \qquad (6)$$

$$\textit{CDI} = a + b\cdot\textit{year} + \textit{plot}\left(0, \sigma^2_{plot}\right) + \textit{year}\left(0, \sigma^2_{year}\right) + \textit{month}\left(0, \sigma^2_{month}\right) + \varepsilon\left(0, \sigma^2_{\varepsilon}\right) \qquad (7)$$

$$\textit{Foliar conc.} = a + b\cdot\textit{year} + \textit{plot}\left(0, \sigma^2_{plot}\right) + \textit{year}\left(0, \sigma^2_{year}\right) + \varepsilon\left(0, \sigma^2_{\varepsilon}\right) \qquad (8)$$

All statistical analyses were carried out with the SAS MIXED and GLMSELECT procedures (version 9.3; SAS institute Inc., Cary, N.C.).

3. Results

3.1. SOC stocks in the forest floor and in the mineral soil

The SOC stocks measured during the first soil campaign varied significantly among tree species for the forest floor but not for the mineral soil (Table 1). The largest SOC stocks in the forest floor were recorded under pine (25.4 MgC ha^{-1}) and Norway spruce (16.1 MgC ha^{-1}) and the lowest were recorded under broadleaved species (5.7 MgC ha^{-1} for both oak and European beech), with Douglas and silver firs showing intermediate values (10.7 and 7.3 MgC ha^{-1}, respectively). The total stock (down to 1 m) was higher under coniferous than under broadleaved stands (109.5 vs 88.5 MgC ha^{-1}, $p = 0.006$). On average, three quarters of this total SOC stock was located in the forest floor and in the upper 40 cm of mineral soil (Table 1).

3.2. Estimating the SOC sequestration rate by comparing stocks

On average between the two soil surveys, the SOC stock significantly increased in the forest floor (+0.10 MgC ha^{-1} yr^{-1}; $p < 0.01$) and in the 0–10 cm layer of the mineral soil (+0.25 MgC ha^{-1} yr^{-1}; $p < 0.001$) but no significant temporal change was observed in the 10–20 cm and 20–40 cm layers (Table 2). All together, the SOC sequestration rate amounted to 0.35 MgC ha^{-1} yr^{-1} (Table 2).

3.3. Effect of ecological factors on SOC dynamics

The model obtained by stepwise forward selection accounted for 14% of the variability in SOC sequestration rate in the forest floor and in the mineral soil down to 40 cm depth. This model showed that SOC sequestration rate was higher in uneven-aged than in even-aged stands ($p < 0.001$, Fig. 3) and decreased in both with stand age ($p < 0.001$). As all uneven-aged stands were older than 80 years in 1995 while even-aged stands covered the whole range of ages (15–182 years), we used an unpaired t-test to compare even- and uneven-aged stands for a same age range (>80 years old) and obtained a significantly higher SOC sequestration rate in uneven-aged stands ($p < 0.05$). However, it is worth mentioning that stand structure distribution was

Table 1
Soil organic carbon (SOC) stocks (MgC ha^{-1}) in the forest floor and five mineral layers measured during the initial soil survey, summarized for the seven dominant tree species. Values in parentheses are standard deviations. For a given soil layer, carbon stocks with common letters are not significantly different (Tukey-Cramer multiple comparison test, $\alpha = 0.05$).

Tree species	N	Forest floor (FF)		Mineral soil (MS)										Total (FF + MS)
				0–10 cm		10–20 cm		20–40 cm		40–80 cm		80–100 cm		
Quercus sp.	30	5.7^{c}	(5.0)	28.8^{a}	(9.0)	16.0^{a}	(5.6)	18.5^{a}	(7.0)	13.5^{a}	(7.2)	5.7^{a}	(5.6)	88.2
Fagus sylvatica	20	5.7^{c}	(3.1)	32.1^{a}	(11.3)	18.2^{a}	(6.3)	20.2^{a}	(8.4)	14.1^{a}	(8.9)	4.1^{a}	(2.7)	94.4
Picea abies	10	16.1^{ab}	(12.1)	34.2^{a}	(7.7)	22.2^{a}	(8.2)	26.1^{a}	(13.6)	19.9^{a}	(8.3)	3.9^{a}	(2.2)	122.4
Abies alba	11	7.3^{bc}	(4.5)	29.1^{a}	(11.6)	17.5^{a}	(7.0)	23.5^{a}	(8.7)	19.4^{a}	(11.2)	4.0^{a}	(2.0)	100.8
Pseudotsuga menziesii	6	10.7^{bc}	(4.3)	31.3^{a}	(13.7)	21.5^{a}	(11.1)	27.7^{a}	(17.1)	20.7^{a}	(17.2)	6.2^{a}	(5.4)	118.1
Pinus sp.	23	25.4^{a}	(14.8)	31.6^{a}	(15.2)	18.0^{a}	(10.7)	21.0^{a}	(14.4)	15.4^{a}	(12.6)	4.0^{a}	(4.0)	115.4
Larix decidua	1	6.1^{abc}		25.0^{a}		10.4^{a}		14.3^{a}		21.0^{a}		5.5^{a}		82.3

quite unbalanced, with 94 even-aged and only 8 uneven-aged stands represented.

3.4. Temporal changes in litter production and decomposition

While no temporal trend in litter production was detected between 1994 and 2008, the main factors influencing litter decomposition changed over the two decades of the study. The climate decomposition index (CDI) decreased by 7.9% between 1992 and 2009 ($p < 0.001$) and foliar Nitrogen (N) concentration decreased by 6.9% between 1994 and 2008 ($p < 0.05$). No change in foliar calcium (Ca) concentration was observed.

According to the model of Adair et al. (2008), the decrease in CDI we observed would induce a reduction of the decay rates (k') of above- and below-ground litter by 3.2% between 1994 and 2002. For the above-ground litter compartment, the decline in foliar N we detected would mean an 8% decrease in decay rate (k') according to the model of Jacob et al. (2010) (Eq. (3)). Based on the model of Silver and Miya (2001) (Eq. (4)), this decline in foliar N would result in a 2.2% reduction in the decay rate (k') of below-ground litter.

According to the flux approach we used to estimate the SOC budget in the middle of the monitoring period (2002), the forest soil down to 40 cm in depth accumulated on average 0.14 MgC ha^{-1} yr^{-1} (Table 3), which is less than the sequestration rate obtained based on the resampling method (0.35 MgC ha^{-1} yr^{-1}, Table 2).

4. Discussion

4.1. SOC stocks

According to our results, SOC stocks (down to 1 m in depth) were on average higher under conifers (109.5 MgC ha^{-1}) than under broadleaf woodlands (88.5 MgC ha^{-1}) in France. Differences between coniferous and broadleaved stands were mainly observed in the forest floor layers where carbon stocks reached 17.5 and 5.7 MgC ha^{-1}, respectively. A higher SOC stock in the forest floor of coniferous stands has been observed in many previous studies. Some of these studies have reported a possible compensation between SOC storage in the forest floor and in the mineral soil, with no overall difference in total SOC stock between coniferous and broadleaved forests (Cienciala et al., 2006; Vesterdal et al., 2008; Wiesmeier et al., 2013) while others have found higher SOC stocks under conifers in both forest floor and mineral soil layers (Ovington, 1954; Ovington, 1956; Galka et al., 2013; Gurmesa et al., 2013). We found higher SOC stocks under conifers for both layer types but the functional type effect was significant only for the forest floor layers. In a recent review of tree species influence on SOC stocks in temperate forests using data from single-tree plots, paired adjacent stands and common garden experiments, Vesterdal et al. (2013) also observed that functional type effects on SOC stocks were weaker and less consistent for the mineral soil than for the forest floor.

Table 2
Soil organic carbon (SOC) stocks at the first soil survey and the annual change in stocks for each soil layer between the two soil surveys. SOC changes were estimated based on the fitted linear mixed models (standard error in brackets). The *p* value indicates whether the SOC sequestration rate is significantly different from zero.

Soil layer	SOC stock (MgC ha^{-1})	SOC change (MgC ha^{-1} yr^{-1})	*p* value
Forest floor	11.70 (1.17)	0.10 (0.04)	0.006
0–10 cm	30.78 (1.13)	0.25 (0.05)	<0.001
10–20 cm	17.91 (0.79)	0.02 (0.02)	0.328
20–40 cm	21.12 (1.09)	−0.02 (0.02)	0.237
Total	80.94 (2.98)	0.35 (0.06)	<0.001

4.2. Estimating SOC sequestration rate based on stock comparison

The SOC stocks to 40 cm in depth in our study forests increased significantly over 15 years (+0.35 MgC ha^{-1} yr^{-1}; $p < 0.001$). This rate of accumulation is somewhat lower than the range reported in the literature for neighbouring countries (0.55–0.73 MgC ha^{-1} yr^{-1}

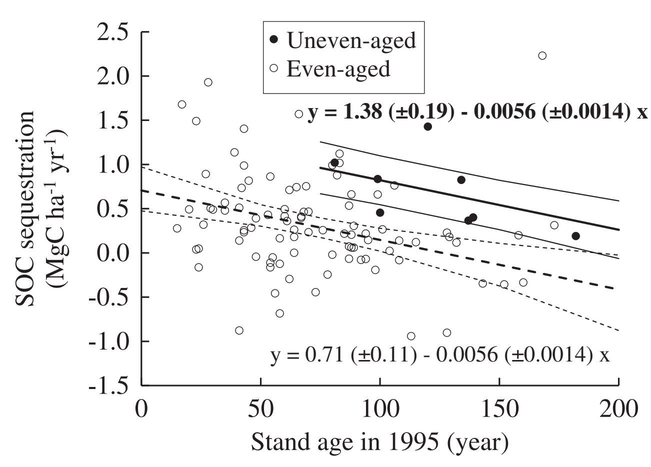

Fig. 3. Effects of stand structure ($p < 0.001$) and stand age ($p < 0.001$) on the soil organic carbon (SOC) sequestration rate in the forest floor and in the mineral soil down to 40 cm. The dashed and black lines represent model predictions (with confidence intervals) for even and uneven-aged stands, respectively.

Table 3
Estimated soil organic carbon (SOC) budgets. Above-ground and below-ground production and decomposition were estimated by considering a steady state at the beginning of the monitoring period (1994) and a transient state in the middle of the monitoring period (2002). The middle of the monitoring period was chosen in order to obtain average fluxes representative of the whole period (supposing linear temporal changes in litter production and decomposition). Values in bold can be compared with the observed total SOC sequestration rate (Table 2).

Carbon flux (tC ha^{-1} yr^{-1})	1994	2002
Measured above-ground litter production	2.15	2.15
Estimated above-ground litter decomposition	2.15	2.05
Above-ground SOC balance	0.00	0.10
Estimated below-ground litter production	1.81	1.81
Estimated below-ground litter decomposition	1.81	1.77
Below-ground SOC balance	0.00	0.04
Total SOC balance	**0.00**	**0.14**

down to 30 cm in depth; Lettens et al., 2005; Grüneberg et al., 2014) and is very similar to that estimated for France by Liski et al. (2002) using the ForClim-D model (+0.33 MgC ha^{-1} yr^{-1} down to 20 cm depth). Extrapolating the SOC sequestration rate to the whole of France, based on the forest area reported by the French forest inventory (http://inventaire-forestier.ign.fr/spip/) provides an estimate of 5.5 TgC yr^{-1}; this rate offsets about 5.4% of country's annual CO_2 emissions from fossil fuel combustion (Oliver et al., 2013). Still, this extrapolated national estimate of the SOC sequestration rate in French forests should be considered with caution and regarded only as a rough approximation of the magnitude to which forest soils contribute to carbon storage in France. Since the French monitoring plots were mainly selected in mature public forests (excluding stands undergoing regeneration during the first 30 years of the RENECOFOR network) and do not include some less abundant forest ecosystems (e.g. Mediterranean forests), their representativeness of the French forest as a whole could be questioned. Concerning disturbances, eight plots were damaged by storms in 1999 and 2009; four of which were replanted while the others naturally regenerated. One can therefore consider that disturbances such as clear-cuts and plantations were accounted for during the monitoring period.

4.3. Effect of ecological factors on SOC dynamics

Among all the potential influencing factors, only stand age and stand structure were retained by the selection procedure. The two factors explained 14% of the variability in SOC sequestration rate (Fig. 3). Plot characteristics can indeed explain only part of this variability; the rest is due to the large spatial heterogeneity of SOC stocks within a same plot (Bekele et al., 2013; Andivia Munoz et al., 2016). By comparing the part of the variance ascribed to intra-plot variability to the total variance, we estimated that only 64% of the total variance could potentially be explained by plot factors while the remaining part (36%) is due to intra-plot variability.

Previous studies based on chronosequences have found an erratic pattern for SOC dynamics with stand age (Covington, 1981; Federer, 1984; Yanai et al., 2003; Mujuru et al., 2014; Cheng et al., 2014; Li et al., 2015), but results from chronosequence studies are often questionable because of their space-for-time assumption. Some patterns ascribed to stand age might in fact be due to spatial effects. Covington (1981) and Federer (1984) observed that forest floor mass declined by 50% in 20 years following timber harvesting, and then increased for the next 50 years. Yanai et al. (2003) argued that the post-harvest decline in SOC was an artefact arising from the fact that, with time, improved skidders reduced the burial of forest floor matter into the mineral soil during logging, but the subsequent rise in SOC has ever been questioned and could be attributed to a SOC stock rebuilding after disturbance and to an increase in total litterfall with stand age (Covington and Aber, 1980; Lebret et al., 2001). Thanks to our repeated soil sampling, we observed that SOC stocks did increase over time. We also observed that the SOC sequestration rate declined with stand age, reaching a value close to zero in even-aged stands >100 years old, while remaining positive in uneven-aged stands whatever the age of the dominant trees (Fig. 3).

Since the broadleaved stands in our study were on average 30 years older than coniferous ones, the stand age effect partly explains the higher SOC sequestration rate under conifers than under broadleaves (+0.49 vs +0.20 MgC ha^{-1} yr^{-1} down to 40 cm in depth, respectively; $p < 0.001$). The broadleaved stands had been forested for >200 years while between 35 and 75% of the coniferous plots were planted within the 20th century on former grasslands, heathlands or croplands or were created by converting low-productivity forests into conifer plantations (Ponce et al., 1998). Grasslands are known to favour below-ground SOC accumulation, and coniferous stands installed on former grasslands probably had a higher below-ground SOC stock at the time of planting than those installed on croplands or than broadleaved stands (Guo and Gifford, 2002; Paul et al., 2002). Afforestation on grasslands was more common in France and this could explain why we found larger SOC stocks under conifers, especially for the deeper soil layers (<20 cm depth). This does not explain the higher SOC stock in the forest floor of coniferous stands, which is more likely to result from the lower decomposability of coniferous litter (Ovington, 1954; Berg and McClaugherty, 2003; Vesterdal et al., 2013; Augusto et al., 2015).

We also found that stand structure affects SOC dynamics, with uneven-aged structures being more favourable to SOC sequestration than even-aged stands. The reasons for these contrasted sequestration rates could lie in the fact that forest cover is maintained continuously in uneven-aged stands and that soil disturbance during harvesting is limited (Jandl et al., 2007; Nave et al., 2010). It may also be that niche complementarity allows trees of different sizes to use resources more efficiently, leading to higher productivity in uneven-aged than in even-aged stands (Jucker et al., 2014; Jucker et al., 2015).

These new insights into the influence exerted by stand structure, stand age and functional type on SOC dynamics may be of help in designing forest management systems able to mitigate climate change impacts. Forest management can influence SOC dynamics by acting on rotation length, stand structure and stand composition to create silvicultural systems that store carbon as effectively as possible. Coniferous stands seem to have a higher capacity to sequester SOC than broadleaved forests. However, this larger SOC sequestration capacity is partly due to carbon storage in the forest floor which is prone to natural and human disturbances. Planting mixed stands of broadleaves and conifers is worth exploring, as this might combine the high SOC sequestration rate of conifers with the broadleaf capacity to transfer carbon into deeper horizons (Andivia Munoz et al., 2016). Silvicultural systems (e.g. uneven-aged stands) and practices which limit soil disturbance during harvesting and replanting, and which retain woody debris on the forest floor must also be considered. However, before using our results to elaborate forest management guidelines, further studies with controlled trials should be carried out to better understand the underlying processes.

4.4. Using a budget approach to test hypotheses

We used a simplified budget approach based on a steady-state assumption to determine whether recent environmental changes or a preexisting imbalance between litter production and decomposition were primarily responsible for SOC sequestration patterns. When analyzing the results of this approach, several limitations must be kept in mind: (i) changes in above- and below-ground litter production were assumed to be positively correlated; (ii) organic matter transfers from the forest floor to the mineral soil were not accounted for and (iii) only nutrient concentrations were used to determine litter quality effect on decomposition. The approach was not designed to accurately reproduce the SOC budget but rather to test whether the steady-state assumption was plausible.

For the above-ground compartment, the average SOC sequestration rate estimated by the budget approach corresponds to that obtained by comparing actual SOC stocks in the forest floor (0.10 ha^{-1} yr^{-1}) and can be attributed to a decrease in above-ground litter decomposition (Table 3). During the monitoring period, climatic conditions became less favourable for litter decomposition (significant decrease in climate decomposition index, CDI) and litter quality probably declined as tree nutrition deteriorated in France (Jonard et al., 2009) and in Europe (Jonard et al., 2015). This deterioration in tree mineral nutrition may be due to a higher nutrient demand from faster growing trees (CO_2 fertilisation effect) whose requirements are not fully satisfied by existing soil nutrient resources. In addition, the decline in atmospheric N deposition certainly contributes to reduce soil N availability and consequently affects negatively foliar N nutrition (Waldner et al., 2014). The models developed by Adair et al. (2008), Jacob et al. (2010) and Silver and Miya (2001) suggest that decreases in CDI and litter quality could have slowed down decomposition and reduced C release by 4.7%. Jacob et al. (2010) and Silver and Miya (2001) used litter N and Ca to describe the litter quality effect on decomposition. Berg and McClaugherty (2003) showed that mass loss rate in the early stages is positively influenced by litter N and P concentrations and pedoclimatic conditions, while high N concentrations in litter could limit the degradation of recalcitrant compounds during the later stages. However, the overall effect of N on late-stage decomposition is difficult to predict since lignin-degrading enzymes are down-regulated by N while cellulose degradation is enhanced (Kutsch et al., 2009). Furthermore, late-stage decomposition is positively affected by litter Ca, which improves bioturbation and litter degradability by favouring earthworm abundance and diversity (Holdsworth et al., 2012; Reich et al., 2005). All in all, we considered litter N and Ca to be acceptable indicators of litter quality effect on decomposition (Holdsworth et al., 2012; Mueller et al., 2015). This said, our objective was not to accurately predict decomposition rate but rather to have a rough estimate of the possible changes in decomposition rate due to change in litter quality. For the forest floor, the budget approach confirmed that the steady-state assumption is plausible and that the observed SOC sequestration rate was likely due to recent environmental changes.

For the below-ground compartment, the average SOC sequestration rate estimated by the budget approach strongly underestimated the rate obtained by comparing SOC stocks in the mineral soil (0.04 vs 0.25 MgC ha^{-1} yr^{-1}). We assumed that below-ground litter production did not change over time since no change was observed for the above-ground litter production. However, allocation patterns could have been modified over time, with, for example, fine root production and turnover being stimulated due to increased atmospheric CO_2 concentrations and decreased tree nutritional status (Lichter et al., 2005). As the budget approach was unable to replicate the observed SOC sequestration rate in the mineral soil, our assumption that the SOC stock was in a steady-state at the beginning of the monitoring period is most probably incorrect for this soil compartment. To explain the observed SOC sequestration rate in the mineral soil, we must rather consider that SOC stocks had not yet reached equilibrium with litter inputs at the time of the first soil survey. This transient state is supported by the fact that the observed SOC sequestration rate decreased with stand age (Fig. 3).

5. Conclusion

Forest soils sequester a substantial amount of SOC in France, with a much higher SOC sequestration rate under conifers than broadleaves; this difference can partly be explained by a stand age effect: the older the stand, the slower the rate. Indeed, the coniferous stands in our study were younger than the broadleaved stands and some of them were afforested much more recently. If indeed stand age is the dominant driver at play, the SOC sequestration rate in France could still be maintained provided that an equilibrium in stand age classes is preserved with no overall aging of the French forest. If, on the other hand, other factors such as land use history and time since afforestation also affect SOC dynamics, one can expect an overall decrease in the SOC sequestration rate in France in the future. Our results show that forest management may have the potential to influence SOC dynamics by acting on rotation length, stand structure and stand composition. However, further research based on experiments conducted in controlled trials is needed to confirm our results and to better understand the underlying processes, thus making it possible to assess whether SOC sequestration will continue at the same rate in the future and to characterize the stability of the newly sequestered carbon.

6. Acknowledgements

Many thanks to all the people who contributed to setting up and maintaining the RENECOFOR network, to collecting data and to ensuring its quality. RENECOFOR is part of the ICP Forests monitoring program and was continuously supported by French public funds (Office National des Forêts, Ministry of Agriculture, Ministry of Ecology, ADEME) and by the European Union from 1991 until 2006. We also thank the INRA Soil Analysis Lab of Arras (LAS) and the Departmental Analysis and Research Lab in the Aisne (LDAR 02) for treating and analyzing the samples and for fruitful discussions on soil analysis methods.

Appendix 1

Range of values for selected stand characteristics (measured in 1995), soil properties (0–40 cm layer, first soil survey), topographic and climatic variables of the French forest monitoring plots classified according to the dominant tree species.

Dominant tree species	Number of plots	Stand age (year)	Stand density (stems/ha)	Basal area (m^2/ha)	Dominant height (m)	pH_H_2O	Cation exchange capacity (cmolc/kg)	Base saturation (%)	Altitude (m)	Annual precipitation (mm)	Mean annual air temperature (°C)
Quercus robur	9	35–134	240–2781	18–32	18–28	4.6–5.1	1.1–21.3	27–90	20–370	651–1163	9.7–13.4
Quercus petraea	19	55–139	296–1338	23–35	21–31	4.2–5.0	1.5–6.8	9–39	55–330	663–1102	9.2–11.7
Q. robur & *Q. petraea*	2	76–113	584–1079	25–31	25–28	4.8–4.8	1.0–1.9	16–45	80–350	698–920	9.8–10.8
Pseudotsuga menziesii	6	20–48	243–1188	16–46	20–39	4.3–4.9	3.2–7.4	9–49	375–700	906–1522	9.1–12.2
Picea abies	11	23–182	371–1258	30–63	17–35	4.2–6.0	3.2–27.0	5–99	480–1700	1043–1987	5.6–10.1
Fagus sylvatica	20	41–160	222–961	18–38	19–30	4.2–7.7	3.0–48.8	10–100	50–1400	736–1894	4.9–13.3
Larix decidua	1	132	388	28	26	6.2	10.5	98	1850	922	6.7
Pinus nigra subsp. *Laricio*	2	45–173	314–806	33–60	23–38	4.6–5.4	1.4–4.1	16–76	140–1100	743–1566	9.6–10.9
Pinus pinaster	7	15–62	511–947	20–76	11–23	4.2–8.6	0.5–6.8	19–100	5–850	775–1328	11.0–13.6
Pinus sylvestris	14	39–94	479–1109	28–46	17–27	4.0–5.3	1.4–4.8	6–66	38–1670	699–1144	7.9–11.8
Abies alba	11	41–168	396–806	31–60	22–29	4.2–6.5	2.2–22.6	10–99	400–1360	925–1564	6.1–10.0

Appendix 2

Information on environmental factors (source of data, number of plots and replicates per plots, monitoring period, measurement frequency and references in which the methods are described in details).

Site factors	Source	Number of plots	Replicates per plot	Sampling period	Measurement frequency/ temporal resolution	Reference
Meteorology	Nearby stations of Météo-France	102	NA	1992–2009	Monthly values used for this study	Ferretti et al. (2014)
	AUREHLY model (Météo-France)	102	NA	1971–2000	Annual values used for this study	Benichou & Le Breton (1987)
Soil profile description	RENECOFOR[a]	102	2 soil profiles	1994–1995	Once	Brêthes and Ulrich (1997)
Soil chemical properties	RENECOFOR	102	4 layers, 25 sampling points, 5 analyses per layer	1993–2012	Twice	Ponette et al. (1997)
Atmopsheric deposition	RENECOFOR	27	1	1993–2011	Weekly collection, Monthly analysis	Ulrich et al. (1998)
	Geostatistical model	102	NA	1993–1998	Mean annual values	Croisé et al. (2005)
Stand age	RENECOFOR	102	30 cored trees	1995–1996	Once	Lebourgeois et al. (1997)
Tree growth	RENECOFOR	102	all trees	1995–2009	Every 5 years	Cluzeau et al. (1998)
Forest history	RENECOFOR	102	NA	NA	Once	Ponce et al. (1998)
Litterfall	RENECOFOR	102	10 traps	1994–2008	Every three months	This study
Foliar chemistry	RENECOFOR	102	8 sampled trees	1993–2009	Every two years	Jonard et al. (2009)

[a] RENECOFOR is the name of the French forest monitoring network composed of 102 level II plots and is part of ICP Forests.

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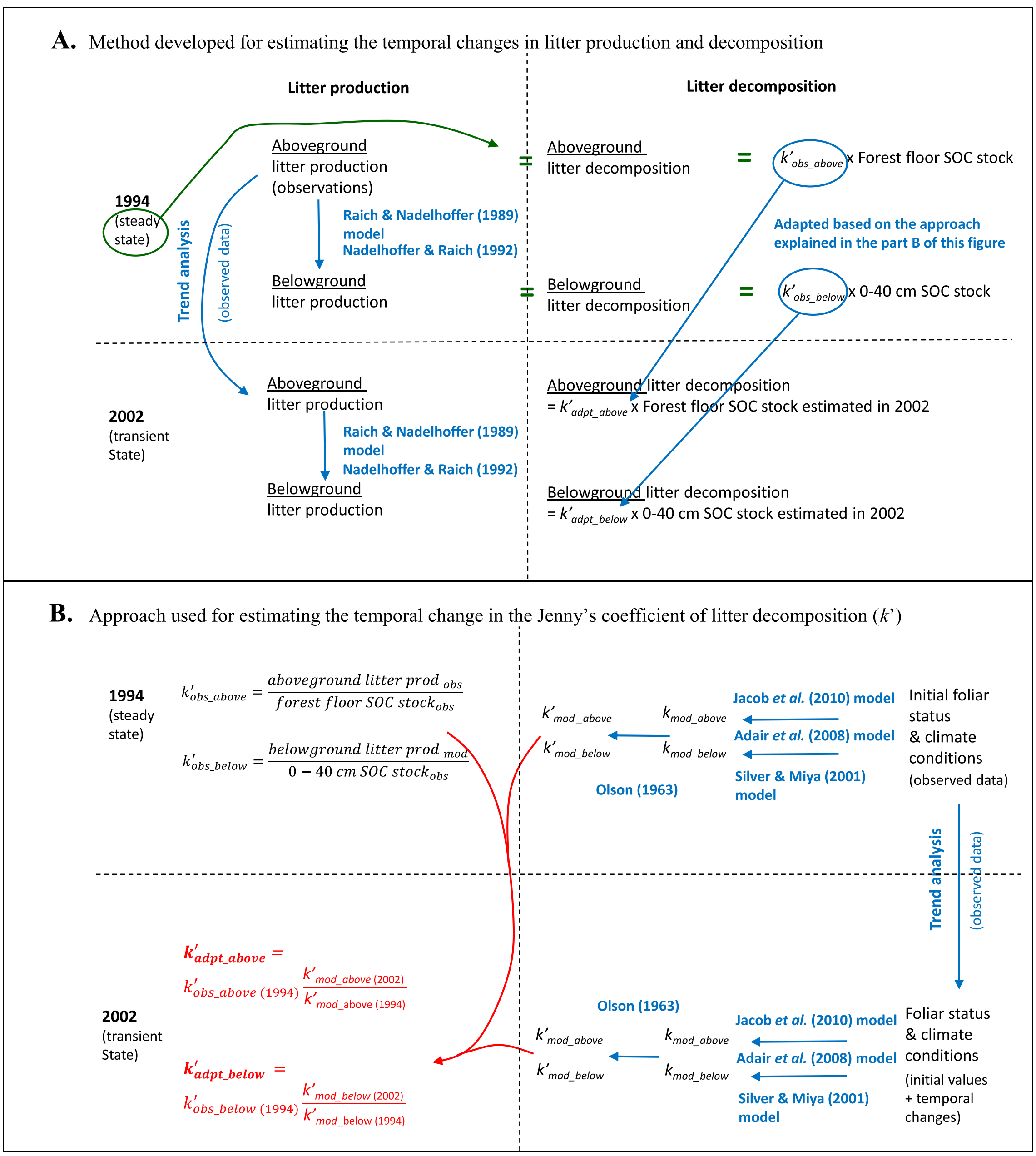
Appendix 3



Appendix 3. Schematic representation of the method developed to estimate temporal changes in litter production and decomposition (A), with a special emphasis on the approach used for estimating the temporal change in Jenny's coefficient of litter decomposition (B). A detailed description of these methods is provided in the Materials and Methods section (2.5 Estimating SOC sequestration based on C fluxes). "obs" and "mod" mean calculated based on observations and on model predictions, respectively; "above" and "below" refer to the above- and below-ground compartment; k and k' are the exponential and Jenny's coefficient of litter decomposition.

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