20th Century Carbon Budget of Forest Soils in the Alps

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ABSTRACT

Dendrochronological studies and forest inventory surveys have reported increased growth and biospheric carbon (C) sequestration for European forests in the recent past. The potential of concomitant changes in forest soil C stocks are not accounted for in the IPCC guidelines for national greenhouse gas inventories. We developed a model-based approach to address this problem and assess the role of soils in forest C balance in the European Alps. The decomposition model FORCLIM-D was driven by long-term (that is, 1900–1985 AD) litter input scenarios constructed from forest inventory data, region-specific dendrochronological basal area indices, and time series of anthropogenic litter removal. The effect of spatial climate variability on organic matter decomposition across the case study region (Switzerland) was explicitly accounted for by constant long-term annual means of actual evapotranspiration and temperature. Uncertainties in forest development, litter removal, fine root litter input, and dynamics of forest soil C were studied by an explorative factorial sensitivity analysis. We found that forest soils contribute substantially to the biospheric C sequestration for Switzerland: Our "best estimate" yielded an increase of 0.35 Mt C/y or 0.33 t C/(ha y) in forest soils for 1985, that is, 27% of the C sequestered by forest trees (BUWAL 1994). Uncertainties regarding C accumulation in forest soils were substantial (0.11–0.58 Mt C/y) but could be reduced by estimating forest soil C stocks in the future. Whereas soils can be important for the C balance in naturally regrowing forests, their C sequestration is negligible (less than 5%) relative to anthropogenic CO_2 emissions in Western Europe at present.

Key words: European forests; greenhouse gas inventory; forest soils; carbon dynamics; soil organic carbon accumulation; forest inventory data; dendrochronology; forest litter harvesting.

INTRODUCTION

The contemporary man-made rise in greenhouse gases and its potentially detrimental effect on global climate have been recognized as a major threat to the environment and the world's economics. As a consequence, the United Nations Framework Convention on Climate Change was established at the 1992 United Nations Conference on the Environment and Development in Rio de Janeiro. Signing parties committed themselves to quantify emissions and sinks of greenhouse gases as well as to preserve and enhance existing national sinks of greenhouse gases. To meet national obligations, the Intergovernmental Panel on Climate Change (IPCC) has established guidelines to estimate greenhouse gas balances (Houghton and others 1997a). Because CO_2 has been recognized as the dominant greenhouse gas with respect to human use and alteration of the biosphere (Houghton and others 1997b), CO_2 emissions and removals from forests and land-use change are included in these guidelines in addition to fuel combustion, emissions from industrial processes, anthropogenic emissions from agriculture or waste management, and others. Houghton and others (1997a) have specified greenhouse effect–relevant

aspects of changes in forest and other woody biomass stocks, forest and grassland conversion, and abandonment of managed lands.

Forests play a major role in the exchange of CO_2 between atmosphere and biosphere: 60–80% of the global terrestrial carbon (C) is sequestered by forest plants and soils (Perruchoud and Fischlin 1995). Deforestation, mainly occurring in the tropics, therefore reduces C stocks at global scales (1.6 ± 1.0 Gt C/y in the 1980s) whereas forest regrowth (0.5 ± 0.5 Gt C/y in the 1980s) on the Northern Hemisphere has the opposite effect (Schimel and others 1996). Forest regrowth has been reported for Europe (Kauppi and others 1992; Kuusela 1994) and Switzerland (Brassel and Brändli 1999) by repeated forest inventories and is attributed to enhanced forest area, improved growth conditions at tree and stand level, and altered harvesting practices. This is supported by forest dendrochronology studies that have provided evidence for a modern long-term increase in radial growth (Innes 1991; Bräker 1996a; Spiecker and others 1996). Possible mechanisms of this effect include shifts in forest age–class structure induced by forest disturbances (Kohlmaier and others 1995; Kurz and others 1995) and plant fertilization by increased atmospheric CO_2 concentration or nitrogen deposition (Melillo and others 1996).

Globally, C sequestration in forests has been hypothesized to explain an "imbalance" in the anthropogenic C budget (Schimel and others 1995) and has become a high priority research area. Many studies still exclude soil organic carbon (SOC) though forest soils sequester 69% of the global forest C (Dixon and others 1994), that is, more than the amount present in the atmosphere, and can respond rapidly and substantially under land-use changes (Johnson 1992; Davidson and Ackerman 1993). This has been acknowledged in the guidelines of the IPCC (Houghton and others 1997a), which include land-use change–induced shifts of nonliving organic carbon (NLOC) with special attention to organic soils and CO_2 emissions from agricultural soils through liming. Also included are SOC changes induced by managed land abandonment or set-aside strategies. Changes in NLOC pools brought about by changes in forest growth are not considered in the guidelines. However, under the assumption of constant plant tissue mortality, the increase of forest stocks observed over the past decades in Europe implies higher plant litter production. If breakdown and mineralization processes also remained unchanged, a substantial net accumulation of NLOC would result and thus an increase of the forests' net C sequestration potential.

The goal of our study was to develop a method to assess the role of soils in the C balance in national greenhouse gas inventories. We hoped to determine the importance of observed increases in timber stocks for forest soil C and the contemporary C balance of Swiss forests. Due to the lack of appropriate soil carbon data for Swiss forests, a spatially referenced modeling approach was chosen: We used Swiss forest inventory data (EAFV 1988; Brassel and Brändli 1999) in combination with estimates of plant tissue longevity, dendrochronological data (Bräker 1996a, 1996b), and historical reconstructions of litter removal (Alveteg and others 1998) for the 20th century to build site-specific time series of litter input and drive NLOC dynamics. Breakdown, mineralization, and humification of organic matter (OM) were simulated with FORCLIM-D (Perruchoud 1996; Perruchoud and others 1999). Existing uncertainties with respect to fine root litter input, forest biomass development, and SOC dynamics were addressed by a factorial sensitivity analysis.

METHODS

Study Area

Forests cover approximately 29% or 12,000 km² of Switzerland (EAFV 1988; SAEFL 1997) and are divided into five productivity regions based on elevation, geology, climate, and land use. These regions (Jura, Plateau, Pre-Alps (lower Alps), Alps (high Alps), and Southern Alps) also differ in size and stocking density. Most areas at lower elevations have a complex vegetation history due to their intensive management, while more natural forests prevail at higher elevations. Spruce, beech, and fir are the dominant species in Switzerland making up approximately 80% of total timber volume reserves (EAFV 1988). Spruce is typical for forests in the Pre-Alps and Alps but also contributes substantially on the Plateau where beech is dominant. The relative contribution of needleleaf trees by region increases with altitude at the cost of broadleaf trees. Climate is characterized by a strong altitudinal gradient in Switzerland and ranges from intra-alpine and continental (annual precipitation sum less than 500 mm) to insubrian (July temperature higher than 20°C, annual precipitation sum greater than 1600 mm) or from temperate (Plateau) to cold climate (Alps) (Brzeziecki and others 1993). All simulation results refer to an area of 10,544 km²
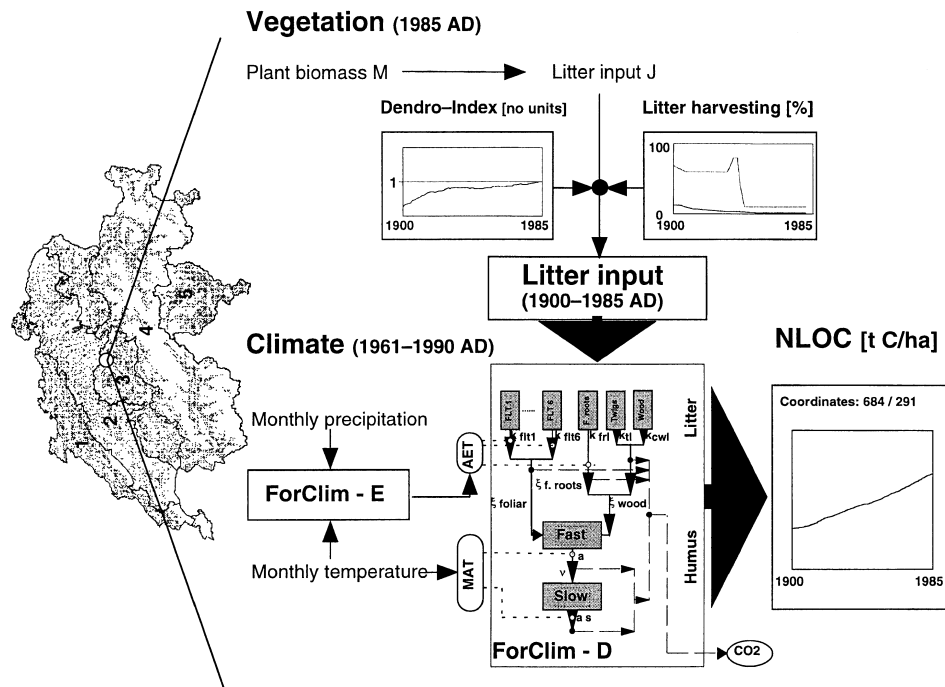
Figure 1. Modeling concept for assessing the role of soils in the C balance of Swiss forests. Plant biomass was estimated on the basis of forest inventory data (EAFV 1988; Brassel and Brändli 1999) and converted to annual litter input for 1985 via plant tissue longevities. The reconstruction of litter inputs for the period 1900–1985 was achieved with an age-corrected dendrochronological basal area index (see Dendro-Index inset). Litter input scenarios were finally corrected for anthropogenic litter removal (see Litter harvesting inset for foliage and fine wood) modified from Alveteg and others (1998) and used to drive FORCLIM-D (Perruchoud 1996; Perruchoud and others 1999), a model of NLOC dynamics with explicit representation of climatic controls (**dotted lines** between FORCLIM-E and FORCLIM-D). In FORCLIM-D, **shaded boxes** denote state variables, and **ovals** are auxiliary variables. **Solid arrows** indicate C-mass fluxes, and **dashed arrows** describe CO_2 losses associated with heterotrophic respiration. Region-specific differences in biomass history and growth trends were accounted for via stratification by productivity regions (**1**, Jura; **2**, Plateau; **3**, Pre-Alps; **4**, Alps; **5**, Southern Alps).

that represents approximately the area of accessible forests without brushwood in Switzerland.

Modeling Concept

The role of forest soils in the Swiss national C balance was assessed by single-site simulations for "accessible forests without brushwood" of the Swiss National Forest Inventory (SNFI) (Brassel and Brändli 1999) (Figure 1). Tree data were used to estimate biomass ($\mathcal{M}_n$) for above- and below-ground plant parts (n) by allometric functions (see *Contemporary Litter C Fluxes*). Litter production was calculated from longevity estimates (τ_n) via $\mathcal{T}_n = \mathcal{M}_n/\tau_n$ following King and others (1997) for $t_0 = 1985$ and reconstructed for 1900–1985 by using a regional tree ring–based basal area index ($I_{i,gen.,reg.}$) for coniferous and deciduous trees in Switzerland (see *Retrospective Extrapolation of Litter C Fluxes*). Anthropogenic forest litter removal was accounted for by plant tissue–specific correction functions (η_n) (see *Litter Harvesting Scenarios*). Thus, annual litter inputs for every grid-point and year were calculated

according to (see APPENDIX E):

$$\mathcal{T}_n(t) = \frac{\mathcal{M}_n(t_0)}{\tau_n} \cdot I_{i,gen.,reg.}(t) \cdot \eta_n(t). \qquad (1)$$

These scenarios were used to drive NLOC decomposition simulations with FORCLIM-D (see FORCLIM-D Model Description). Variations of organic matter decomposition induced by differences in abiotic controls were included by site-specific long-term annual means of air temperature, precipitation sums, and simulated actual evapotranspiration (see *Bioclimatic Parameters*). National estimates of NLOC dynamics between 1900–1985 were obtained by aggregating grid-point information from 5272 sites and assuming a representability of 2 km² for each sample point.

FORCLIM-D Model Description

FORCLIM-D (Perruchoud 1996; Perruchoud and others 1999) was originally developed as submodel of the forest gap model FORCLIM (Bugmann 1996) to

simulate species composition and C dynamics in forests of the temperate zone under current and altered climatic conditions. FORCLIM-D includes a climate and litter quality–specific model of foliar litter decomposition and discriminates foliar (six litter types), fine root, twig, and woody litter (Figure 1). The decomposition of litter is represented as a first order kinetic reaction:

$$\dot{c}_n(t) = -k_n \cdot c_n(t) + \mathscr{T}_n, \qquad (2)$$

where c_n is the carbon mass, k_n the turnover rate, and $\mathscr{T}_n$ the scenario input flux for compartment n. A fraction ξ_n of the C flux from decomposing litter is transferred to the soil while the rest $(1 - \xi_n)$ is respired as CO_2. The total C flux entering the soil is given by the sum of the humification fractions ξ_n multiplied by the litter decomposition fluxes (that is, turnover rate k_n times litter mass c_n):

$$u(t) = \sum_n \xi_n \cdot k_n \cdot c_n(t). \qquad (3)$$

The decomposition of humified organic carbon (SOC) is described by coupling a fast (c_{fH}) and a slow (c_{sH}) overturning soil humus compartment:

$$\dot{c}_{fH}(t) = -a \cdot c_{fH}(t) + u(t), \qquad (4)$$

$$\dot{c}_{sH}(t) = -a \cdot s \cdot c_{sH}(t) + v \cdot a \cdot c_{fH}(t), \qquad (5)$$

where u is the input from the litter compartments, a and $a \cdot s$ denote turnover rates for fast and slow humus, and s is the ratio of their turnover times. v controls the fraction of fast humus that is passed to the slow humus compartment (Figure 1). In the current parameterization obtained with soil ^{14}C data, these boxes refer to rapid (c_{fH}) and recalcitrant (c_{sH}) SOC in the 0–20 cm topsoil layer (Perruchoud and others 1999). Abiotic controls on foliar and fine root litter decomposition were expressed by actual evapotranspiration (Meentemeyer 1978; Berg and others 1993), and mean annual temperature was used as sole climatic control of humus mineralization here (Trumbore and others 1996).

Input Data

Bioclimatic parameters.   Actual evapotranspiration (AET) and mean annual temperature (MAT) were derived for every forested grid-point at a 1.4 km × 1.4 km spatial resolution. We used long-term monthly mean records of temperature and precipitation (base period: 1961–1990) from Swiss climate stations and spatial extrapolation with a 25-m digital terrain model (Kienast 1998). AET was determined with a simplified spatial version of FORCLIM-E (Bugmann and Cramer 1998), spatially uniform monthly climate variabilities, and a fixed field capac-

ity parameter value of 15 cm (H. Lischke, WSL Birmensdorf personal communication). We assumed constant climate throughout the simulation.

Contemporary litter C fluxes.   Swiss forest inventory data (EAFV 1988; Brassel and Brändli 1999) were used to estimate biomasses for twig (diameter less than 7 cm), branches (diameter 7–12 cm), bark, and other woody tissue (coarse wood). Four classes were used for leaf and needle biomass, respectively, based on longevity and decomposability (see APPENDIX A). Fine roots were defined by a threshold diameter of 5 mm; all other roots were treated as coarse wood. Allometric models were used for aboveground stemwood volume (Kaufmann 1996) and branch volume estimated from tree genus, productivity region, and tree diameter at breast height (dbh). Similarly, twig biomass was expressed by genus and dbh (Kaufmann and Brassel 1999). Biomass conversions of volume data were obtained with published wood density estimates (see APPENDIX B). Additionally, genus-specific estimates were introduced for leaf, needle, and root biomass (see APPENDIX C). In contrast to all other plant tissues, fine root biomass was not determined at tree level but at stand level (that is, on a hectare basis) and approximated as a constant fraction of coarse root or total foliage biomass (Table 1).

Biomass figures on a hectare basis were extrapolated from single tree data and averaged by genus. The sum of twigs, branches, and bark was replaced by fine wood. Longevity estimates of coarse wood, required to derive litter inputs, were derived from region-specific tree mortalities monitored over a 10-y period (Kaufmann and Brassel 1999) and ranged between 200 (South Alps) and 700 y (Jura). For fine wood turnover time, we assumed 25 y and for fine roots (less than or equal to 5 mm in diameter) 1.361 y according to Kurz and others (1996). Estimates for needles were based on expert knowledge (M. Sieber, ETH Zürich, personal communication) assuming 3 y for *Pinus,* 7 y for *Picea,* and 10 y for *Abies.* Foliar litter was aggregated by decomposability (see APPENDIX A) by using a modified version of the litter classification scheme of Perruchoud (1996).

Litter input of harvesting residues left on-site were estimated by consideration of trees, which had disappeared between the first (1983–1985) and the second SNFI inventory (1993–1995) assuming removal after 5 y (WSL 1999). Additional coarse woody litter input was thereby obtained on 3065 out of 5272 forest sampling plots. For each, annual litter input of fine, woody roots, leaves, needles, twigs, and bark was subsequently determined. Due to the lack of data, we assumed no changes for the

Table 1. Characteristics of Factorial Sensitivity Experiment

Experiment	Biomass Trend	Litter Harvesting	Fine Root Biomass	Comment
1	$I_{2,gen.,reg.}$	A, CWLH = FLH	5% of CRB	Base scenario
2	$I_{2,gen.,reg.}$	A, CWLH = FLH	**10% of CRB**	Effect of fine root biomass
3	$I_{2,gen.,reg.}$	A, CWLH = FLH	**TFB**	Effect of fine root biomass
4	$I_{1,gen.,reg.}$	A, CWLH = FLH	5% of CRB	Alternative dendro-index
5	$I_x(t_0) = 0.25$	A, CWLH = FLH	5% of CRB	Strong biomass trend
6	$I_x(t_0) = 0.50$	A, CWLH = FLH	5% of CRB	Medium biomass trend
7	$I_x(t_0) = 0.75$	A, CWLH = FLH	5% of CRB	Weak biomass trend
8	$I_x(t_0) = 1.00$	A, CWLH = FLH	5% of CRB	Zero biomass trend
9	$I_{2,gen.,reg.}$	**A, CWLH = 2 × FLH**	5% of CRB	Altered litter harvesting
10	$I_{2,gen.,reg.}$	**A, CWLH = 3 × FLH**	5% of CRB	Altered litter harvesting
11	$I_{2,gen.,reg.}$	**A, CWLH = FWLH**	5% of CRB	Altered litter harvesting
12	$I_{2,gen.,reg.}$	**no litter harvesting**	5% of CRB	Altered litter harvesting
13	$I_{2,gen.,reg.}$	**A, customized harvest**	5% of CRB	Altered litter harvesting
14	$I_{2,gen.,reg.}$	A, CWLH = FLH	5% of CRB	**High humus accumulation**
15	$I_{2,gen.,reg.}$	A, CWLH = FLH	5% of CRB	**Low humus accumulation**

The factorial experiment was used to assess the sensitivity of C dynamics in Swiss forest soils for the 20th century. Experiments 1–3, fine root biomass was assumed as varying fraction of coarse root or total foliage biomass. Experiments 4–8, alternative indices ($I_{i,gen.,reg.}$) were used as proxy for past biomass trends in Swiss forests. I_x refer to synthetical linear biomass increases between $t_0 = 1900$ and 1983. Experiments 9–13, litter harvesting was modified from Alveteg and others (1998) (A). Parameter changes for experiments 14 and 15 are given in the text in Simulation Experiments.
FLH, foliage litter harvesting; FWLH, fine woody litter harvesting; CWLH, coarse woody litter harvesting; CRB, coarse root biomass; TFB, total foliar biomass.
Experiment 1 was used as base scenario, factorial changes in the other experiments are indicated by bold letters.

relative contribution of litter from harvesting residues over the entire simulation period. Litter inputs were calculated at a 1.4 km × 1.4 km spatial resolution, and organic matter converted to C by using factors of 0.45 for foliar and fine root litter and 0.5 for woody litter (Vogt 1991).

Retrospective extrapolation of litter C fluxes. Litter inputs were back extrapolated to 1900 on the basis of tree-ring chronologies by using an age-corrected and productivity region-specific basal area index of tree development. Sample trees from generally fully stocked even- and uneven-aged stands were taken on a 4 km × 4 km grid (Sanasilva 1984, 371 sites) and a 50-km transect (Sanasilva 1992, 58 sites). A total of 1336 cores were sampled from beech ($n = 55$), fir ($n = 328$), and spruce ($n = 953$) trees, which represent the most abundant species and account for 80% of the standing volume in Swiss forests (EAFV 1988). The number of tree-cores varied between one and eight cores per site (Bräker 1996b). Dominant, codominant, subdominant, and suppressed trees with a minimum diameter at breast height of 20 cm were included for deriving tree-ring indices. See Bräker (1996b) for details.

Our approach for deriving tree-ring indices was traditional in that age-related biases were removed by calculating ratios of actual and modeled tree growth. However, because we were interested in estimating tree biomass, we used basal area not tree-ring width for calculation of the dendrochronological index. Methodological uncertainties in the calculation of a tree-ring biomass index were met by two alternative approaches and a subsequent comparison with forest inventory biomass increase estimates. First, basal area was calculated according to $\pi/4 \cdot d^2$ where d is tree diameter for every sample tree. Second, basal area was plotted against physiological age (pa) and averaged for all sample trees. Third, this record was smoothed by nonlinear regression (SAS 1990) with a triple-exponential model [that is, $exp\ (b_1 \cdot pa + b_2 \cdot\ pa^2 + b_3 \cdot pa^3)$] and the resulting signal used as a first reference. A second reference signal was obtained by sorting single tree-ring data, averaging by physiological age, smoothing with the above triple-exponential model, and converting mean tree-ring width to basal area under the assumption of a circular tree cross-section. The reference signals were used to derive basal area indices in "physiological time representation" taking the ratio of single tree basal area and reference signal 1 and 2, respectively. Finally, these indices were averaged in absolute time over all sample trees and normalized to one for the reference year 1983. Stratifying trees by genus (beech, spruce, and fir) and productivity region, we thus obtained $I_{1,gen.,reg.}(t)$, $I_{2,gen.,reg.}(t)$ with $I_{i,gen.,reg.}(1983) = 1$.

The indices for beech and spruce were assumed as representative for the lateral growth history of Swiss

Table 2.   Stand Level Plant C Density by Productivity Region for Swiss Forests

Region	Number	Plant C Sequestration [t C/ha]					
		Foliage	Fine Wood	Stemwood	Fine Roots	Coarse Roots	Total Tree
Jura	943	2.8	19.5	65.1	1.2	29.5	114.5
Plateau	1098	3.2	26.4	76.8	1.3	27.9	135.6
Pre-Alps	1005	4.2	20.4	71.0	1.3	29.3	126.3
Alps	1616	3.4	14.6	48.6	1.1	23.7	91.3
S-Alps	610	2.0	13.3	35.5	1.1	24.6	76.6
Switzerland	5272	3.3	18.9	60.2	1.2	26.2	109.7

Based on EAFV (1988). Stand level C densities refer to the inventory period 1983–1985 (EAFV 1988) and represent above- and belowground C stocks of forest trees in Switzerland (accessible forests only). The "number" of forest plots was determined from a 1.4 km × 1.4 km grid. "Foliage" denotes leaves and needles, "fine wood" subsumes twigs, branches, and bark, and "stemwood" stands for woody biomass with diameter greater than 12 cm. Biomass of "fine roots" (diameter greater than or equal to 5 mm) represents 5% of coarse root biomass here. Total tree C differs slightly from the sum of individual plant parts due to rounding errors.

broadleaf and needleleaf trees, respectively. We adopted the same trends as proxy for past tree biomass history to reconstruct litter input scenarios via Eq. (1) neglecting variations in longitudinal tree growth or forest structure. The limitations of this approach are commented on below (see Discussion). Alternatively, four synthetical indices (I_x) were constructed to simulate linear biomass increases of 0, 25, 50, and 75%, respectively, between 1900 and 1983. They were used to assess the sensitivity of NLOC dynamics to uncertainties in forest biomass history and make extrapolations for European forests.

Litter harvesting scenarios.   Plant litter removals for this century (Bürgi 1997) were modified from Alveteg and others (1998) who specified the percentage of foliar and fine woody (branch) litter harvesting. We assumed multiples of foliar and branch litter harvesting for coarse woody litter removal. Changed harvesting conditions (namely, no litter harvesting and customized litter removal with an increase around World War I and a delayed decrease after World War II) were considered additionally to assess the sensitivity of NLOC dynamics (Table 1 and Figure 1, insets).

Simulation Experiments

Model initialization.   The model was initialized in AD 1900 assuming that the system had previously equilibrated under the constant litter inputs $\mathscr{T}_n(t = 1900)$ obtained via Eq. (1). This procedure was conducted for each grid-point.

Experimental design.   A factorial simulation experiment was set up to assess the sensitivity of NLOC dynamics with respect to model uncertainties (Table 1), such as the effect of changes in fine root litter input, forest biomass trends, litter harvesting, and soil humus dynamics. For the latter case, variations

of model parameters controlling NLOC dynamics were assumed, and high vs low humus accumulation simulated changing humification ratios ξ_i by ±10%, humus decomposition a by ∓10%, and humus transfer v by ±10%.

Modeling and simulation tools.   The model ForClim-D was developed with the interactive modeling and simulation software Ramses (Fischlin and others 1994) on Apple's Power Macintosh computers. All applications of the model were performed on SUN workstations in batch mode under Rass (Thöny and others 1994), and statistical analyses were performed with the SAS package, version 6.11 (SAS 1990) on SUN workstations.

Results

Present-Day Plant C Pools and Litter C Fluxes in Swiss Forests

To derive litter C fluxes, we estimated plant C stocks for accessible forests from the first SNFI (EAFV 1988). At stand level (Table 2), C stock estimates varied by a factor of two across productivity regions with lowest C density in forests of the Southern Alpine region. North of the Alps, plant C decreased with altitude from the Plateau over the Pre-Alps to the Alps, whereas plant C in forests of the Jura was intermediate. Calculations of tree C allocation (data not shown) yielded a maximum estimate of 55% for below- to aboveground plant C ratios in Southern Alpine forests. In all other regions, a substantially lower fraction of belowground tissues (26–40%) was obtained, which decreased with altitude. Seventy-one to seventy-four percent of the aboveground plant C was sequestered in the stem, foliage held 3–6% C, and the rest was stored by twigs, branches, and bark. At the national level, C stocks

Table 3. Nationwide Plant C Sequestration by Productivity Region for Swiss Forests

	Forested Area		Plant C Stocks	
Region	Absolute (km²)	Relative (%)	Absolute (Mt C)	Relative (%)
Jura	1886	17.9	21.6	18.7
Plateau	2196	20.8	29.8	25.8
Pre-Alps	2010	19.1	25.4	22.0
Alps	3232	30.7	29.5	25.6
S-Alps	1220	11.6	9.3	8.1
Switzerland	10,544	100.0	115.6	100.0

Based on EAFV (1988). Estimates represent above- and belowground C stocks of forest trees in Switzerland for 1983–1985 (EAFV 1988) in accessible forests only. Region areas were determined assuming a representability of 2 km² for each sample plot (Table 2). Percentages do not add up to 100.0 due to rounding errors.

Table 4. Stand Level C Litter Inputs by Productivity Region for Swiss Forests

	Plant Litter Inputs [t C/(ha y)]			
Region	Foliage	Fine Roots	Fine Wood	Coarse Wood
Jura	1.21	0.87	1.08	0.65
Plateau	1.47	0.94	1.58	1.01
Pre-Alps	1.27	0.98	1.14	0.85
Alps	1.34	0.79	0.78	0.69
S-Alps	1.26	0.82	0.64	0.55

Based on EAFV (1988). Litter production refers to the inventory period 1983–1985 (EAFV 1988) and was calculated as ratio of biomass (Table 2) and longevity (King and others 1997). Figures are corrected for residues left on-site after harvesting. "Foliage" refers to leaf and needle litter; "fine roots" includes belowground litter with a maximum diameter of 5 mm; "fine wood" debris comprises twig, branch, and bark litter; and "coarse wood" stands for stemwood and coarse root litter.

sequestered in Southern Alpine forests were least important (Table 3), whereas forests in the Alps contributed as much as forests on the Plateau (nearly equal to 30%) to the national Swiss forest C stock of 116 Mt due to their large area.

We derived plant litter input estimates for 1983–85, which were additionally corrected for residues left on-site after harvesting (Table 4), based on stand level C densities and tissue longevities from the literature. The highest inputs resulted for foliage and fine roots due to their fast turnover. In contrast to the respective biomass estimates (Table 2), regional differences of litter input between foliage and fine roots were less pronounced due to the sizeable fraction of coniferous trees with high needle longevities (that is, 3 y for *Pinus,* 7 y for *Picea,* and 10 y for *Abies*) in all regions. Lowest litter inputs were found for coarse and fine woody debris.

Retrospective Plant Biomass Dynamics

Dendrochronological analyses for basal area yielded a positive long-term trend with strong regional discrimination (Figure 2). Over the short term, this trend was, however, negative for all genera and regions. Regional patterns of NBAI were also different in timing and amplitude for all genera; the increase of normalized basal area index (NBAI) for spruce (Figure 2, middle right), for example, was in general less pronounced at high elevations (Pre-Alps and Alps) than on the Swiss Plateau or in the Jura and also contrasted with the behavior of fir. A methodological comparison (Figure 2, left vs right) showed that $I_{1,gen.,reg.}$ exceeded $I_{2,gen.,reg.}$ for all genera and regions over the long term. To be conservative with respect to the simulated NLOC accumulation, we used $I_{2,gen.,reg.}$ as default for reconstructing past biomass trends in the factorial experiment. A detailed discussion of these dendrochronological analyses will be given in a follow-up article (O. U. Bräker, WSL Birmensdorf, personal communication).

NLOC Dynamics of Swiss Forests in the 20th Century

The base simulation run for NLOC accumulation in accessible Swiss forests without brushwood (Table 1, experiment 1) is shown in Figure 3. NLOC increased monotonously from 44 Mt C in 1900 to 71 Mt C in 1985 supporting a NLOC sink of 0.35 Mt C/y for 1985. Thus, organic matter sequestered by litter and soil humus (0–20 cm) represented 61% of plant C stocks in Swiss forests (Table 3). Annual NLOC fluctuations (Figure 3, bottom) were approximately several tenths of a percent of NLOC stocks (Figure 3, top), which explains the latter's smooth trajectory. Forest soils were a sink for atmospheric CO_2 over the entire simulation period, although the sink effect of NLOC was reduced during World War II in response to enhanced litter harvest. ΔNLOC remained positive in the early 1940s thanks to the delayed and dampened soil humus response that balanced negative changes of litter organic carbon. Regional contributions to national NLOC accumulation in Swiss forests varied according to differences in area extent (Figure 4): Forests in the Jura, Plateau, and Pre-Alps region stored similar amounts of NLOC and lay between NLOC stocks for the Southern Alps at the low end and Alpine forests at the high end.

At stand level, forest soils in the Pre-Alps sequestered more C than any other region followed by the Alps and the Plateau (Table 5). Because litter inputs on the Plateau in 1985 were distinctively higher than in the Alps, the latter's high NLOC pools reflect the combined effect of reduced decomposition due
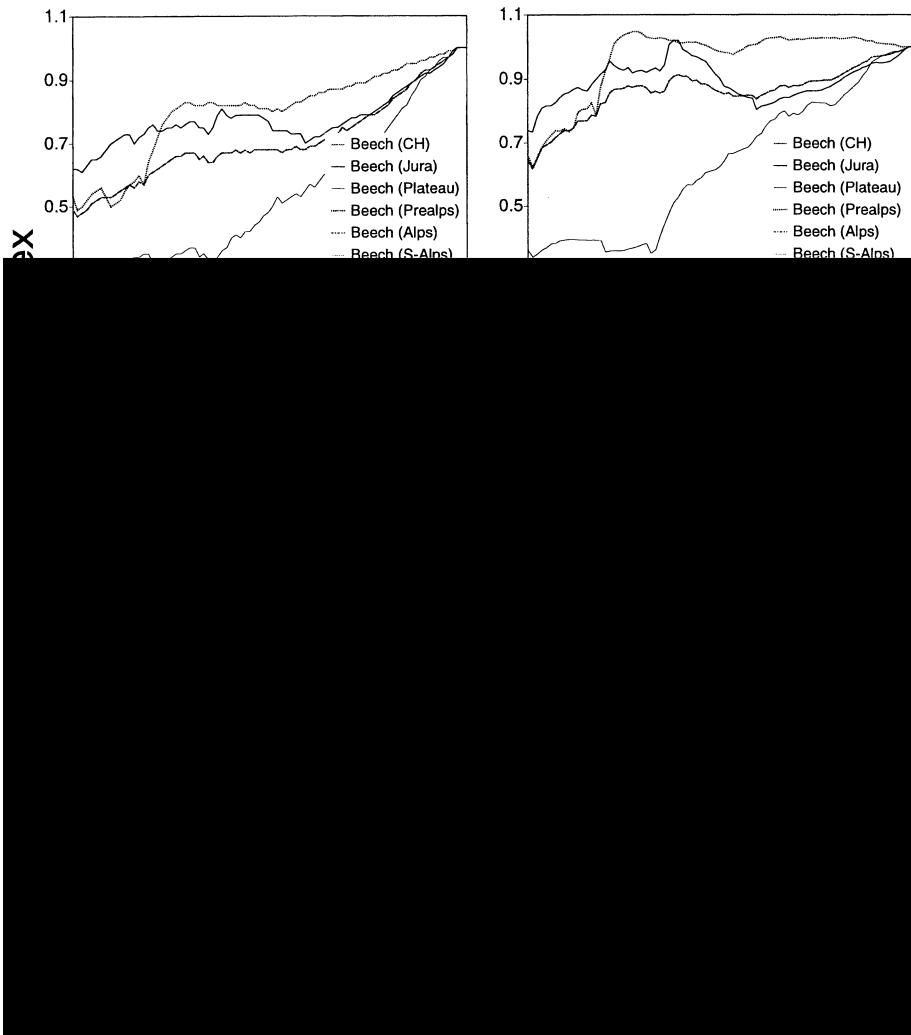
Figure 2. Normalized basal area indices by genus and productivity region were used as proxy for past biomass trends in Swiss forests in this study. Top, middle, and bottom figures denote indices for beech, spruce, and fir and different productivity regions in Switzerland. $I_{1,gen.,reg.}$ (**left**) and $I_{2,gen.,reg.}$ (**right**) refer to different calculation methods (see METHODS for details). Note, that the conservative index ($I_{2,gen.,reg.}$) was used in all simulation experiments except for No. 4.

to low temperature and high litter inputs for the period before 1985 derived via $I_{2,gen.,reg.}$. Forests on the Swiss Plateau revealed, however, the highest C flux for 1985. Simulated distributions of NLOC pools (Figure 5) were skewed to the right and shallow with maxima approximately 20–60 t C/ha. A similar situation was obtained for annual NLOC changes with maximum ΔNLOC of 0.1–0.3 t C/(ha y).

Sensitivity Analysis

We investigated the sensitivity of NLOC dynamics for different sources of uncertainty to assess the reliability of simulated C pools and fluxes for Swiss forest soils in 1985 (Table 6). Results were compared with the base scenario run (experiment 1) with NLOC stocks of 71 Mt C and NLOC accumulation of 0.35 Mt C/y. Assumptions regarding fine root biomass did considerably affect NLOC pool and flux estimates (Figure 3 and Table 6). Doubling fine root biomass (experiment 2) relative to the base scenario

increased Swiss forests' NLOC pool by 28% and their C sink by 17% (Table 6). Variations of NLOC pools and fluxes induced by uncertainties in forest biomass history (experiments 4–8) varied between 57–84 Mt C and 0.11–0.58 Mt C/y for 1985, respectively. The most pronounced biomass increase (experiment 5) yielded the lowest C pool and highest C sink estimate for Swiss forest soils (Figure 6). Unlike the uncertainties in forest biomass history, the considered litter harvesting scenarios induced a converging band of NLOC fluxes in the range 0.36–0.44 Mt C/y (Figure 6). Again highest C accumulation in forest soils was related to the lowest NLOC pool estimate (experiment 13) in response to the pronounced shift in litter harvesting between the first and second half of the century. In view of the uncertainty concerning litter harvesting and biomass history for the present century, we find that experiment 12 (no litter harvesting) and experiment 8 (zero biomass trend) are of particular interest. For both cases, NLOC accumulation was re-
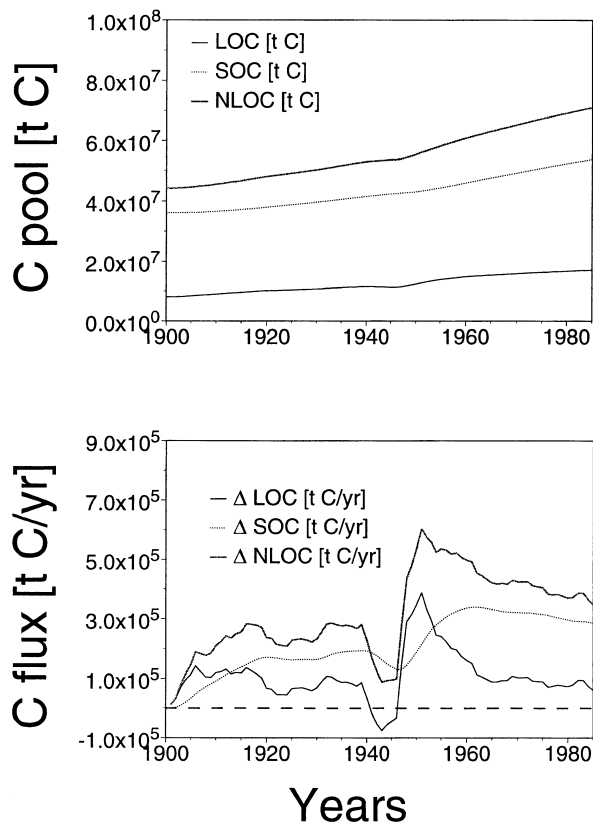
Figure 3. Simulated trends of C pools (**top**) and C changes (**bottom**) in Swiss Forest soils since 1900. Figures represent simulated trends of C pools and fluxes for litter, soil humus, and nonliving organic matter (litter plus soil humus) obtained under the assumptions of experiment 1 (Table 1). Positive fluxes denote C accumulation in forest soils.
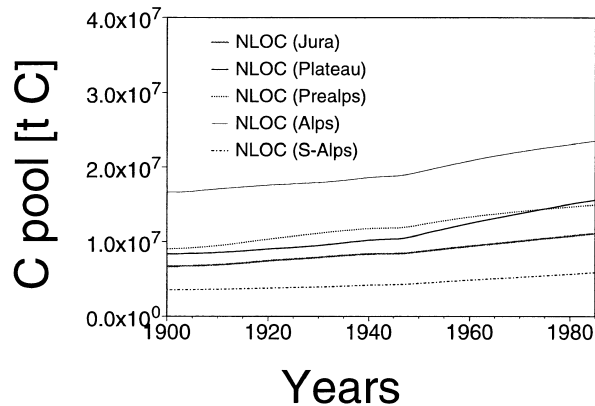

Figure 4. Simulated regional trends of C pools in litter, soil humus, and nonliving organic matter (litter plus soil humus) in Swiss Forest soils since 1900. Same as Figure 3 with regional stratification, that is, simulated C pools and fluxes for litter, soil humus, and nonliving organic matter (litter plus soil humus) obtained under the assumptions of experiment 1.

Table 5. Stand Level C Pools and Fluxes by Productivity Region for Swiss Forests in 1985

Region	C pool [t C/ha]			C flux [t C/(ha y)]		
	LOC	SOC	NLOC	ΔLOC	ΔSOC	ΔNLOC
Jura	14.7	44.0	58.8	0.06	0.26	0.32
Plateau	20.7	50.3	71.0	0.08	0.38	0.46
Pre-Alps	17.7	56.8	74.5	0.05	0.23	0.27
Alps	14.9	57.7	72.7	0.04	0.24	0.27
S-Alps	11.7	36.6	48.3	0.08	0.26	0.35

Estimates for litter, soil humus, and nonliving organic matter (litter plus soil humus) refer to assumptions of experiment 1 (Table 1). Annual C changes (Δ) were derived by difference of figures simulated for 1985 and 1984.

duced but is still on the same order of magnitude as in all other simulations. It is to be noted that uncertainties in the parameterization of organic matter decomposition (experiments 14 and 15) had a minor effect on model simulations within the ranges considered. Symmetrical 10% variations of the parameters controlling SOC dynamics had comparable effects on NLOC dynamics: high (low) NLOC accumulation enhanced (reduced) pools and fluxes by 17% (14%) relative to the base scenario run.

DISCUSSION

Present-Day Plant C Pools and Litter C Fluxes in Swiss Forests

The presented method for national scale assessments of C dynamics in forest soils relied on an estimation of Swiss growing stocks per hectare that are among the highest in Europe (EAFV 1988). Grid-point information (1.4 km × 1.4 km resolu-

tion) was integrated to arrive at a national estimate for plant C in forests. Differences between our (115.6 Mt C) and earlier estimates of plant C by BUWAL (1994) (113.7 Mt C) or Paulsen (1995) (120.7) are not surprising, because the latter refer to slightly different forest area. Additionally, these studies differed in the way root, young growth, and understory biomass were accounted for, but final estimates varied by less than 5% relative to ours.

C allocation into stemwood and the distribution of above- and belowground C were in agreement with published data. The relative contribution of stemwood to total tree C obtained here (47–56%) was somewhat lower than the published estimates derived from Cannell (1982) (60 ± 10%) or Turner and others (1995) (58 ± 7%). Our figure for root C to total tree C (20–35%) compared well with estimates of Cannell (1982) for roots to total biomass, in European forest stands older than 50 years
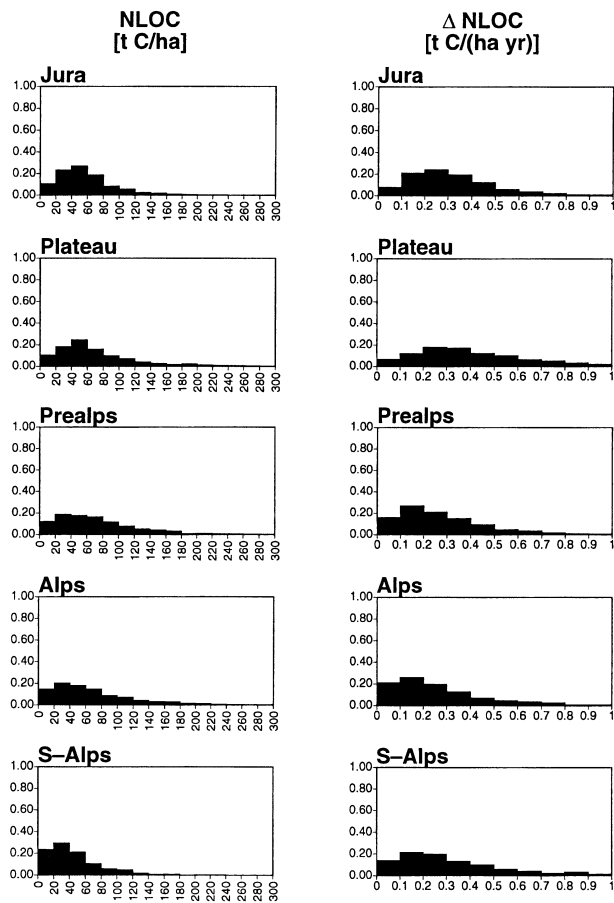
Figure 5. Regional distribution of simulated C pools (**left**) and annual C changes (**right**) in Swiss Forest soils for 1985. Frequency distributions (in [%/100]) of NLOC pools and fluxes are stratified by productivity region. Simulations were obtained by assumptions of experiment 1 (Table 1). Annual C changes for litter plus soil humus (ΔNLOC) were derived by difference of figures simulated for 1985 and 1984.

Table 6. Sensitivity of Simulated Pools and Fluxes of Swiss Forest Soil C for 1985

Experiment	NLOC 1985 (Mt C)	ΔNLOC 1985 (Mt C/y)
1	71	0.35
2	81	0.38
3	91	0.41
4	64	0.50
5	57	0.58
6	66	0.42
7	75	0.27
8	84	0.11
9	69	0.36
10	67	0.38
11	66	0.40
12	80	0.27
13	65	0.44
14	83	0.41
15	61	0.30

Under the factorial experiment shown in Table 1.The factorial experiment includes variations of fine root biomass (experiments 1–3), forest biomass trends (experiments 4–8), litter harvesting (experiments 9–13), and SOC dynamics (experiments 14 and 15). See Table 1 and text for more details.

(20 ± 8%). It also agreed with Burschel and others (1993) value for German forests (25–30%) but was somewhat higher than the global assessments (19–21%) of Cairns and others (1997). This is of particular importance because we used root biomass to estimate biomass and litter inputs from fine roots, which are an important driver of C dynamics in forest soils (Nadelhoffer and Raich 1992).

Different assumptions were made to estimate fine root biomass and litter production. When we set fine root biomass equal to foliage biomass (experiment 3), our regional averages of topsoil fine root biomass [4.5–9.6 t dry weight (d.w.) organic matter/ha] clearly exceeded the estimates of 1.9–2.8 t d.w. OM/ha given for live fine root biomass in the upper 30 cm of temperate and boreal forests (Jackson and others 1997). Relating fine to coarse root biomass

led, however, to reasonable estimates if a proportionality factor of 5% (experiment 1) was assumed, namely, 1.9 t d.w. OM/ha (Jura), 2.1 t d.w. OM/ha (Plateau), 2.2 t d.w. OM/ha (Pre-Alps), 1.8 t d.w. OM/ha (Alps), and 1.8 t d.w. OM/ha (S-Alps). Although published fine to total root biomass ratios were somewhat higher in the top 30 cm of soil (8–10% for fine roots with diameters less than or equal to 2 mm) (Jackson and others 1997), a 5% proportionality factor seemed reasonable to quantify fine root biomass and obtain a conservative estimate of fine root litter input given that our coarse root biomass estimate was at the high end of published values.

Estimates of litter inputs (Table 4) were plausible but could not be validated with field data due to the paucity of data, large intersite and interannual variability, and methodological reasons. Simulations matched litterfall data for foliage in the Jura but exceeded measured field data at higher elevations (Lüscher 1991). Coarse woody debris pools have been estimated for a small number of forest sites in Switzerland (Bretz Guby and Dobbertin 1996), but data on woody litter inputs are currently unavailable. Compared with coarse woody litterfall for temperate forests in the US [2.7 ± 5.4 t d.w. OM/(ha y), $n = 36$] (Harmon and others 1986), our figures were rather low. Note, that a verification of estimated woody litter inputs was also hampered by differences of the threshold size diameter used to
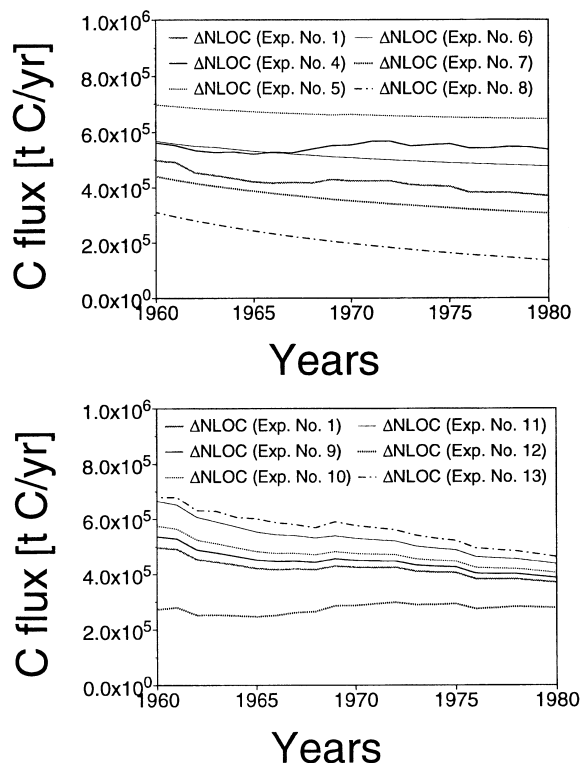
Figure 6. Sensitivity of NLOC fluxes to uncertainties of forest biomass history (**top**) and litter harvesting (**bottom**) between 1960 and 1980. **(Top)** Simulations refer to methodological differences in the derivation of forest biomass trends from dendrochronological data (experiment 1 vs 4) and synthetic linear biomass increases by 75% (experiment 5), 50% (experiment 6), 25% (experiment 7), and 0% (experiment 8) since 1900 (see Table 1). **(Bottom)** Litter harvesting scenarios were modified after Alveteg and others (1998), that is, coarse woody residue removal was alternatively assumed to equal foliage (experiment 1), fine woody litter removal (experiment 11), and multiples of foliage litter harvesting (experiments 9 and 10). Experiments 12 and 13 refer to forest soil C dynamics without and with customized litter harvesting, respectively (see METHODS for more details).

define twig litter among field surveys (Matthews 1997).

Finally, our NLOC pool and accumulation estimates could be changed if litter inputs from ground vegetation are considered. Whereas the herbaceous layer can contribute as much as 25% of total litterfall in some boreal ecosystems (J. Liksi, personal communication), lower mean estimates of 5% have been reported for temperate forests (Raich and Nadelhoffer 1989) and intensively managed forests in Central Europe (Burschel and others 1993). Therefore, a small effect is to be expected for Switzerland and could even reverse direction if litter

input decreases in parallel with understory biomass during stand development.

Retrospective Plant Biomass Dynamics

Characteristic time scales involved in NLOC cycling are believed to be on the order of a few decades for more than half of the C sequestered by topsoils (Harrison and others 1993; Townsend and others 1995; Trumbore and others 1996; Perruchoud and others 1999). Thus, the soil's contribution to the contemporary C balance of terrestrial ecosystems depends on the system's history. This explains why we could not determine NLOC changes for 1985–1995 from tree data of national forest inventories covering the same period but needed retrospective litter input scenarios. Use of dendrochronological data could be a means of reconstructing forest biomass history and model changes of forest soil C in cases where repeated soil inventory data are missing. For Switzerland, this approach allowed for an estimation of region- and tree type–specific growth trends at high temporal resolution.

However, the dendrochronological method can be criticized for several reasons. First, it is questionable how appropriate a tree-ring–based basal area index is for deriving biomass dynamics at tree or stand level, particularly if a dominant life form, such as deciduous trees, is poorly represented. Second, standard statistical procedures for the derivation of dendrochronological indices do not exist, and different methods lead to significant discrepancies in NLOC dynamics (experiment 1 vs 4). Third, uncertainty in long-term growth trends exists due to potential sampling biases (Cherubini and others 1998). The risk of overestimating biomass due to unaccounted for postsuppression releases was probably not high because subdominant and suppressed trees were included in the sample collective, but stand productivity (and litterfall from living trees) could have been overestimated due to neglect of stand mortality. However, the absence of this process in the derivation of dendrochronological indices also resulted in an underestimation of litter inputs to the soil, which represents, thus, a compensating effect with respect to the litter input signal. Information such as temporal changes in stand density or diameter distribution that could help determine the quality of the dendrochronological index as representative stand biomass proxy data was not available. We therefore used sensitivity experiments (experiments 5–8) to quantify the effect of past biomass trends. Despite all of this, our assessment of forest biomass history and litter production seems to be conservative: The estimated increase of forest vegetation C in 1982–83 deter-

mined as product of $I_{2,gen.,reg.}$ respectively. $I_{1,gen.,reg.}$ and tree C stocks (0.97 resp. 1.63 Mt C/y) was lower than the respective figures in the Swiss forest C balance for the same period [2.73 Mt C/y, see BUWAL (1994)], and our long-term trends are comparable to assessments given for growing stocks in Europe (Kuusela 1994).

Litter Harvesting Scenarios

Extra land-use activities, such as litter raking, forest pasturing, pig breeding, or forest agriculture, were common in Switzerland in the 19th century and in remote areas even in the 20th century (Stuber 1996; Bürgi 1997). This not only affected the nutritional status of forest soils (SAEFL 1998) and hence tree growth but forest soil C stocks directly (Burschel and others 1993). In our simulations, NLOC accumulation was enhanced by 30% through gradual renunciation of litter removal as compared with the case without litter harvesting (Table 6, experiment 1 vs 12). Both NLOC accumulations might be underestimations if past usage of coarse woody litter had in fact been higher (experiment 13). Reliable data for litter harvesting are unfortunately missing for Swiss forests, and the scenarios used are of qualitative character (D. Kurz, EKG Geoscience Berne, personal communication). Our NLOC simulations should thus be interpreted with caution at the national and subregional scale because region-specific differences in private usage or agricultural demand for litter were neglected here. Some improvement could be achieved by reconstruction of regional forest litter harvesting scenarios from agricultural demand and cattle stock records (M. Stuber, personal communication), although this approach would not account for other kinds of litter removal (for example, "Schneiteln" and "Bettlauben"). The importance of litter harvesting is likely to decrease in the context of NLOC cycling in Swiss forests in the future due to current forest management practices but remains an important issue at present due to the delayed response of NLOC under environmental changes.

NLOC Dynamics of Swiss Forests in the 20th Century

Assessments of NLOC dynamics are affected by a variety of uncertainties, one reason that forest soils have rarely been included in national C balances and primarily assessed as static C pools (Nabuurs and Mohren 1993; Liski and Westman 1996; Milne and Brown 1997; Nabuurs and others 1997). Burschel and others (1993) recognized the importance of forest soil C as a dynamic part of the ecosystem based on its potential to respond to "past devastative practices," giving a crude estimate of present NLOC accumulation in German forest soils: Their assumed NLOC increase is 18% of the C increment in living forest biomass and thus lower than our "best estimate" of 27% (experiment 1, Table 6) relative to the 1.28 Mt C/y increase of Swiss forest vegetation in 1985 (BUWAL 1994). However, both studies support the hypothesis that forest soil carbon has been accumulating in the recent past and thus cannot be neglected in national forest C balances.

Simulated estimates of forest soil C pools per hectare (Table 5) were plausible in view of earlier estimates for topsoil (0–20 cm) SOC of 40–63 t C/ha (Haber 1985; Huntington and others 1988; Ziegler 1991; Grigal and Ohmann 1992; Hohmann and others 1995). Their spatial distribution across Switzerland arose from complex spatial patterns in vegetation and stemwood volume (EAFV 1988), forest management, and altitudinal temperature distribution, which we assumed as the primary abiotic decomposition control (Tate and others 1995; Townsend and others 1995; Trumbore and others 1996) at the national scale. Additional modifications of the spatial NLOC distribution were related to genus-specific longevities: Although forests in the Pre-Alps had highest foliage stand biomass (Table 2), its litter input was considerably lower than for forests on the Plateau or in the Alps (Table 4) and attributable to region-specific fractions of deciduous vs coniferous stands and the distribution of conifers with different needle longevity (for example, fraction of *Abies* and *Pinus* in Pre-Alps and Alps) (EAFV 1988). Finally, the temperature-induced altitudinal decrease of decomposition rates narrowed regional differences in NLOC pools (Table 5) beyond what was expected on the basis of plant C stocks.

Uncertainties not considered in our assessment include changes in forest area, successional changes in litter production, and the influence of edaphic factors or climatic variations on organic matter decomposition. Our analysis was based on a forest area of 10,544 km² without inaccessible forests and brushwood, which is approximately 10% less than the forest area of EAFV (1988), that is, 11,863 km². Changes in forested area of 30–40% since 1900 (SAEFL 1997) were treated implicitly due to missing land-use history data and large uncertainties regarding differences of vegetation and soil C dynamics between native forests and afforestations: Because deforestation can be excluded as major land-use change process in Switzerland due to the Forest Police Act of 1902, stands with presently low biomass were interpreted as recent reforestations, and past biomass and litter inputs were derived by use of the dendrochronological basal area index. Although

the area-related error cannot be quantified reliably, it is to be noted that NLOC accumulation could be underestimated if timber production in regenerating forests is higher than in native forests (Nabuurs and Mohren 1995) and if SOC dynamics in reforestations is faster than for near-natural systems (Harrison and others 1995). Further research on this last topic is urgently needed because afforestation, reforestation, and deforestation are included as carbon sequestering activities under the Kyoto Protocol.

Additional changes would result if edaphic controls on C dynamics of forest soils, such as soil structure (Van Veen and Kuikman 1990), mineralogy (Torn and others 1997), soil water status (Davidson 1995; Hohmann and others 1995), or clay content (Balesdent and others 1988), were introduced. These were, however, not considered because of controversial discussions regarding their influence on NLOC dynamics (Davidson and others 1995) and missing data for our study region.

Finally, the effect of climatic variations on organic matter decomposition was neglected despite the long-term increase of approximately 1.5°C in mean annual temperature since 1900 (Brang 1998) and regional warming trends across Switzerland (Beniston and others 1994). Warming could in fact reduce C sequestration by forest soils as a consequence of enhanced microbial respiration. However, a gradual temperature change is probably less important than the biomass increase for the time period considered; Perruchoud (1996) has investigated the effect of a 1°C warming on C stocks in forest soils by soil warming analogy studies (Kirschbaum 1995; Townsend and others 1995; Trumbore and others 1996). The equilibrium reduction in soil C was approximately 7–12% with higher sensitivity at low temperatures. Soils would reach a new C equilibrium only after several centuries under an instantaneous climate change. A gradual warming as experienced today would delay the soil's response and thus probably have little effect on SOC dynamics over decades.

Carbon Accumulation in European Forest Soils

Growing stocks have substantially increased between 1950 and 1990 not only in Switzerland but in European forests in general (Kuusela 1994). Development of growing stocks for forests in "Central" (Denmark, Germany, Poland, and Czechoslovakia) and "Alpic" Europe (Austria and Switzerland) sensu Kuusela (1994) are comparable and exceed the linear trend assumed in experiment 6 slightly. We extrapolated the estimated 33% annual NLOC accumulation relative to the C sequestration by forest vegetation (experiment 6) obtained for Switzerland to Central and Alpic Europe (see Appendix D). The net forest increment of 23.4 Mt C/y (Kuusela 1994) implied an annual C accumulation of 7.7 Mt C/y in Central and Alpic Europe forest soils for the year 1990. The same rationale yielded for European forests (149.3 × 10^6 ha) a forest tree C sink of 89.5 Mt C/y (Kuusela 1994) and an annual C accumulation of 29.5 Mt C/y in forest soils for 1990, although consideration of ecological suitability in terms of soils, climate, or forest history were excluded here. Compared with the gain in soil organic carbon obtained by afforestations of 30% of surplus arable lands in Europe (19.2 Mt C/y) estimated by Smith and others (1997), our projection for NLOC accumulation in European forests is high. It, however, accounts only for approximately 4% of the anthropogenic CO_2 production in Western Europe (829 Mt C/y) in 1990 (Marland and others 1994).

Such extrapolations are afflicted with considerable uncertainties due to distinct abiotic regimes and country-specific silvicultural treatments not considered here. Given reliable data to estimate C litter inputs, our approach could, however, be used to improve our understanding of the role of soils in the C balance of European forests. Two final notes: first, C accumulation in forest soils is tightly linked to increases in the vegetation C compartment and therefore a transient effect. Any change in the disturbance regime or climate-induced changes of net primary production will imply changes of soil C stocks. Thus, terrestrial ecosystems that are now sinks for CO_2 can transform into CO_2 sources in the future (GACGC 1998). Second, our estimates of C accumulation in soils refer to natural forest regrowth, a process not counted as a carbon sequestering activity in the Kyoto Protocol. Refined analyses of the change in C dynamics following afforestation, reforestation, and deforestation are now urgently needed to provide a sound base for C accounting under Article 3.3 of the Kyoto Protocol.

Conclusions

The observed C accumulation in European forests (Kauppi and others 1992; Kuusela 1994) is not restricted to vegetation only but is likely to affect forest soils as well. This not only refers to land-use conversions such as afforestation of arable lands (Smith and others 1997). It also includes the accumulation of nonliving organic matter in soils of forests with increased tree growth and litter production induced by changing environmental conditions and altered harvesting practices. For 1985 we estimated a net C sink from the atmosphere into the soil

that represents more than 25% of the forest vegetation C sink in Switzerland (BUWAL 1994). Variations of this best soil sink estimate were in the range of 10–50%, indicating existing uncertainties in forest biomass history, litter harvesting, and soil organic carbon dynamics. Soil data from which to estimate C stocks in soils at a national scale were not available in Switzerland but could be used in the future to cross-check our simulations and reduce the above uncertainties.

Because repeated national soil inventories are still rare in contrast to tree inventory data, our approach represents an alternative for a preliminary assessment of the role of forest soils in the national C balance from tree data. However, before making our model applicable for assessments of C sequestering activities included in the Kyoto Protocol, a refined quantification of changes in SOC dynamics under altering land use is needed. Although this work gives evidence that C dynamics in forest soils should not be excluded from national forest C balances, consideration of the C sequestration potential of today's European forest soils does not defuse the problem of anthropogenic CO_2 production in Western Europe.

ACKNOWLEDGMENTS

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Table A1.   Model Coefficients for Estimating Foliage Biomass from Tree Diameter at Breast Height

Tree Genus	Sample Number	$R^2_{adj.}$	$\alpha_{0,gen.}$	$\alpha_{2,gen.}$	$\alpha_{4,gen.}$
Fagus	91	0.93	0.372238	0.006653	$9.78 \cdot 10^{-7}$
Quercus	53	0.93	0.402990	0.007293	$2.82 \cdot 10^{-7}$
Abies	88	0.93	2.056995	0.024814	$-1.54 \cdot 10^{-7}$
Picea	189	0.86	1.413701	0.024182	$-1.067 \cdot 10^{-6}$
Pinus	210	0.82	1.138795	0.007911	$8.639 \cdot 10^{-9}$

Biomass is given as kilograms dry weight organic matter; diameter at breast height is in centimeters. Leaf biomass for Castanea was estimated using parameters for Quercus, for all other deciduous trees the Fagus parameters were used. Similarly, Larix was treated as Pinus, while needle biomass for all other coniferous genera were estimated by the Picea function. All models were highly significant ($P > F = 0.0001$). (Eq. 6).

Table A2.   Model Coefficients for Estimating Coarse Root Biomass from Tree Diameter at Breast Height

Life form	$\beta_{0,lf.}$	$\beta_{3,lf.}$	$\beta_{4,lf.}$
Deciduous	48.425782	0.003077	-0.000005217
Coniferous	48.796249	0.003077	-0.000005217

Biomass is given as kilograms dry weight organic matter; diameter at breast height is in centimeters. The model ($R^2 = 0.995$, $P > F = 0.0001$) was derived from data of Santantonio and others (1977) providing 16/46 samples for deciduous/ coniferous trees with only few samples for dbh greater than 30 cm. (Eq. 7).

Appendix A   Leaf and Needle Biomass Classes

Needle biomass was first classified for litter production calculations according to needle longevity: We assumed 3 y for *Pinus,* 7 y for *Picea,* 10 y for *Abies,* and 1 y for *Larix.* For all other conifers needle longevity was set to 3 y whereas broadleaf trees were assumed to loose foliage annually.

Slow litter decomposition was assumed for *Pinus, Abies,* and all other conifers based on mean initial litter lignin concentration data (Perruchoud 1996) and higher decomposition for *Picea* and *Larix.* For leaf litter, four decomposition classes were used (sorted by increasing decomposability): (a) *Fagus,* (b) *Betula, Quercus, Salix,* (c) other broadleaf trees, (4) *Alnus, Carpinus, Fraxinus, Acer, Castanea, Populus, Sorbus, Tilia,* and *Ulmus.* See Perruchoud (1996) for details.

Appendix B   Wood Density

We used a variety of sources (Trendelenburg and Mayer-Wegelin 1955; Knigge and Schulz 1966; Niemz 1993; Lakida and others 1995; FOEFL 1997) to convert fresh volume data of woody biomass to dry weight mass. Estimates (expressed as kilograms of dry weight organic matter per cubic meter fresh volume) were found for *Abies* (339), *Larix* (487),

Picea (332), *Pinus* (431), and *Pseudotsuga* (412), and 384 kg/m³ was assumed for all other conifers. More wood density data were available for broadleaf trees, namely, *Acer* (522), *Alnus* (411), *Betula* (505), *Carpinus* (620), *Castanea* (523), *Fagus* (554), *Fraxinus* (564), *Juglans* (554), *Malus* (601), *Quercus* (561), *Populus* (377), *Prunus* (601), *Pyrus* (601), *Robinia* (647), *Salix* (362), *Sorbus* (601), *Tilia* (386), and *Ulmus* (556).

Appendix C   Estimation of Foliage and Woody Root Biomass

Foliage biomass was estimated via:

$$m_{fol.gen.} = \alpha_{0,gen.} + \alpha_{2,gen.} \cdot (dbh)^2 \\ + \alpha_{4,gen.} \cdot (dbh)^4 \quad (6)$$

and fitted to Swiss tree data (Burger 1940, 1947, 1948, 1950, 1951, 1953). Similarly woody root biomass was determined from:

$$m_{wr.lf.} = \beta_{0,lf.} + \beta_{3,lf.} \cdot (dbh)^3 + \beta_{4,gen.} \cdot (dbh)^4, \quad (7)$$

with data of Santantonio and others (1977) (*lf.* denotes tree life form, that is, deciduous or coniferous). Model coefficients are listed in Tables A1 and A2.

Appendix D   Carbon Accumulation in European Forest Soils

Potential annual C sequestration in forest soils of Central and Alpic Europe were calculated from estimates of gross annual increment, timber removal under bark [Table 2.8 in Kuusela (1994)], and the fraction of coniferous trees [Table 2.7 in Kuusela (1994)]. The latter was used to average wood densities for hard- and softwood (FOEFL 1997) at the country level. Stemwood volume was converted to dry weight organic matter and expanded by 1.45 (FOEFL 1997) to account for other

woody parts (for example, roots and branches). We assumed a factor of 0.5 (Vogt 1991; FOEFL 1997) to convert from organic matter to carbon mass. The resulting annual C sequestration by forest trees in 1990 was 20.2 Mt C/y for Central Europe and 3.2 Mt C/y for Alpic Europe. NLOC accumulation for these forests was derived assuming an annual C sequestration of 33% of the C amount bound by forest vegetation in 1990. This fraction represents the C accumulation in Swiss forest soils induced by a biomass doubling between 1900 and 1985 (experiment 6), which is qualitatively in line with the development of Central and Alpic European forest since 1950 (Kuusela 1994). The same rationale was used to arrive at a first assessment for European forest soils.

Appendix E   List of Abbreviations

OM	Organic matter
SOM	Soil organic matter
LOC	Litter organic carbon, that is, C sequestered in freshly shed litter
SOC	Soil organic carbon, that is, C sequestered in humified form
NLOC	Nonliving organic carbon, that is, C sequestered in litter and soil humus with a maximum soil depth of 20 cm
MAT	Mean annual temperature (°C)
AET	Actual evapotranspiration (mm/y)
NBAI	Normalized basal area index (dimensionless)
SNFI	Swiss National Forest Inventory
n	Plant tissue type, for example, leaves, stemwood, and twigs
$\mathcal{M}_n$	C mass of plant tissue type n (t C/ha)
$\mathcal{I}_n$	C litter input of plant tissue type n [t C/(ha y)]
$I_{i,gen.,reg.}$	Genus and region-specific normalized basal area index (dimensionless)
τ_n	Longevity of plant tissue n (y)
η_n	Plant tissue-specific litter harvesting index (dimensionless)
t_0	Reference year, that is, 1985 AD
dbh	Diameter at breast height (cm)
$m_{fol.,gen.}$	Biomass of foliage (kg d.w. OM)
$m_{wr.,lf.}$	Biomass of coarse roots (kg d.w. OM)
$\alpha_{i,gen.}$	Polynomial coefficients for determining $m_{fol.,gen.}$
$\beta_{i,lf.}$	Polynomial coefficients for determining $m_{wr.,lf.}$
Mt	Mega tonnes 1 Mt = 10^6 t
gen.	Tree genus
lf.	Life form, that is, coniferous or deciduous
d.w.	Dry weight
f.v.	Fresh volume