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# Long-term tracing of whole catchment $^{15}$N additions in a mountain spruce forest: measurements and simulations with the TRACE model

Kim Krause · Isabelle Providoli · William S. Currie · Harald Bugmann · Patrick Schleppi

**Abstract** Despite numerous studies on nitrogen (N) cycling in forest ecosystems, many uncertainties remain, particularly regarding long-term N accumulation in the soil. Models validated against tracer isotopic data from field labeling experiments provide a potential tool to better understand and simulate C and N interactions over multiple decades. In this study, we describe the adaptation of the dynamic process-based model TRACE to a new site, Alptal, where long-term N-addition and $^{15}$N-tracer experiments provide unique datasets for testing the model. We describe model parameterization for this spruce forest, and then test the model with 9- and 14-year time series of $^{15}$N-tracer recovery from control and N-amended catchments, respectively. Finally, we use the model to project the fate of ecosystem N accumulation over the next 70 years. Field $^{15}$N recovery data show that the major sink for N deposition is the soil. On the control plot, tracer recovery in the soil increased from 32 % in the second year to 60 % in the ninth year following tracer addition, whereas on the N-saturated plot, soil recovery stayed almost constant from 63 % in the third year to 61 % in the twelfth year. Recovery in tree biomass increased over the decadal time scale in both treatments, to ca. 10 % over 9 years on the control plot and ca. 13 % over 14 years on the N-amended plot. We then used these time series to validate TRACE, showing that the adaptation and calibration procedure for the Alptal site was successful. Model-data comparison identified that the spreading method of $^{15}$N tracers needs to be considered when interpreting recovery results from labeling studies. Furthermore, the ground vegetation layer was recognized to play an important role in controlling the rate at which deposited N enters soil pools. Our 70-year model simulation into the future underpinned by a Monte-Carlo sensitivity analysis, suggests that the soil is able to immobilize a constant fraction of 70 and 77 % of deposited N for the treated and the control plot, respectively. Further, the model showed that the simulated increased N deposition resulted in a relatively small elevated C sequestration in aggrading wood with an N use efficiency of approximately 7 kg C per kg N added.

**Keywords** N cycling · $^{15}$N tracer · Simulation model · Mountain forest · Norway spruce · N deposition

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## Introduction

Deposition of oxidized ($NO_y$) and reduced ($NH_x$) forms of reactive nitrogen (N) to terrestrial ecosystems has risen sharply since the industrial revolution; in some parts of the globe N deposition is even projected to continue to increase (Galloway et al. 2003; Gruber and Galloway 2008). This

human-induced high input can shift the N status of forest ecosystems from naturally N limited to N saturated (Aber et al. 1989, 1998; Dise and Wright 1995; Fenn et al. 1998). Such a change in N status can have serious environmental consequences by changing soil and water chemistry, changing vegetation composition and productivity, and by altering the fluxes of radiatively active trace gases ($N_2O$, $CO_2$, $CH_4$) exchanged between forests and the atmosphere (Aber 1992; Butterbach-Bahl et al. 1997; Priha and Smolander 1995). N additions to forest soils have been shown to reduce C/N ratios in leaves and litter (Dise and Wright 1995; Gundersen et al. 1998; Magill et al. 1997) and to stimulate tree growth and productivity (De Vries et al. 2006; Högberg et al. 2006; Hyvonen et al. 2008). High N deposition rates increase $NO_3^-$ leaching from forest soils to groundwater (Borken and Matzner 2004; Dise and Wright 1995; Gundersen et al. 2006; Jussy et al. 2004; Schleppi et al. 2004), and accelerate soil acidification due to increased nitrification, ammonium uptake (Högberg et al. 2006; Likens et al. 1979) and base cation leaching (Currie et al. 1999a). High rates of N deposition can also change the ground vegetation (Fangmeier et al. 1994; Hulber et al. 2008) and thus lead to a decline in biodiversity (Phoenix et al. 2006). Although the impact of N on terrestrial ecosystems is an intensively studied research field, many uncertainties remain on how ecosystems will respond, especially in the longer term (i.e. over decades to centuries).

Dynamic biogeochemical process-based models can improve our understanding of long-term N effects on ecosystems. They provide an interconnected set of hypotheses about how fine-scale processes interact to produce whole-system N cycling and C–N interactions. However, modeling complex C–N interactions in a biogeochemical process model could produce whole-system C and N cycling that appear correct but do not necessarily capture the correct fine-scale interactions that cause ecosystem-level patterns. Most simulation analyses of N cycling and C–N interactions have limited ability to determine if the process interactions are captured correctly (Larocque et al. 2008). A powerful tool for testing model formulations of C–N interactions is to compare predicted movement of the stable isotope $^{15}N$ between ecosystem pools with the redistribution of field-applied $^{15}N$ tracers. With models that consider constraints from stable isotopes, we can achieve a deeper understanding than can be achieved with non-isotopic models (Currie et al. 2004).

In this study, the process-based model TRACE, with the ability to simulate $^{15}N$ redistribution in forest ecosystems, was applied for its first time to a different temperate forest type (subalpine, open-canopy spruce forest at Alptal, Switzerland) than where the model was developed and validated, i.e. closed-canopy temperate oak and pine forests

at the Harvard Forest, MA, USA (Currie and Nadelhoffer 1999; Currie et al. 1999b, 2004).

Our aim was to test TRACE's representation of whole-system C and N dynamics by applying it to a new site, Alptal, which is an open spruce forest with ground vegetation and low permeability soil. The Alptal experimental site hosts a long-term low-dose N-addition ($NH_4NO_3$) experiment initiated in 1995. The site consists of two small catchments, one receiving +25 kg N/ha/a and the second is the control. On the catchment scale, regular pulses of a $^{15}N$ tracer were applied for 1 year starting in 1995 on the fertilized plot and in 2000 on the control plot.

Thus, our objectives were (1) to evaluate N partitioning in forest ecosystem compartments with field $^{15}N$-tracer recoveries; (2) to adapt TRACE to a different type of temperate forest (Alptal); and (3) to compare model results at Alptal against field-observed $^{15}N$ recoveries. Finally, we used model-based projections to project the expected fate of elevated atmospheric N deposition on ecosystem N status over the time scale of several decades.

## Field methods

### Site description

The experimental site is located in the Alptal valley, on the northern edge of the European Alps in central Switzerland (47°02′N, 8°43′E) at 1200 m a.s.l. It lies within the Erlenbach headwater catchment, which covers 0.7 km² and consist of 40 % naturally regenerating forest and 60 % bedding meadow, neither ever fertilized. The climate is cool and wet with a mean annual temperature of 6 °C and a mean annual precipitation of 2,300 mm (30 % as snow) reaching a maximum in June (270 mm) and a minimum in October (135 mm). The growing season lasts from May to September. Atmospheric inorganic N deposition is moderate with 12 kg N/ha/a bulk deposition and 17 kg N/ha/a in throughfall, equally divided between $NO_3^-$ and $NH_4^+$ (Schleppi et al. 1999a). Parent rock material is Flysch, and major soil types are clay-rich Gleysols with an average 48 % clay, 46 % silt and 6 % sand. This leads to low permeability with a water table close to the surface throughout the year (Hagedorn et al. 1999). The two major soil types are determined by the distinct microtopography: (1) umbric gleysol with mor (raw humus), Ah and oxidised or partly oxidised Bg or Br horizons on mounds; and (2) mollic gleysols, with an anmoor (muck humus) topsoil, a thin Lf horizon and an almost permanently reduced Bg or Br horizon in depressions where the water table can reach the surface (Hagedorn et al. 2001). On average, soils are covered with snow from mid-November to April. The slope is ca. 20 % with a west-facing aspect. The stand consists of

Norway spruce (*Picea abies*) ($\sim 85$ % of basal area), along with silver fir (*Abies alba*). The stand regenerated naturally after selective logging and includes trees up to 260 years old. The stand's relatively low leaf area index (LAI) of 3.8 allows a well-developed layer of ground vegetation, which forms patches of botanical associations that vary by humus type and light conditions (Schleppi et al. 1999b). Ground vegetation is dominated by *Caltha palustris* (L.), *Petasites alba* ((L.) Gaertner), *Poa trivialis* (L.) and *Carex ferruginea* (Scop.) (Schleppi et al. 1999b). The moss layer is well developed with *Hylocomium splendens* ((HEDW.)B.S.G.) and *Sphagnum quinquefarium* ((LINDB. EX BRAITHW.) WARNST.) as the dominant species.

### N addition and $^{15}$N-tracer experimental design

A low-dose N-addition experiment has been conducted since April 1995 in a paired-catchment design. Within the spruce forest, two small catchments (each ca. 1,500 m$^2$) were delimited by trenches. Due to the impermeable gleyic subsoil, the water is assumed not to infiltrate below the depth of the trenches (80 cm) and the yearly water budget of each catchment is approximately balanced (Schleppi et al. 1998). One catchment is subjected to an increased deposition of 25 kg N/ha/a as NH$_4$NO$_3$ added to rain water and sprinkled 1.5 m above ground, i.e. under the tree canopy but above the ground vegetation (Schleppi et al. 1998). The other catchment acts as a control, receiving only rainwater with ambient N deposition.

Several $^{15}$N labeling experiments have taken place in this paired-catchment design. On the N-treated plot, the nitrogen added during the first year of the experiment (between April 1995 and March 1996) was labeled with $^{15}$NH$_4$$^{15}$NO$_3$ (219 mmol/m$^2$; 0.88 atom %) and distributed by sprinklers (Schleppi et al. 1999a). On the control plot, two $^{15}$N labeling experiments took place (described in Providoli et al. 2005). First, K$^{15}$NO$_3$ (0.17 mmol/m$^2$; 99 atom %) was applied between July 2000 and June 2001. After a 1-year gap, $^{15}$NH$_4$Cl (0.7 mmol/m$^2$; 99 atom %) was applied from July 2002 to June 2003. On the control plot, the tracers were applied on a weekly basis in summer and every 2 weeks in winter with a backpack sprayer directly above the ground vegetation. A timeline of tracer addition and sampling can be found in Figs. 4, 5 and 6.

### Field $^{15}$N-tracer recovery

We compared simulated $^{15}$N-tracer recoveries with the 9- and 14-year data of field $^{15}$N recoveries from the control and N-addition catchments, respectively. We considered $^{15}$N recovery in the following pools: wood, branches, foliage, ground vegetation, coarse and fine roots, soil litter 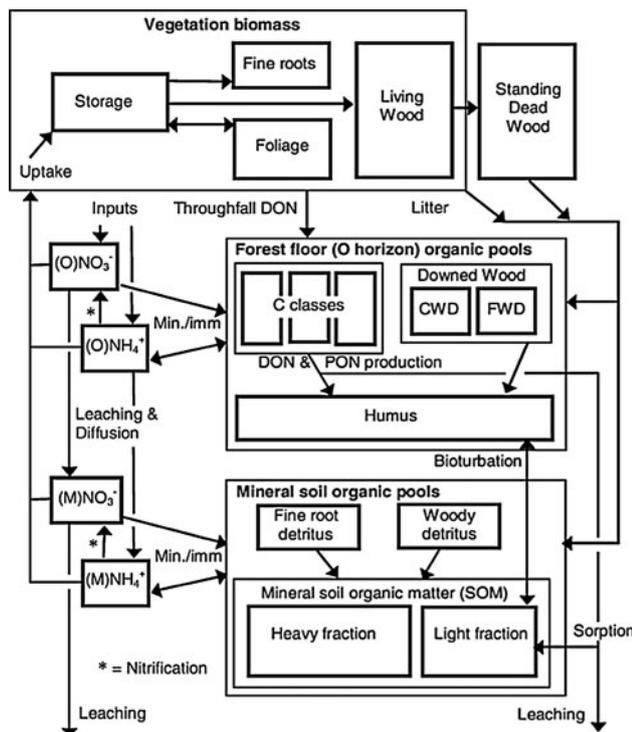layer, soil organic horizon and mineral soil horizon. In addition, the cumulative fluxes of $^{15}$N tracers in foliar litterfall and nitrate leaching were considered. All recoveries were calculated in proportion to the applied tracer (Providoli et al. 2005). For the N-treated plot, $^{15}$N recovery data for the year 1997 are from Schleppi et al. (1999a) following 1 year of N addition and labeling. For this year, separate data for fine roots and litter are not available as they were bulked for the analysis. For the years 2002 and 2009, we present new $^{15}$N recovery data. Sampling and analyses for soil and ground vegetation pools for these new data were conducted according to Providoli et al. (2005), and wood sampling and analyses were conducted according to Schleppi et al. (1999a). For the control plot, $^{15}$N recovery rates for the years 2001 and 2003 are from Providoli et al. (2005); for 2009, we provide new data.

For $^{15}$N recoveries in foliage, needle cohorts were taken each year from the seventh whorl of five dominant trees per plot. Annual cohorts were analyzed separately and later combined to obtain $^{15}$N percent recovery per year to compare with model results. We did this because the model considers only the youngest cohort and the sum of older ones as distinct pools. For the yearly recovery of $^{15}$N in litterfall, the content of four litter collectors per plot were bulked, analyzed quarterly and combined. To account for the cumulative tracer flux in nitrate leaching, weekly bulked runoff-proportional water samples were collected at the discharge weirs at both catchments since 1995 (Schleppi et al. 2004).

## TRACE model

### Model overview

Tracer Redistribution Among Compartments in Ecosystems (TRACE) is a biogeochemical process model of C, N and water fluxes in forest ecosystems. The crucial feature of TRACE is the prediction of the redistribution of $^{15}$N and $^{14}$N isotopes through time by simulating $^{15}$N:$^{14}$N ratios of individual N pools and of the N transferred between pools, incorporating the principles of pool dilution and mass balance (Wessel and Tietema 1992). TRACE calculates the mixing and redistribution of $^{14}$N and $^{15}$N as NH$_4$$^+$ and NO$_3$$^-$ and organic N in the soluble and solid phases, while linking the fluxes of C, N and water in forest vegetation and soil (Fig. 1). Thus, TRACE allows for comparisons with large-scale $^{15}$N-labeling studies, as it simulates the timing, isotopic abundance and forms of $^{15}$N across the major pools in the ecosystem added to large pools. TRACE runs on a monthly time step and can be used to project forest change over decades to centuries, including the effect of climate change and altered N deposition. TRACE combines the vegetation processes of PnET-CN (Aber and

**Fig. 1** Schematic diagram of pools and fluxes of N in TRACE. Plant N uptake, detrital N dynamics and N transformations are calculated separately in each soil layer. Pools of available N are separated by soil layer: O, organic horizon; M, mineral horizon; DON, PON, dissolved and particulate organic nitrogen; CWD, FWD, coarse and fine woody debris; Min./imm., mineralization/assimilation. Inputs: $NO_3^-$ and $NH_4^+$ in atmospheric deposition, fertilizer, and isotopic tracer additions. For clarity, not all fluxes are shown in detail (adapted from Currie et al. 2004)

Driscoll 1997) with the soil processes of DOCMod (Currie and Aber 1997). PnET-CN emphasizes the links between vegetation physiology, biogeochemistry, and hydrology. PnET-CN incorporates photosynthesis, stomatal conductance and transpiration as a function of foliar N content, radiation, temperature, and soil water availability (Aber and Federer 1992). DOCMod is a model of litter decomposition, humification and production of dissolved organic C and N in the forest floor. Detailed information about the fundamental vegetation and soil processes in TRACE and PnET-CN can be found in Aber et al. (1997), Currie and Aber (1997), Currie and Nadelhoffer (1999) and Currie et al. (1999b).

Model adaptation to the Alptal site

Our analysis is based on TRACE v4.5. Since TRACE was initially developed for well-drained soils like Inceptisols on coarse-loamy texture at Harvard Forest (Aber et al. 1993), we made some structural changes to the model to account for known site-specific features at Alptal. Our changes

incorporate (1) the gleyic soil conditions with low permeability and high water tables and (2) the preferential water flow (Schleppi et al. 2004).

First, during their inverse modeling analyses, Currie et al. (2004) had changed tree N uptake to be preferentially from the mineral soil pools. To account for the low permeability and high water tables resulting in a low rooting depth at Alptal, we changed this to the organic soil horizon. Second, in the original model, the $NO_3^-$ concentration in preferential water flow was zero. In the Alptal model version, $NO_3^-$ concentration from wet deposition and/or from snowmelt in the preferential water flow was added, i.e. a new variable *NO3fastflow* was created. By doing so, a fraction of $NO_3^-$ is leached directly out of the system instead of going into the soil, i.e. a fraction of $NO_3^-$ bypasses the soil pools without interactions. Equation (1) for *NO3fastflow* was added to the water balance procedure (monthly time step):

$$
\begin{aligned}
NO3fastflow = {} & FastFlowFrac \times (NO3WetDep \\
& \times (1 - SnowFrac) + NO3SnowPack \\
& \times Snowmelt
\end{aligned}
$$

(1)

| | |
|---|---|
| *FastFlowFrac* | fast flow fraction, i.e. proportion of water that flows preferentially through the soil; parameter |
| *NO3WetDep* | wet $NO_3^-$ deposition (g N/m²/month); input |
| *SnowFrac* | proportion of precipitation as snow (dimensionless); |
| *NO3SnowPack* | $NO_3^-$ amount present in snow pack (g N m⁻²); state variable |
| *Snowmelt* | proportion of the snow pack that melts and releases $NO_3^-$ within a month (dimensionless). |

Preliminary simulation runs showed a non-negligible accumulation of $NH_4^+$ in the organic soil N pool. The original model nitrified only the fraction of $NH_4^+$ mineralized in the current month rather than the whole $NH_4^+$ pool of the organic soil. We solved this conceptual problem by applying the existing sub-procedure *GrossNitrif* to the whole $NH_4^+$ pool rather than only to the newly mineralized $NH_4^+$.

Current climate data for the Alptal site were derived using local measurements from a nearby open-field meteorological station and represent 25-year means (1982–2007); these data were used to represent 20th century conditions (Table 1). To characterize the strong increase in N deposition over the 20th century, we estimated a total deposition of inorganic N that increased

**Table 1** Long-term mean climate data for the Alptal site

| Month | Daily min. temperature (°C) | Daily max. temperature (°C) | Photosynthetically active radiation (μmol/m$^2$/s) | Precipitation (cm) |
|---|---|---|---|---|
| 1 | −3.2 | 2.7 | 224 | 15 |
| 2 | −4.1 | 2.9 | 304 | 16.1 |
| 3 | −3.2 | 4.9 | 414 | 19.3 |
| 4 | −0.1 | 8.6 | 485 | 17.7 |
| 5 | 4.5 | 13.9 | 494 | 20.9 |
| 6 | 7.5 | 16.6 | 510 | 25.2 |
| 7 | 9.6 | 19.0 | 542 | 25.5 |
| 8 | 9.6 | 18.4 | 492 | 25.1 |
| 9 | 6.6 | 15.1 | 427 | 19.6 |
| 10 | 3.7 | 11.9 | 324 | 13 |
| 11 | −1.6 | 5.6 | 227 | 17 |
| 12 | −3.7 | 3.4 | 191 | 16 |

Data represent 25-year means (1982–2007) from a nearby open-field meteorological station



**Fig. 2** Scenarios of $CO_2$ concentration, bulk N deposition and N addition for the control and the N-treated plot for the years 1920–2080. Varying values for N addition from 1995 to 2008 are due to real data, for the following years values are a mean of the 1995–2008 data
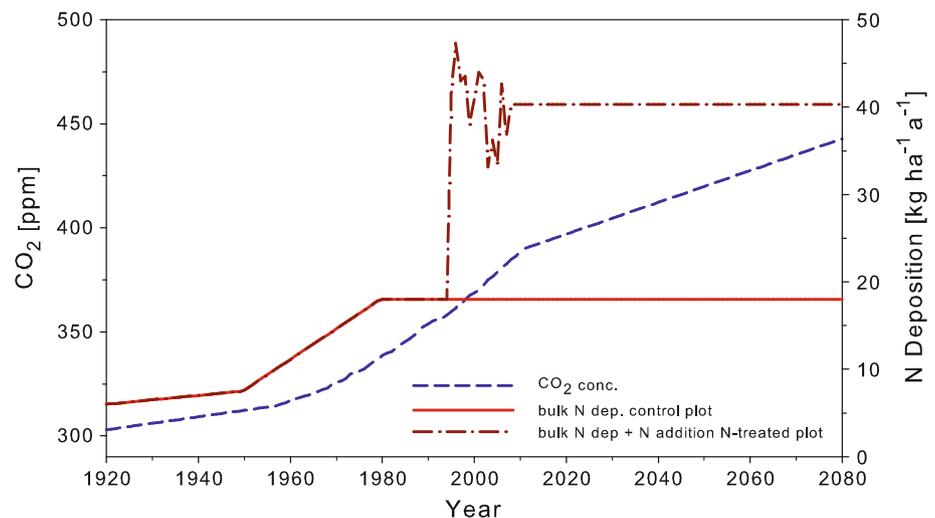
linearly from 5 kg N/m$^2$/a in 1900 to 7.6 kg N/m$^2$/a in 1950; from there, deposition increased more steeply to 18 kg N/m$^2$/a in 1975 and onward had constant values to reflect the effect of legal measures taken to control N deposition (Fig. 2). Historical $CO_2$ data from 1900 to 1958 were taken from the Law Dome ice core (Meure et al. 2006). Data between 1958 and 2010 are from Mauna Loa (*Dr. Pieter Tans, NOAA/ESRL*; http://www.esrl.noaa.gov/gmd/ccgg/trends/). For future projections, the IPCC WRE Stabilization Profile 450 (IPCC 2001) was chosen. This optimistic scenario assumes an emission reduction that stabilizes atmospheric $CO_2$ concentration in the year 2090 at 450 ppm and is tied to a change in maximum/minimum temperature of 2 °C relative to 1960–1990. After all of the changes described above, we checked model integrity to ensure that TRACE maintained C and N mass balance throughout all simulations.

Finally, it should be noted that the OiOe horizon in TRACE corresponds to the LF horizon at Alptal, the Oa

horizon corresponds to the O humus horizon at Alptal and the M (for mineral soil) horizon in TRACE corresponds to the sum of the A and B horizons at Alptal (Providoli et al. 2005).

Model parameterization and calibration

TRACE is a complex model based on more than 100 parameters and initial conditions for state variables. As a basis for our parameterization procedure we used the input data for the red pine (*Pinus resinosa*) stand of Harvard Forest because it is the only conifer stand for which the model has been parameterized to date (Currie et al. 2009). The changes we made compared to the red pine parameterization are summarized in the Appendix. The simulation was initialized for the year 1900. Since for the initial values of state variables no historical records were available, we estimated these based on circumstantial evidence as follows. At the Alptal site, the *Picea abies* forest was similar

to today, i.e. a relatively open-canopy stand at least since 1925. Due to the proximity to a road, selective harvests (single trees) took place regularly (Gimmi et al. 2009). The most striking changes in the model parameterization based on empirical data from the Alptal site were the following (cf. "Appendix"): average foliar retention time (FolReten) is longer for *Picea* than for *Pinus* and was changed to 6 years, based on branch dissections (variable names in the model code, e.g. FolReten, are listed here in parentheses). Specific leaf weight, i.e. leaf mass per area, at the canopy top (SLWmax) was changed to 440 g m$^{-2}$ based on annually collected needle samples at the canopy top (Schleppi et al. 1999b). The change in specific leaf weight with canopy depth (SLWdel) was increased to 0.21 g m$^{-2}$ g, based on branch and needle harvests (Schleppi et al. 1999a, b). Initial maximum foliar mass [variable FolMass(2)] was increased to 1090 g OM m$^{-2}$, based on LAI measurements and yearly needle samples at the canopy top (Schleppi et al. 1999b). Water holding capacity (WHC) was reduced to 4 cm based on estimations from hydrographs in combination with measured rooting depth. The leaching fraction of available $NO_3^-$ (MNitleach) was set to 0.3 (Hagedorn et al. 2001). According to $^{15}N$ recovery data from a microsite labeling experiment by Providoli et al. (2006), the fraction of inorganic N leaching from the organic to the mineral horizon (ONH4leachProp and ONO3leachProp) were set to 0.12 and 0.23, respectively. Because of the lack of soil permeability at Alptal, we did not include diffusion of isotopes between available inorganic N pools in the organic and mineral soil horizons as used by Currie et al. (2004) for different soils.

Having incorporated climate and N deposition scenarios as well as the changes to parameters and initial conditions based on empirical data, we calibrated the following key variables (independently of $^{15}N$ recovery) before making model-data comparisons: foliar and woody production, tissue, fine root and wood N concentrations, O horizon mass and C/N ratio, net nitrification and leaching of $NO_3^-$. We chose those variables because (1) they are central fluxes and pools in the model that are highly indicative of model behavior (Currie et al. 2009) and (2) they can be measured in the field. The resulting most striking parameter changes were the following (cf. "Appendix"): the minimum ratio of wood production to foliar production (Min-WoodFolRatio) was reduced to 0.75. To adjust LAI for light extinction in clumped canopies, the parameter LAIadj was set to 1.11. LAIadj corresponds to 1/Ω, Ω being the canopy clumping factor (cf. Nilson 1971). The parameters NImmobA and NimmobB were set to 160 and −24, respectively. These parameters adjust the relationship between soil N concentration and re-immobilization in organic matter and serve to calibrate the C/N ratio in the different soil horizons. Model-data comparison for the key variables is shown in Table 2. Results for the entire simulation period after the model calibration for the key variables and for both plots are shown in Fig. 3.

To evaluate model sensitivity to uncertainty in the parameter estimates, a multivariate Monte-Carlo analysis was conducted. We stochastically altered 63 parameters to test model behavior. The parameters that were altered were those that were not initially calculated, whose values are not well known, or did not belong to the initial conditions or climatic data. A detailed list of the altered parameters can be found in the TRACE user guide (Currie et al. 2009). Each of the chosen parameters was altered stochastically assuming a normal distribution around the default value of the parameter and a standard deviation of 10 %. After 100 model runs, with each considering a different altered

**Table 2** Model-data comparison after calibration to assess model accuracy prior to the analysis of $^{15}N$ redistribution

| | Model results (2000) | Field data, control plot | Reference for field data |
|---|---|---|---|
| Foliar production (g OM/m/a) | 231 | 300 | Calculated using LAI, spec. leaf weight, needle life time |
| Wood production (g OM/m/a) | 567 | 410 | From dendrometers and height growth |
| N concentration in green foliage (%) | 1.15 | 1.14 | Needle sampling (2000) |
| N concentration in fine roots (%) | 0.98 | 0.74 | Soil sampling (2009) |
| N concentration in wood (%) | 0.07 | 0.08 | From tree-rings (2009) |
| Soil O horizon OM mass (g OM/m$^2$) | 3,715 | 2,730 | Soil sampling (1997) |
| Soil O horizon C/N ratio (g/g) | 20.9 | 19.7 | Soil sampling (2009) |
| Soil O horizon net nitrification (g N/m$^2$/a) | 0.38 | 0.12 ± 0.24 | Hagedorn et al. (1999) |
| $NO_3^-$ leaching from M horizon (g N/m$^2$/a) | 0.30 | 0.31 | Runoff sampling, Schleppi et al. (2004) |

*OM* organic matter (ash-free, oven-dry weight)
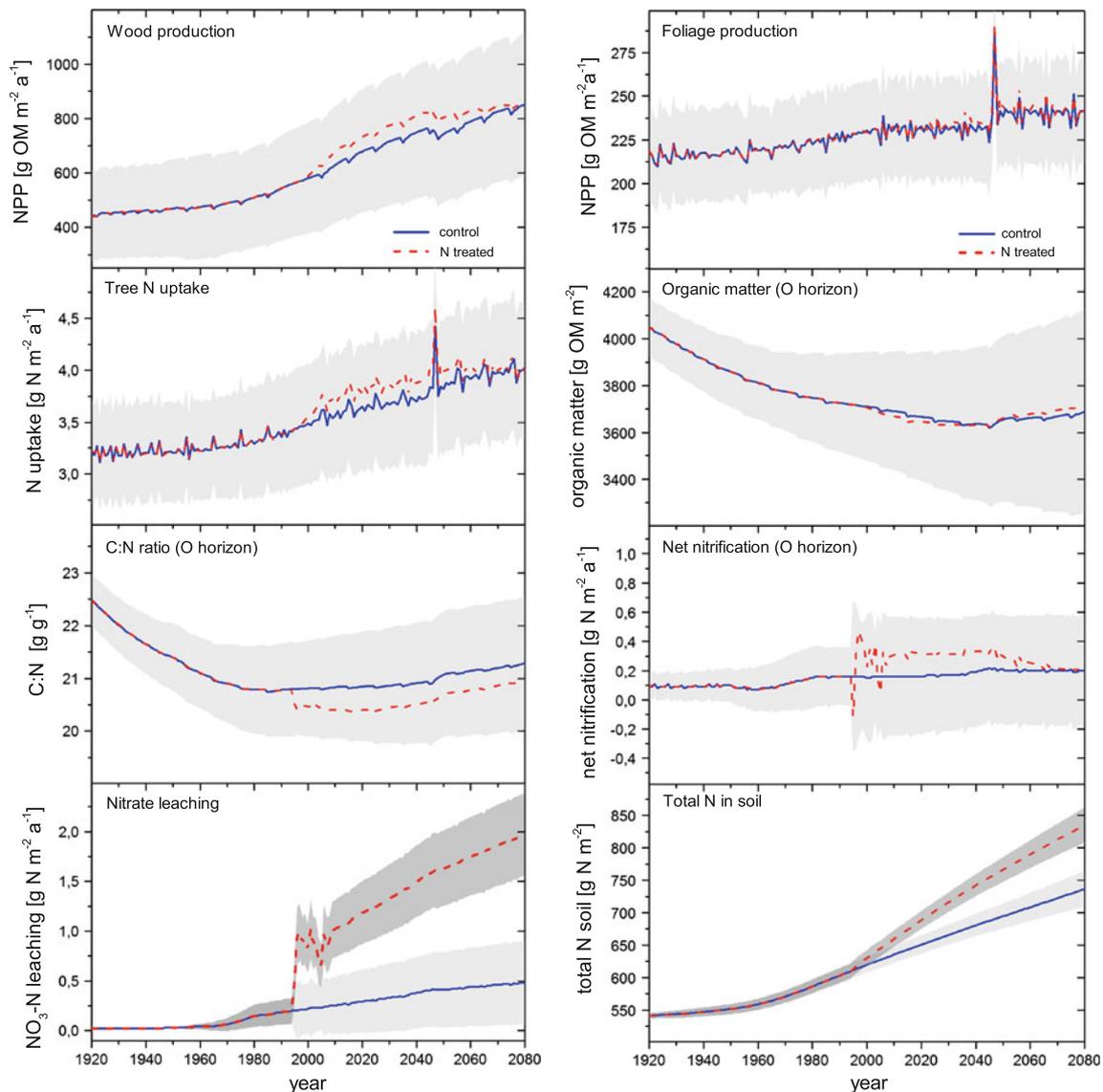
**Fig. 3** Simulation of the main fluxes in the calibrated model for the years 1920–2080 for the control (*solid line*) and for the N-treated plot (*dashed line*). *Shaded areas* represent ±standard deviation (SD) from 100 Monte-Carlo runs with randomly altered parameters. Only the SD of the control plot is shown where it overlaps that of the N-treated plot and does not differ from it by more than 1 %. The spike in foliage production and tree N uptake in 2047 is a discretization effect corresponding to the warming-induced advancement of a phenological stage (end of needle growth) by one time step, i.e. 1 month

parameter set, means and standard deviations within the ensemble of the model runs were calculated for each simulated year and selected model result.

## Results

### Recovery of $^{15}$N tracer in field samples

Total recovery of the applied $^{15}$N tracer for the new data presented here (2002 on the N-treated plot and 2009 for both plots) varied between 60 and 75 % (Tables 3, 4, 5). In all cases, the soil was the dominant sink for the $^{15}$N. On the control plot, tracer recovery in the soil increased almost linearly from 8 % in 2001 to 60 % in 2009 (Fig. 4). Recovery in the ground vegetation first increased from 4 % in 2001 to 32 % in 2003, and then decreased to 4 % in 2009. Trees showed a slight increase in the $^{15}$N tracer from 0.1 % in 2001 over 6 % in 2003 to 10 % in 2009.

On the N-treated plot, tracer recovery in the soil decreased from 63 % in 1997 to 47 % in 2002 (also Fig. 4) and then increased to 61 % in 2009. In the ground vegetation, $^{15}$N-tracer recovery decreased from 5 % in 1997 to 1.5 % in 2002 and less than 1 % in 2009. Trees showed a

**Table 3** Partitioning of the added $^{15}$N labeled nitrogen for 2002, 6 years after tracer addition on the N-treated plot (+25 kg/ha/a) in major ecosystem pools, as means

Pool sizes as dry matter, N concentrations, N pools, tracer fractions and tracer recoveries. $^{15}$N-tracer recoveries are estimated according to "Field methods"

[a] Recovery rates for trees (including bark, wood branches and needles) were estimated by a linear interpolation between recovery rates from 1997 and 2009

| N-treated plot 2002 | | | | | |
|---|---|---|---|---|---|
| Pool | Pool size (kg/m$^2$) | N conc. (%) | N pool (g/m$^2$) | Tracer | |
| | | | | Fraction (mmol/mol) | Recovery (%) |
| Trees | | | | | |
| Bark, wood, branches, needles | | | | | 9.3[a] |
| Ground vegetation | | | | | |
| Mosses | 0.9 | 2.1 | 1.9 | 12 | 0.6 |
| Monocotyledons | 0.4 | 2.0 | 0.8 | 8 | 0.2 |
| Dicotyledon herbs | 0.6 | 2.1 | 1.3 | 8 | 0.3 |
| Dicotyledon shrubs | 0.4 | 1.3 | 0.5 | 19 | 0.3 |
| Others species | 0.2 | 1.9 | 0.4 | 2 | 0.1 |
| Roots | | | | | |
| LF fine roots | 0.3 | 0.9 | 0.2 | 20 | 1.6 |
| A + B fine roots | 0.5 | 0.8 | 0.4 | 12 | 1.0 |
| LF medium roots | 0.3 | 0.4 | 0.1 | 9 | 0.4 |
| A + B medium roots | 1.0 | 0.4 | 0.4 | 6 | 1.0 |
| Soil | | | | | |
| Litter | 0.5 | 1.4 | 0.7 | 12 | 2.6 |
| LF | 6.9 | 1.2 | 8.3 | 10 | 26.7 |
| A | 28.5 | 0.7 | 20.3 | 2 | 15.4 |
| B | 75.8 | 0.3 | 200 | 0 | 0 |
| Total recovery | | | | | 59.5 |

slight increase in the $^{15}$N tracer from 8 % in 1997 to 13 % in 2009.

### Model results compared against $^{15}$N field data

After calibration, the model was compared against the results of the $^{15}$N-tracer study conducted in both experimental catchments. Because total N pools and fluxes had been adjusted in the parameterization and calibration phase, the main criteria to judge model performance in this new forest type were the tracer recoveries. We considered the following pools: foliage (most recent cohort and sum of the older ones), fine roots (<2 mm diameter), living wood, soil litter layer, organic soil horizon and mineral soil horizon. The cumulative fluxes of tracer in litterfall as well as in nitrate leaching were also considered.

On the control plot TRACE calculated a sharp increase in recovery of the $^{15}$N tracer in current-year foliage (Fig. 5) with a peak after 2 years once 100 % of the tracer had been applied. Field data (also Fig. 5) for this variable on the control plot showed much lower values and no clear peak 8 years after the last tracer dose was applied. Fine root $^{15}$N recovery was slightly overestimated by TRACE and field data did not show the same clear peak simulated 3 years after the first tracer application. The peak 4 years after the application of $^{15}$NO$_3^-$ in the litter layer was captured well

by the model. Recovery rates in the organic horizon were not well captured (Fig. 6). In the first years after the beginning of tracer application, TRACE over-predicted $^{15}$N recovery rates, whereas 9 years later, TRACE under-predicted them.

On the N-treated plot, calculated $^{15}$N recovery in foliage fits well with field observations. Recovery data for fine roots showed good agreement between simulation and measurements 7 years after tracer application, but 14 years after tracer application, field recovery was underestimated in the model by a factor two. For the litter layer simulated recovery agreed well with field results. For the organic horizon, TRACE under-predicted recovery rates throughout the simulation run with nearly constant rates, whereas field recovery rates were more variable.

On both the control and the N-treated plot, recovery of the cumulated litterfall flux was over-predicted by TRACE, which suggested a peak in litterfall fluxes of $^{15}$N about 3 years after tracer addition. In the field data, litterfall fluxes of $^{15}$N showed no clear peak or decline even after 14 years. In addition, simulated wood $^{15}$N recovery rates on both plots were consistent with field data, and they lay within the calculated sensitivity range.

Simulated recoveries of $^{15}$N tracer in the litter layer on both plots showed good agreement with field data (Fig. 5). The simulated cumulative $^{15}$N recovery of the NO$_3^-$

**Table 4** Partitioning of the added $^{15}$N labeled nitrogen for 2009, 9 years after tracer addition on the control plot (no N addition) in mayor ecosystem pools, as means

| Control plot 2009 | | | | | |
|---|---|---|---|---|---|
| Pool | Pool size (kg/m$^2$) | N conc. (%) | N pool (g/m$^2$) | Tracer | |
| | | | | Fraction (μmol/mol) | Recovery (%) |
| Trees | | | | | |
|   Wood | 20 | 0.1 | 16 | 30 | 0.7 |
|   Bark | 2 | 0.3 | 6.3 | 38 | 2.3 |
|   Branches | 3 | 0.4 | 12 | 19 | 1.9 |
|   Needles | 1.1 | 1.2 | 14 | 34 | 3.7 |
| Ground vegetation | | | | | |
|   Mosses | 0.3 | 2 | 6.5 | 103 | 2.1 |
|   Monocotyledons | 0.04 | 2 | 0.7 | 37 | 0.1 |
|   Dicotyledon herbs | 0.07 | 1.9 | 1.4 | 61 | 0.4 |
|   Dicotyledon shrubs | 0.1 | 1.2 | 1.7 | 79 | 0.5 |
|   Others species | 0.03 | 1.6 | 1.7 | 120 | 0.7 |
| Roots | | | | | |
|   LF fine roots | 0.4 | 1 | 0.02 | 79 | 2.5 |
|   A + B fine roots | 0.4 | 0.8 | 0.02 | 21 | 0.6 |
|   LF medium roots | 0.2 | 0.6 | 0.01 | 48 | 0.5 |
|   A + B medium roots | 0.8 | 0.5 | 0.02 | 13 | 0.6 |
| Soil | | | | | |
|   Litter | 0.6 | 1.3 | 8.4 | 53 | 3.7 |
|   LF | 7 | 1.4 | 104 | 48 | 38.9 |
|   A | 23 | 0.9 | 178 | 6 | 13.3 |
|   B | 64 | 0.3 | 145 | 0 | 0 |
| Total recovery | | | | | 72.5 |

Pool sizes as dry matter, N concentrations, N pools, tracer fractions and tracer recoveries. $^{15}$N-tracer recoveries are estimated according to "Field methods"

leaching flux for both catchments was consistent with field measurements, showing that the majority of the tracer leaching occurs within the first 2–3 years (Schleppi et al. 2004). The only difference in $^{15}$N–NO$_3$ leaching between treatments is that twice as much tracer was leached on the N-treated catchment than on the control.

On both plots, TRACE predicted the mineral soil horizon as the major sink for the applied tracer with nearly 40 % recovery of the applied tracer after ca. 3–4 years. Field recovery showed a much smaller N sink in the mineral horizon. On the control plot, field recovery of $^{15}$N in the mineral soil was below 5 % in the first 3 years, and reached a maximum of about 14 % 9 years after the beginning of the tracer application. On the N-treated plot, $^{15}$N recovery was ca. 20 % at both 2 and 14 years after application.

After the successful calibration and validation with $^{15}$N field data, the model run for 70 years into the future showed that the soil has the ability to immobilize an ongoing constant rate of 77 % (15 kg/ha/a) of the N load on the control plot and 70 % (18 kg/ha/a) of the N load on the treated plot (Fig. 3).

### Modeled N impact on C sequestration

Model results showed that the additional N clearly increased forest net primary production (NPP). Before the start of N addition in 1995, both experimental plots showed similar values for NPP of about 550 g OM/m$^2$/a (where OM is organic matter). Followed by the start of N addition in 1995, simulated wood NPP increased characterized by a sigmoid curve for approximately 13 years by almost 10 %, stayed constant on that level for another 60 years and returned linearly almost to the control level at the end of our simulation period in 2080. In contrast to wood NPP, foliar NPP did not change due to the additional N input in our simulations.

Model results for the ecosystem C pools indicated an increased C sequestration especially in standing wood (living plus standing dead) and, to a lesser extent, in the soil O horizon. The increase in standing wood peaked in 2055 with 1,080 g C/m$^2$ or 6.4 % over the control. Soil C storage on the N-treated plot started to increase after a time lag of approximately 15 years, increased by approximately 6.5 g C/m$^2$/a and peaked after 60 years before returning

**Table 5** Partitioning of the added ^{15}N labeled nitrogen for 2009, 14 years after tracer addition on the N-treated plot in mayor ecosystem pools, as means

| N-treated plot 2009 | | | | | |
|---|---|---|---|---|---|
| Pool | Pool size (kg/m$^2$) | N conc. (%) | N pool (g/m$^2$) | Tracer | |
| | | | | Fraction (mmol/mol) | Recovery (%) |
| Trees | | | | | |
| Wood | 11.6 | 0.08 | 9.3 | 11 | 1.1 |
| Bark | 1.4 | 0.3 | 4.6 | 9 | 2.0 |
| Branches | 2.5 | 0.4 | 10.3 | 10 | 3.3 |
| Needles | 1.3 | 1.2 | 16 | 9 | 5.0 |
| Ground vegetation | | | | | |
| Mosses | 0.06 | 2.5 | 1.4 | 2 | 0.1 |
| Monocotyledons | 0.1 | 1.8 | 2.3 | 5 | 0.3 |
| Dicotyledon herbs | 0.1 | 2 | 2.1 | 4 | 0.2 |
| Dicotyledon shrubs | 0.1 | 1.4 | 2.1 | 4 | 0.2 |
| Others species | 0.06 | 1.9 | 1.0 | 1 | 0.1 |
| Roots | | | | | |
| LF fine roots | 0.4 | 1.2 | 0.02 | 10 | 1.7 |
| A + B fine roots | 0.4 | 0.8 | 0.02 | 7 | 1.0 |
| LF medium roots | 0.2 | 0.6 | 0.005 | 8 | 0.3 |
| A + B medium roots | 0.7 | 0.5 | 0.02 | 6 | 0.9 |
| Soil | | | | | |
| Litter | 0.8 | 1.4 | 12.4 | 7 | 2.9 |
| LF | 7.8 | 1.5 | 126 | 9 | 36.7 |
| A | 23.3 | 0.8 | 163 | 3 | 16.8 |
| B | 75.8 | 0.3 | 200 | 1 | 2.1 |
| Total recovery | | | | | 74.7 |

Pool sizes as dry matter, N concentrations, N pools, tracer fractions and tracer recoveries. ^{15}N-tracer recoveries are estimated according to "Field methods" section

almost to control levels in 2080. While modeled NPP converged between N-treated and the control plot until the end of our model simulation in 2080, differences in C pool sizes remained.

## Discussion

In model-data comparisons using the TRACE model, if C, N, and ^{15}N results for ecosystem compartments are simulated correctly, we can gain increased confidence in our understanding of how fine-scale processes combine to produce whole-system C and N cycling. Applying TRACE at a new site is worthwhile, particularly where field data for ^{15}N recoveries are available at multiple points in time, because this allows us to assess our understanding from monthly to decadal timescales and across a greater range of forest types. Compared to other models, TRACE has the advantage that it is able to simulate the redistribution of ^{15}N tracers in major ecosystem compartments. This provides investigators with the ability to discover where disagreements arise between field-measured and modeled ^{15}N redistributions.

However, before evaluating the simulation results in more detail (below) the following has to be taken into account. While model results are constrained by a mathematical mass balance of the isotope such that tracer percent recovery after accounting for system losses always total 100 %, field observations typically scale-up recovery rates from fine-scale samples and do not necessarily recover the entire amount of tracer in the study system; thus, tracer recovery rates from field studies typically do not total 100 %, but usually lie between 60 and 90 % (Buchmann et al. 1996; Lamontagne et al. 2000; Nadelhoffer et al. 2004; Providoli et al. 2005; Templer et al. 2012). In both the field and the model study, gaseous N losses through denitrification for example are not taken into account, which may be a reason why field recoveries do not total 100 %. For our study site Alptal, Mohn et al. (2000) showed that the total gaseous N loss through denitrification is of minor importance (1.7 kg N/ha/a on the control and 2.9 kg N/ha/a for the treated plot) and thus represents a small part of the ^{15}N not recovered.

### Field recovery of the ^{15}N tracer

The results of ^{15}N-tracer recovery for the 9- and 14-year resampling are consistent with earlier results from the same site, that the soil pool was the most important sink for all

three applied tracer forms and for all sampling times. This agrees well with a meta-analysis by Templer et al. (2012), which compares ecosystem-level ^{15}N-tracer studies across vegetation biomes, soil types, and plant functional types. As a general pattern, in the short-term (<1 week) as well as in the longer term (3–18 month) the soil is the largest sink for ^{15}N tracers in terrestrial ecosystems. Our 14- and 9-year time series of ^{15}N-tracer recovery for all major ecosystem N pools are unique because most of the ^{15}N studies in forest ecosystems either have sampling periods no longer than 3 years or do not account for all major N pools (Buchmann et al. 1996; Lamontagne et al. 2000; Morier et al. 2008; Nadelhoffer et al. 1995; Perakis et al. 2005; Providoli et al. 2005; Templer et al. 2005; Tietema et al. 1998). The only study we are aware of with longer sampling periods in all major N pools is a 7-year resampling at Harvard Forest (Nadelhoffer et al. 2004). Their long-term study and our results provide evidence that the immobilization of inorganic N input to forest soils is not a short-term response (1–3 years); in actual fact, after entering soil pools, deposited N has mean residence times greater than a decade.

In our results, a main difference between catchment responses for ^{15}N recovery in soil shortly after ^{15}N additions was that the N-treated plot had high recovery in the soil (63 %) in the year 1997, whereas the control plot had much lower recovery in 2003 (33 %) (Figs. 4, 6). One potential cause of this difference might be the different ^{15}N-tracer forms that were used. In a meta-analysis of ^{15}N field tracer studies across a broad range of terrestrial ecosystems, Templer et al. (2012) showed that the form of the added tracer has a significant influence on total ecosystem ^{15}N-tracer recovery. Studies in which the tracer was added as [15]$NH_4$ had significantly lower total ecosystem [15]N

recovery (53.4 %, $n = 23$) compared to those where ^{15}N was added as [15]$NH_4$[15]$NO_3$ (85.3 %, $n = 15$) or [15]$NO_3$ (80.2 %, $n = 10$). Another, and in our opinion more likely cause of the difference we observed may be the differences in tracer application methods. On both catchments the ^{15}N tracer was applied directly on the ground or ground vegetation where present, but on the N-treated plot this was done during rain events with an automatic irrigation system (Schleppi et al. 1999a). As a result, the precipitation along with the irrigation water allowed the tracer to rapidly infiltrate into the soil, and contact time with plant tissues remained short. However, on the control plot, the tracer was applied independently of rain events using a backpack sprayer (Providoli et al. 2005) leaving the tracer on plant and soil surfaces for an extended period of time. Recovery rates from the ground vegetation support this hypothesis: On the control plot, where the tracer had longer retention time on plant tissues, tracer recovery in ground vegetation was almost 20 % while on the N-treated plot only 5 % of the tracer was recovered. An N saturation of the ground vegetation within the first year of (labeled) N treatment can be ruled out since the N concentration in plant tissues did increase during this time (Schleppi et al. 1999a). Another argument supporting the fact that the different application methods influence the retention time of the applied tracer in the soil is nitrate leaching during the first year of tracer addition: In the fertilized catchment, Schleppi et al. (1999a) recovered 10 % of the tracer in runoff, whereas in the control catchment Providoli et al. (2005) recovered only ca. 1 % of the tracer in runoff. One might argue that the N fertilization has caused this increase in nitrate leaching due to N saturation (Tietema et al. 1998) but Schleppi et al. (1999a) showed that the leached nitrate was hydrologically driven and mainly coming directly from the additional N

**Fig. 4** Recoveries of the ^{15}N tracer in major ecosystem pools in proportion to the total amount of applied tracer (soil, trees and ground vegetation) on the N-treated and the control plot. Trees comprise coarse roots and soil comprises fine roots. Total recovery for the year 2001 on the control plot is low because only 24 % of the total tracer has been applied since then. *Vertical bars* indicate timing, form and amount of the applied tracers. N addition began in 1995 and continued throughout the course of measurements. Detailed recovery data for all ecosystem pools can be found in the Tables 3, 4 and 5
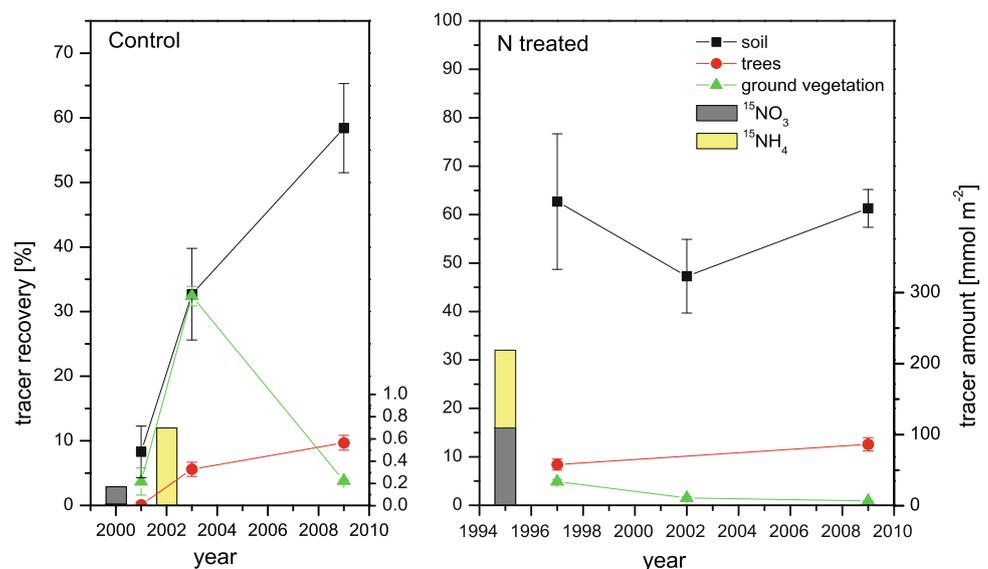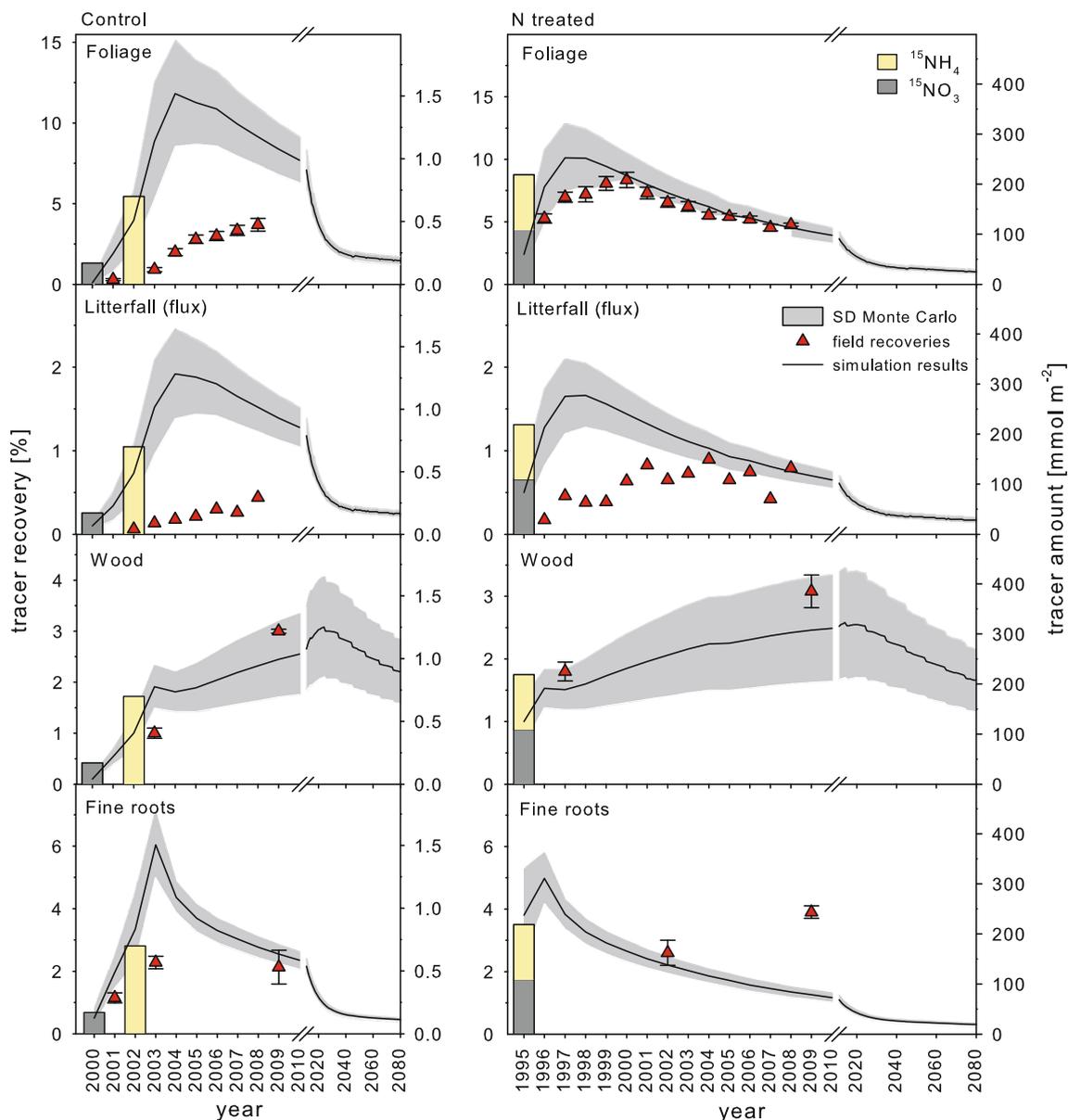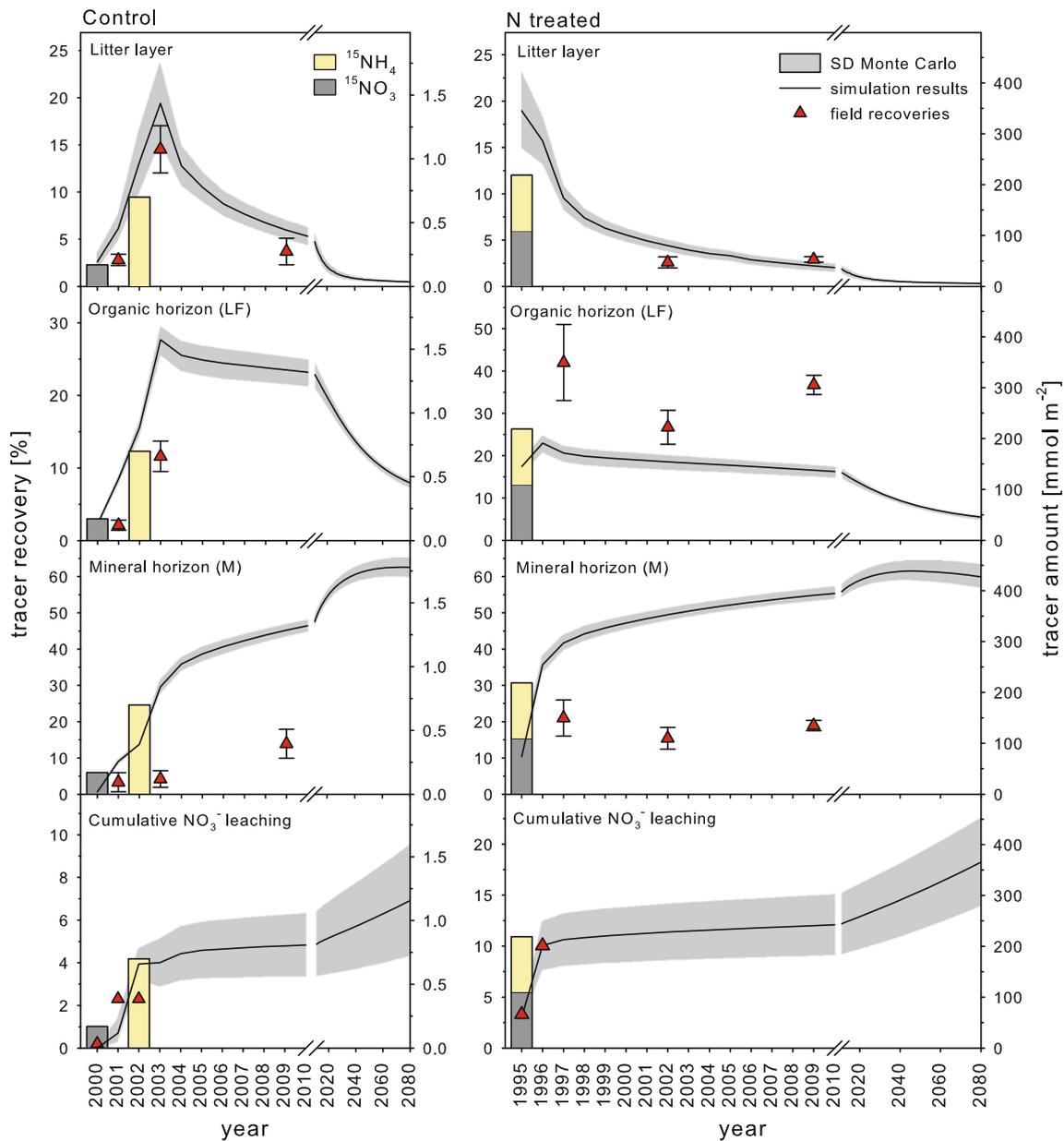
**Fig. 5** Simulation results compared to field data for the recovery of ${}^{15}$N tracers in plant N pools and foliar litterfall flux. Field study results are shown as *triangles* with *error bars* as means ± standard deviation (SD). Some SD values are too low to be visible. Simulated mean values are shown as *solid lines*. The *shaded area* represents ±SD based on a set of 100 Monte-Carlo runs with altered model parameters (see text). 'Foliage' results are sums of all yearly cohorts in living foliage. Wood refers to living wood. *Vertical bars* show form, amount and timing of the ${}^{15}$N-tracer application. Note that after the year 2010 the scaling of the *x* axis changes

fertilization even during single rainfall events (Schleppi et al. 2004). At Alptal, >80 % of the total N deposition occurs as wet deposition (Schleppi et al. 1998). Given all of these factors, we expect that the application of the tracer on the N-treated plot with sprinklers during rain events, as well as recovery rates obtained in N-treated plot, were more realistic.

In tree biomass, tracer recoveries on both plots were small relative to recoveries in the soil (Fig. 4). On both plots, trees accumulated about 10 % of the tracer by 14 or

9 years after ${}^{15}$N application which is consistent with findings by Nadelhoffer et al. (2004) where trees (red pine) accumulated 6.8–15.5 % of the tracer by 7 years after application. Their long-term tracer study as well as our results showed that after approximately a decade, trees were still taking up some of the ${}^{15}$N tracer. Considering the fact that a part of the atmospheric N deposition to forests can be taken up directly by the canopy, our ${}^{15}$N recovery rates for trees might be slightly underestimated (Sievering 1999; Sievering et al. 2000; Nadelhoffer et al. 1999).

**Fig. 6** Simulation results compared to field data for recovery of $^{15}$N tracer in soil N pools and cumulative nitrate leaching. Field study results are shown as *triangles* with *error bars* as means ± standard deviation (SD). Some SD values are too low to be visible. Simulated mean values are shown as *solid lines*. The *shaded areas* represent ±SD based on a set of 100 Monte-Carlo with altered model parameter (see text). *Vertical bars* show form, amount and timing of the $^{15}$N tracer. Note that after the year 2010 the scaling of the *x* axis changes

### Comparison of model simulations against field data

#### Soil

Model simulation correctly showed the dominance of soil pools over vegetation pools as N sinks for $^{15}$N tracers at the Alptal site in both control and N-treated plots. Simulated tracer recovery rates in the litter layer on the control plot matched well with our field results throughout the time series (Fig. 6). Model results slightly overestimated the

organic horizon in 2001 and 2003 but underestimated it in 2009. This underestimation by the model in 2009 can be explained as follows: The model was originally adapted to closed-canopy forests without a significant layer of ground vegetation, or an herbaceous layer, in which N could be retained. The current version of TRACE has no mechanism for N (including $^{15}$N) uptake into the ground vegetation. However, at Alptal the open-canopy spruce forest has a well-developed ground layer, and, in particular, a wide-spread mosaic-like moss layer with more than 30 moss

species (Schleppi et al. 1998). It is well known that mosses use atmospherically deposited inorganic N as a major N source (Bates 1992; Woodin et al. 1985) and therefore modify the chemistry of the percolating water prior to its infiltration into the soil. In the Netherlands, where high ambient N deposition levels prevail, Heijmans et al. (2002) retrieved 63 % of the tracer in the living *Sphagnum* layer 15 months after $^{15}$N addition. For the Alptal experimental site Providoli et al. (2005) found that mosses contain roughly 15 % of the added $^{15}$N after 1 year. This observation indicates that a large part of the $^{15}$N tracer is retained in the moss layer first; only later is it passed to the organic soil as plant litter, with a delay equal to the lifespan of moss tissue.

On the N-treated plot, as on the control plot, simulated recovery rates for the litter layer fit well with field results. Model results for $^{15}$N recovery in the organic horizon overestimated field recoveries for the control plot in the first few years, while underestimating field recoveries on the N-treated plot throughout the sampling period. This difference could be explained by the above-mentioned difference in the method of tracer application. Overestimation of modeled O horizon recovery of $^{15}$N on the control plot may also be due to the absence of a ground vegetation layer in the model. On both plots, recovery rates for the mineral horizon were overestimated in model simulations compared to field data. In their simulation study with TRACE, Currie et al. (2004) thought that the field sampling depth could be a factor that leads to an underestimation in field recovery because any tracer leached below sampling depth is missed. This is not the case in our study because recovery in the B horizon (sampling depth 25 cm) was always low (max. 2 %). The reason for this is certainly because soils at Alptal are waterlogged for much or most of the year, and the infiltration of the tracers into mineral soil is much less important than in permeable soils. This difference highlights how important infiltration into mineral soils is for vertical transport and retention of N.

Despite all discrepancies between model and field recovery rates in the different soil compartments, the comparison of simulation and field results show a rather good match when the soil is considered as a single pool.

Modeled N uptake by plants first takes place in the upper soil horizon but can also take place, if depleted, from the lower horizon. Hence, for simulations of ecosystem-scale C and N cycling, the model-field data discrepancies in the soil that we found are not of key importance. The sensitivity analysis, with its 63 stochastically altered parameters, showed that the model is relatively robust against uncertainties in parameter estimates. This applies to the main N fluxes as well as to $^{15}$N recoveries. Total N content in the soil on the N-treated plot in 2080 varies only by ca. $\pm10$ % within the set of Monte-Carlo simulation undertaken to

assess uncertainty (Fig. 3). This shows the relative precision of our simulation-based prediction that forest soils will continue to immobilize approximately 3/4 of the N load for the next 70 years under the assumed climate change and N deposition scenarios. However, like with every model of this kind, predictions are only realistic as long as basic ecosystem functions are retained. While N is known to make ecosystems more sensitive to abiotic and biotic stresses like drought, frost, pests, diseases or combinations of these (Magill et al. 2004; McNulty and Boggs 2010; Throop and Lerdau 2004), the model does not make predictions about such disturbances. Model results show that N addition results in a significantly lower ratio of C/N in soil (Fig. 3). This could alter N availability and potentially alter the outcome of plant competition over long time scales. The lower C/N ratio can also be expected to promote nitrate leaching and loss to surface waters (Fig. 3; Gundersen et al. 1998).

Plant pools and litterfall fluxes

In their modeling study with TRACE using field data from Harvard Forest (Nadelhoffer et al. 2004), Currie et al. (2004) found a general overestimation of simulated recovery rates from vegetation pools for the pine forest (foliage, wood, roots). Comparing our model results with theirs, we found that all vegetation pools except wood and fine roots on the N-treated plot were slightly overestimated at Alptal. For wood and fine roots, the Alptal version of TRACE shows an even closer match with field data than the original model application. The disagreement of simulated $^{15}$N recovery rates for fine roots may be due to an oversimplified N storage function in the model. TRACE assumes that one-third of the plant internal storage (*VascN*) is recovered in fine roots; Currie and Nadelhoffer (1999) previously pointed out that this is a simplifying assumption and that correctly capturing $^{15}$N-tracer recovery in fine roots requires additional research. Before looking at results for foliage we have to consider that modeling temporal patterns of $^{15}$N recovery rates for foliage with process-based models is also demanding as numerous processes are involved: soil N mineralization and nitrification, uptake of inorganic nitrogen forms of N from the organic and mineral horizons, physiological assimilation, transport, storage and allocation, foliar phenology and N leaching from the canopy. As a result, a certain degree of divergence between measured and simulated recovery is to be expected. Taking this into account, simulated recovery of the $^{15}$N tracer generally agrees well with field recovery. Upon further examination, recovery in foliage on the N-treated plot fits better to field recovery than on the control plot where model results slightly overestimate the field study results and show a stronger peak. Again, this may be explained by

the different application methods of the tracer as mentioned above. When comparing results from tracer studies, not only the application method of the tracer has to be considered but also its form. Several N uptake studies have shown that *Picea abies* prefers $NH_4^+$ to $NO_3^-$ (Buchmann et al. 1995, Ilari 1994, Kronzucker et al. 1997).This might explain the low recovery on the control plot in the first two years after the addition of the $K^{15}NO_3$ tracer followed by a sharp increase in recovery directly after the addition of the $^{15}NH_4Cl$ tracer, compared to the immediate increase after the addition of the $^{15}NH_4^{15}NO_3$ tracer on the N-treated plot.

Because the tracer signal in litterfall is controlled by the signal in foliage, model discrepancies in recovery rates in litterfall fluxes can be partially explained by discrepancies in foliage. However, the mismatch of modeled litterfall $^{15}N$ recovery is also related to the number of foliage cohorts considered in the model. In TRACE, foliage is separated into two cohorts only. The first cohort is defined as current-year foliage, while the second cohort includes foliage from all prior years. Modeled foliar litterfall in conifers then takes place from the second cohort, thus leading rapidly to an increased signal of $^{15}N$ in litterfall from this cohort. In contrast, field observations at the Alptal site show that the foliage of *Picea abies* builds up to 11 cohorts with an average longevity of about 6–7 years. Subsequently, the $^{15}N$-tracer signal in litterfall is expected to be significantly delayed in field results. Approximately 10 years after tracer addition when all foliage cohorts in the field have taken up some of the $^{15}N$ tracer, model and field recovery rates on both plots match well. Therefore, simulation results for litterfall tracer recovery in the longer term showed realistic results, while only short-term patterns disagree and do so for an easily understood reason.

Increased modeled C sequestration by N addition

Beside modeling the fate of added N with TRACE, it is possible to answer the question of the effects of additional N on ecosystem C pools and fluxes. Our simulation showed that the additional N resulted in an increased wood NPP and, thus enhanced forest C sequestration. The simulated continuing N addition of 25 kg N/ha/a on the treated plot (Fig. 2) resulted in a cumulative N input of 1,500 kg N/ha over 60 years, the time at which the differential C sequestration peaked. The ratio of cumulative C sequestration to the cumulative N addition resulted in an N use efficiency (NUE) for aggrading wood of 7.2 kg C per kg N added. A very similar modeling study with TRACE for the Harvard forest hardwood stand by Currie et al. (2004) found a NUE of 5 kg C per kg N of the added N. In a meta-analysis of the above-ground C sequestration in forests induced by enhanced N deposition De Vries et al. (2009) suggest a most possible range of 15–40 kg C per kg N added. Compared to that, the results from Currie et al. (2004) and our results show a relatively low response of the additional N on the ecosystem C sequestration.

## Conclusions

Our time series of $^{15}N$-tracer recoveries from two plots with different N status, unique in their long-term duration, allowed us to track the partitioning of N inputs among forest ecosystem compartments through time. These data show that the combined organic and mineral soil was the major sink for N deposition (60 %), whereas trees (needles, branches, wood, bark) stored about 10 % of the applied tracer 14 and 9 years after tracer addition, respectively. The comparison of field $^{15}N$ recoveries with results from the TRACE model showed some discrepancies, but in general the simulation results for the $^{15}N$ recovery from the various ecosystem compartments were satisfactory. In many respects, discrepancies between model results and field observations provide insight into the particularities of more open subalpine forests with ground vegetation growing on poorly permeable soils (Alptal) compared to more closed temperate North American forests stocking on permeable soils (Harvard Forest) for which TRACE was initially developed. During the model adaptation process we included preferential water flow for nitrate and fixed an ammonium accumulation problem in the organic soil. TRACE is based on more than 100 parameters which make the adaptation process to new sites very much dependent on the availability of data. However, the conducted sensitivity analyses revealed that for the Alptal site, the uncertainty in parameter estimates plays a minor role in causing uncertainty in model results. The inclusion of additional site-specific conditions, i.e. the ground vegetation layer and more than two foliar cohorts in the model should be given much more attention. Beside these potential improvements we conclude that the adapted and calibrated version of TRACE is able to capture N and C cycling well in a very different type of forest than it was first developed for. Consequently, using the model to evaluate the long-term fate of N deposition, our 70-year simulation in the future suggests a constant ongoing ability of the forest soil to immobilize 70 to 77 % of the N load and resulted in an NUE of approximately 7 kg C per kg N added.

# Appendix

See Table 6.

**Table 6** Changes made to the default parameter set for the initialization year 1900 separated into parameters and initialization data

| | | Units | Harvard forest (pine)[a] | Alptal[b] (spruce) | References |
|---|---|---|---|---|---|
| **(a) Parameters** | | | | | |
| *Phenology and physiology* | | | | | |
| PsnTMin | Minimum daily temperature for photosynthesis | °C | 4 | 0 | R. Häsler (WSL, pers. comm.) |
| PsnTOpt | Optimum daily temperature for photosynthesis | °C | 24 | 18 | R. Häsler (WSL, pers. comm.) |
| AmaxFrac | Daily Amax as fraction of instantaneous | Decimal fraction | 0.8 | 0.58 | |
| FolReten | Foliar retention time | Year | 2.25 | 6 | Schleppi et al.(1999a) |
| SLWMax | Specific leaf weight at top of canopy | g/m$^2$ | 200 | 440 | Schleppi et al. (1999b) |
| SLWdel | Change in specific leaf weight with canopy depth | g/m$^2$/g | 0 | 0.21 | Schleppi et al. (1999a, b) |
| GDDFolStart | Growing-degree days for foliar expansion to start | °C day | 900 | 570 | Hallenbacher PhD thesis (2002) |
| GDDFolEnd | Growing-degree days for foliar expansion to end | °C day | 1,600 | 1,400 | Hallenbacher PhD thesis (2002) |
| GDDWoodStart | Growing-degree days for wood growth to start | °C day | 900 | 300 | Schleppi (unpublished data) |
| GDDWoodEnd | Growing-degree days for wood growth to end | °C day | 1,600 | 1,400 | Schleppi (unpublished data) |
| FolRelGrowMax | Max relative growth rate of canopy | | 0.3 | 0.5 | |
| FolNRetrans | Maximum N resorbed (retranslocated) from foliage | Decimal fraction | 0.48 | 0.123 | |
| FolNConRange | Max. relative increase in green foliar N under increased N avail. | g N/g OM mass | 0.7 | 0.1 | |
| MinWoodFolRatio | Minimum ratio of wood production to foliar prod. | Decimal fraction | 0.85 | 0.75 | |
| VascNWprop, | Proportion of VascN that will be counted in wood | | 0.5 | 0.2 | |
| LAIadj | Adjustment to LAI for light extinction in clumped canopies | | 1.5 | 1.11 | |
| *Foliar litter* | | | | | |
| FLPctN | N concentration in foliar litter | g N/g OM | 0.0055 | 0.01 | Schleppi et al. (1999a, b) |
| *Fine root litter* | | | | | |
| RpctACI | Acid insoluble fraction, fine root litter | 100 × (g/g OM) | 47.3 | 24.5 | |
| RpctACS | Acid soluble fraction, fine root litter | 100 × (g/g OM) | 30.7 | 29 | |
| RpctTEX | Total extractives fraction, fine root litter | 100 × (g/g OM) | 22 | 46.5 | |
| RLPctN | In fine roots, N concentration as permanent N that will reside in tissue | g N/g OM | 0.001 | 0.0001 | |
| WLPctN | In wood, N concentration as permanent N that will reside in tissue | g N/g OM | 0.0016 | 0.00065 | |
| *Decomposition related parameters* | | | | | |
| WoodLitCLoss | Ratio of C loss to C transfer | | 0 | 0.25 | |

**Table 6** continued

| | | Units | Harvard forest (pine)[a] | Alptal[b] (spruce) | References |
|---|---|---|---|---|---|
| WoodMRespB | Controls maintenance respiration of living wood | | 0.078 | 0.07 | |
| Kho | Decay rate of humus | Per month | 0.0008 | 0.00042 | |
| Bioturb | Fraction of humus (Oa) mass bioturbated into mineral soil each month | Per month | 0.017 | 0.001 | |
| Klct | Humification of ACI and ACS in litter | | 0.6 | 0.01 | |
| OGNitFrac | O horizon gross nitrification fraction | | 0.2 | 0.13 | |
| MGNitFrac | M horizon gross nitrification fraction | | 0.3 | 0.0012 | |
| LSOMdec, | Ratio of decay rate of SOM to Humus | | 1.8 | 0.9 | |
| AETavg, | Used in calculation of humus decay rate | | 535 | 500 | |
| NImmobA, | Parameters for the relationship between soil %N and re-immobilization | | 151 | 160 | |
| NImmobB, | | | −35 | −24 | |
| LSOMprop | Proportion of mineral SOM that is light-fraction | Decimal fraction | 0.39 | 0.9 | |
| BaseGrossNmin | | | 28 | 23 | |
| *Water balance variables* | | | | | |
| WHC | Soil water holding capacity | cm | 12 | 4 | Schleppi (unpublished data) |
| PrecIntFrac | Proportion of precip intercepted by canopy | Decimal fraction | 0.2 | 0.125 | Schleppi (unpublished data) |
| *Leaching* | | | | | |
| ACIleach | Fraction of ACI mass loss that is leached | | 0.2 | 0.31 | |
| ACSleach | Fraction of ACS mass loss that is leached | | 0.37 | 0.56 | |
| TEXleach | Fraction of TEX mass loss that is leached | | 0.05 | 0.077 | |
| MNitLeach | Fraction of available $NO_3$ in mineral soil that leaches from solum | Decimal fraction | 0.05 | 0.3 | Hagedorn et al. (2001) |
| *Soil parameters* | | | | | |
| ORootFrac | Fraction of fine roots in O horizon | | 0.48 | 0.75 | |
| SoilMoistFact | Soil moisture factor | | −1 | 0 | |
| GRespFrac, | Carbon cost of synthesis | Decimal fraction | 0.25 | 0.28 | |
| *Biomass* | | | | | |
| FolMassMin | Initial minimum foliar mass | g OM/m$^2$ | 460 | 300 | |
| WoodCJan | Wood C storage | | 150 | 250 | |
| PlantC | Plant internal C storage pool for photosynthate | g C/m$^2$ | 800 | 4,000 | |
| RootC | Pool that is used for root production | g C/m$^2$ | 100 | 800 | |
| FolMass(1) | Initial minimum foliar mass | g OM/m$^2$ | 208 | 210 | |
| FolMass(2) | Initial maximum foliar mass | g OM/m$^2$ | 52 | 1,090 | Schleppi et al. (1999b) |
| RootMass | Initial fine root mass | g OM/m$^2$ | 200 | 300 | |
| WoodMass | | g OM/m$^2$ | 5,000 | 12,000 | |
| *Site parameters* | | | | | |
| Lat | Latitude | deg | 42.5 | 47.05 | |
| Lon | Longitude | deg | 72.2 | 8.72 | |
| Elev | Elevation | m | 350 | 1,185 | |

**Table 6** continued

| | | Units | Harvard forest (pine)[a] | Alptal[b] (spruce) | References |
|---|---|---|---|---|---|
| **(b) Initialisation data** | | | | | |
| *SnowPack* | | cm | 13 | 4.3 | |
| Water | Average water equivalent stored in snowpack on Jan 1 | cm | | 4 | |
| SWD | Average water equivalent stored in soil column on Jan 1 | g OM mass/m$^2$ | 12 | 1,000 | |
| | Initial mass of standing dead wood (snags) | | 10 | | |
| ONH4(1) | Pool size: inorganic available N in O horizon | | 0.4 | 0.05 | |
| ONO3(1) | Pool size: inorganic available N in O horizon | | 0.02 | 0.001 | |
| MNH4(1) | Pool size: inorganic available N in M horizon | | 0.5 | 0.1 | |
| MNO3(1) | Pool size: inorganic available N in M horizon | | 0.02 | 0.001 | |
| BL | Mass of nonhumified, nonwoody litter buried in mineral soil | g OM mass/m$^2$ | 260 | 240 | |
| BLN(1) | N pool size in nonhumified, nonwoody litter buried in mineral soil | g N/m$^2$ | 2.45 | 2.9 | |
| OFWD | Pool size (mass) of fine woody debris <10 cm diameter in O horizon | g OM mass/m$^2$ | 100 | 1,500 | |
| OFWDN(1) | N pool size in fine woody debris <10 cm diameter in O horizon | g N/m$^2$ | 0.42 | 2 | |
| HOM | Standing pool size (mass) of humified material in O horizon | g OM mass/m$^2$ | 500 | 3,200 | Schleppi et al. (2004) |
| HON(1) | N pool size in humified material in O horizon | g N/m$^2$ | 16 | 80 | |
| SOM | Standing pool size (mass) of mineral soil organic matter | g OM mass/m$^2$ | 14,231 | 13,200 | Schleppi et al. (2004) |
| SON(1) | N pool size in mineral soil organic matter | g N/m$^2$ | 370 | 380 | |
| ACI | Standing pool size (mass) of acid insolubles in litter + Oe layer | g OM mass/m$^2$ | 335 | 1,055 | |
| ACIN(1) | N pool size within acid insolubles in Litter + Oe layer | g N/m$^2$ | 4.5 | 28 | |
| ACS | Standing pool size (mass) of acid solubles in Litter + Oe layer | g OM mass/m$^2$ | 409 | 1,288 | |
| ACSN(1) | N pool size within acid solubles in litter + Oe layer | g N/m$^2$ | 4.7 | 34 | |
| TEX | Standing pool size (mass) of total extractives in litter + Oe layer | g OM mass/m$^2$ | 427 | 1,345 | |
| TEXN(1) | N pool size within total extractives in litter + Oe layer | g N/m$^2$ | 3.8 | 35 | |

[a] Harvard Forest TRACE 4.5.0 Currie parameter set last modified 4.08.06

[b] Alptal TRACE 4.5.0 Krause parameter set last modified 11.01.11

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