

Simulated soil CO₂ efflux and net ecosystem exchange in a 70-year-old Belgian Scots pine stand using the process model SECRETS

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Abstract – Within the framework of the EU ECOCRAFT (European collaboration on CO₂ responses applied to forests and trees), we developed a stand scale process model to simulate short-term carbon (C) and water fluxes from a mixed coniferous/deciduous forest in Northern Belgium (51°31' N, 4°22' E). The model, termed SECRETS, is a sequential, multi-species and multiple layer simulator that uses process modules adapted from several sources. Namely, we adapted BIOMASS (maintenance respiration and water balance), and coded the sun/shade model (photosynthesis; modified for forest species), and the GRASSLAND DYNAMICS (soil carbon and nitrogen) models. In this contribution we simulate carbon fluxes for a 70-year-old Scots pine (*Pinus sylvestris* L.) stand and we introduce an approach to characterize uncertainty in the model outputs. Simulated, annual gross primary productivity (GPP) for 1997 and 1998 was 1965 and 1888 g C m⁻², respectively. Soil respiration was 25% (495 g C m⁻² a⁻¹) and 27% (505 g C m⁻² a⁻¹) of the GPP in 1997 and 1998, respectively, in this slow growing Scots pine stand. Heterotrophic respiration (R_H) accounted for, roughly, 32% of the total soil C efflux for both years. Simulated daily fluxes for net ecosystem exchange (NEE) suggested C uptake throughout most, but not all, of the spring and summer, but net release during mid-autumn to early winter periods for both years. Our base estimates of NEE ranged from 385 g C m⁻² a⁻¹ in 1997 to 310 g C m⁻² a⁻¹ in 1998. However, the uncertainty in NEE varied from 167 to 509 g C m⁻² a⁻¹ and 138 to 392 g C m⁻² a⁻¹ in 1997 and 1998, respectively. Thus, this stand may be accumulating C at a rate of 138 to 509 g C m⁻² a⁻¹ depending on the assumed stand and site characteristics, tree physiology, and local variation in weather.

net ecosystem exchange / carbon budgets / heterotrophic respiration

Résumé – Utilisation du modèle mécaniste « SECRETS » pour la simulation des efflux de CO₂ du sol et de l'échange net de l'écosystème dans un peuplement belge de Pin sylvestre de 70 ans. À l'occasion du contrat européen ECOCRAFT (collaboration européenne sur les réponses du CO₂ appliquées aux forêts et aux arbres), nous avons développé, à l'échelle du peuplement, un modèle mécaniste pour simuler les flux à court terme du carbone (C) et de l'eau pour une forêt mélangée feuillus résineux dans le Nord de la Belgique (51°31' N, 4°22' E). Le modèle, nommé SECRETS, est un simulateur séquentiel, multi-espèces et multi-couches qui utilise des modules mécanistes adaptés de différentes origines. Nommément, nous avons adapté les modèles BIOMASS (entretien de la respiration et bilan en eau), et codé le modèle soleil/ombre (photosynthèse; modifié pour les espèces forestières), et GRASSLAND DYNAMICS (carbone et azote du sol). Dans cette contribution nous simulons les flux de carbone pour un peuplement de 70 ans de Pin sylvestre (*Pinus sylvestris* L.) et introduisons une approche pour caractériser les incertitudes dans les sorties du modèle. La production primaire annuelle simulée (GPP) pour 1997 et 1998 était de 1965 et 1888 g C m⁻², respectivement. La respiration du sol représentait 25 % (495 g C m⁻² a⁻¹) et 27 % (505 g C m⁻² a⁻¹) du GPP en 1997 et 1998, respectivement, dans ce peuplement de Pin sylvestre à faible croissance. La respiration hétérotrophe (R_H) représente, environ, 32 % de l'efflux total du carbone du sol pour les deux années. Les flux journaliers simulés pour l'échange net de l'écosystème (NEE) suggère un prélèvement de C pour la plupart de la durée, mais pas pour tout, du printemps et de l'été, alors que la libération nette se ferait pendant la période entre la mi-automne et le début de l'hiver et ce pour les deux années. Notre estimation de base pour NEE variait de 385 g C m⁻² a⁻¹ en 1997 à 310 g C m⁻² a⁻¹ en 1998. Cependant, l'incertitude sur NEE variait de 167 à 509 g C m⁻² a⁻¹ et 138 à 392 g C m⁻² a⁻¹ en 1997 et 1998,

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respectivement. Ainsi, ce peuplement pourrait accumuler du C au rythme de 138 à 509 g C m⁻² a⁻¹ selon les caractéristiques probables du peuplement et du site, de la physiologie de l'arbre, et de la variation locale du temps.

échange net de l'écosystème / bilan de carbone / biomasse microbienne

1. INTRODUCTION

Forest management directives call for an analysis of the current status, and the expected future role, of terrestrial ecosystems in the total global carbon (C) balance (i.e., the United Nations Framework Convention on Climate Change (UNFCCC) and the Kyoto Protocol). This mandate necessitates both an analysis of the current standing stock of C as well as a determination, both in time and in space, of the C flux between forest vegetation and the atmosphere. Stand inventory data, either extant or proposed, as well as harvest inventories may be used to determine the net C storage. However, simulation models or other efforts [e.g., 26], are required to evaluate the spatial and temporal dynamics of terrestrial C fluxes [e.g., 17]. Furthermore, soil organic C, largely ignored in traditional C budget investigations [c.f.r., 18], has become a central focus in "closing" the C budget; over one-half of the C accumulated in forests may reside in the soil as organic matter [31, 41]. Of course, the critical issue is whether forests (and other terrestrial systems) act as sources or sinks of C, and why? Process models serve as one approach to evaluate the potential of a forest to sequester C as a means to help mitigate globally increasing CO₂ concentrations.

Simulating the dynamics of C and water fluxes in European forests presents a unique challenge because many European forests are small and heterogeneous, composed of several species with varying age classes. In addition, and perhaps more important, they are inter-mixed among urban and rural developments which results in a patchy, discontinuous forest landscape. Latitudinal changes in edaphic and climatic variables, and anthropomorphic disturbance along with the patchy mixed-species associations further complicates modeling efforts. Generalized, stand-level models that can be scaled to broader spatial and temporal scales offer distinct advantages in this context. At present, no process models are currently available to assess C and water budgets of these multiple-patch forest ecosystems. The model described here was initially conceived to simulate the canopy carbon fluxes of a very patchy and heterogeneous forest in the Northern Campine region (Belgium). This forest has complex overstory and understory species associations [7]. From this detailed and complex effort a more generic multi-species and multiple patch

model has been developed for homogeneous or heterogeneous forests.

A rigorous C balance requires a complete C cycle; both above- and below-ground processes associated with CO₂ flux must be included. Unfortunately, the contribution of soil microorganisms (heterotrophic respiration, R_H) to total soil CO₂ efflux are not well known. As such, empirical models are often used to estimate soil CO₂ efflux using soil temperature as a driving variable [21, 31]. In this case autotrophic and R_H cannot be evaluated separately. While appropriate in many instances, separating these fluxes may, when feasible, help elucidate the causal mechanisms associated with surface and soil organic matter (SOM) degradation and, therefore, soil CO₂ evolution.

Our objectives were to develop a mass-balance, short-term, stand-scale process model to evaluate C and water fluxes from a mixed coniferous/deciduous Belgian forest. We combined, or coded, "process modules" from several models to develop SECRETS, a patch to ecosystem multiple-species, multi-structure, sequential simulator. To introduce this model and to evaluate model performance we conducted simulations for a pure Scots pine (*Pinus sylvestris* L.) stand in Northern Belgium; we were able to comfortably parameterize the full model for this species using on-site empirical data from numerous studies. In this paper we present model development, C budgets, and simulations of soil respiration (root and R_H) and NEE, along with our estimates of uncertainty in these outputs, for a Scots pine stand.

2. MATERIALS AND METHODS

2.1. Site description

The field site is an even-aged, 70-year-old Scots pine (*Pinus sylvestris* L.) stand, representing a portion of a 150 ha mixed coniferous/deciduous forest – De Inslag – in Brasschaat (51°18'33" N, 4°31'14" E), in the Belgian Campine region, Northern Belgium. Our research (and protocol) was within the framework of the European ECO-CRAFT (European collaboration on CO₂ responses applied to forests and trees) and EUROFLUX (i.e., long-term carbon dioxide and water vapor fluxes of European

Table I. Stand characteristics of a 70-year-old Scots pine (*Pinus sylvestris* L.) stand examined in this study located in the Campine region, Northern Belgium at the beginning of 1997.

Stand parameter	Units	Value	Reference
Average DBH	m	0.27	[4]
Average tree height	m	20.6	"
Average canopy depth	m	3.7	"
Stand density	stems ha ⁻¹	556	[13]
Basal area	m ² ha ⁻¹	31.2	"
Standing wood volume	m ³	300	"
Wood volume increment:	m ³ ha ⁻¹ a ⁻¹		
1988–1995		8.1	[29]
1995–1998		6–7	[13]

forests and interactions with the climate system) networks. The stand is a level II observation plot of the European program for intensive monitoring of forest ecosystems (EC regulation No 3528/86), managed by the Institute for Forestry and Game Management (Flanders, Belgium). Stand structure summary data may be found in *table I*. Mean long-term annual temperature at the site is 9.8 °C, with 3 °C and 18 °C as mean temperatures of the coldest and warmest months, respectively. Mean annual precipitation is 767 mm; rainfall is fairly evenly distributed throughout the year but with slightly higher precipitation often occurring during July or August. The study site has a flat topography (slope less than 0.3%), situated at an elevation of 16 m. The pine forest has an open canopy, with a mean canopy gap fraction of 35% [4] and a peak projected leaf area index (LAI; m² m⁻²), for 1997, of 1.91 [9]. The sparse canopy permitted, in the past, a vigorous undergrowth of black cherry (*Prunus serotina* Ehrh.) and rhododendron (*Rhododendron ponticum* L.), that was completely removed in 1993, leaving only a moss layer dominated by *Hypnum cupressiforme* (Hedw.) covering about 30% of the soil surface area. Needle analysis has shown the stand to be low in magnesium and phosphorus [32, 47]. Needle nitrogen (N) concentrations were optimal as the site is located in an area with high NO_x and ammonia deposition [29, 30].

The upper soil layer is ca. 1.8 m thick, consisting of aeolian Northern Campine cover sand (Dryas III). Beneath this sand layer, at a depth of 1.5 to 2 m, lies a clay lens (Tiglian) and, deeper still, more sand (sands of Brasschaat, Pretiglian; [2]). The soil has been described as a moderately wet sandy soil with a distinct humus and/or iron B-horizon. Due to the clay layer the site has poor drainage. The soil is moist and often saturated, with a high hydraulic conductivity in the upper soil layers (sand). Groundwater is normally at 1.2 to 1.5 m [2].

2.2. Model development

2.2.1. Model structure

The model, termed SECRETS (Stand to Ecosystem CaRbon and EvapoTranspiration Simulator), was written in Digital, visual FORTRAN 95 [37]. The model runs on a daily time step, except for photosynthesis that runs on an hourly (or user defined) time step (*figure 1*). We modified the process model BIOMASS [23], as adapted for loblolly pine (*P. taeda* L.) [36] to create the internal structure for SECRETS. Four major changes to BIOMASS were made. First, the radiation interception, photosynthesis, and C storage and partitioning subroutines were removed. Second, the model was modified to permit multiple input files, one for a simulation control file, and one for each species to be simulated. Third, a common module was written to enable sequential simulation of multiple “patches”, where a patch represents a species, or a combination of species (overstory alone, or overstory with substory or understory species combinations). For patches with more than one species present, biotic and abiotic variables from the overstory species are “passed” to the patch-mate; substory or understory species within the patch have, logically, secondary access to available photosynthetically active radiation (PAR) within the sequence of the daily time step. Access to precipitation and soil available water by substory or understory species (if present) was more difficult to code. Rainfall dynamics and soil water availability and use are discussed in detail below.

For simulations with more than one patch present, patches are area-weighted for the main output variables. Although nine separate patch combinations are possible in the current model structure, in this contribution we address simulations from a Scots pine stand with no substory or understory present. Lastly, process modules from a variety of sources are included to develop a simple, robust model with respect to short-term C and water fluxes. Each of these modules is discussed in appropriate detail below.

2.2.2. Model processes

2.2.2.1. Photosynthesis

The sun/shade photosynthesis model [6], was coded for single-layer and multi-layer options for SECRETS. A minor modification adapted the model for deciduous and coniferous forest applications. Specifically, we modified the input to permit species-specific photosynthetic parameters and structure-specific parameters of the forest canopy.

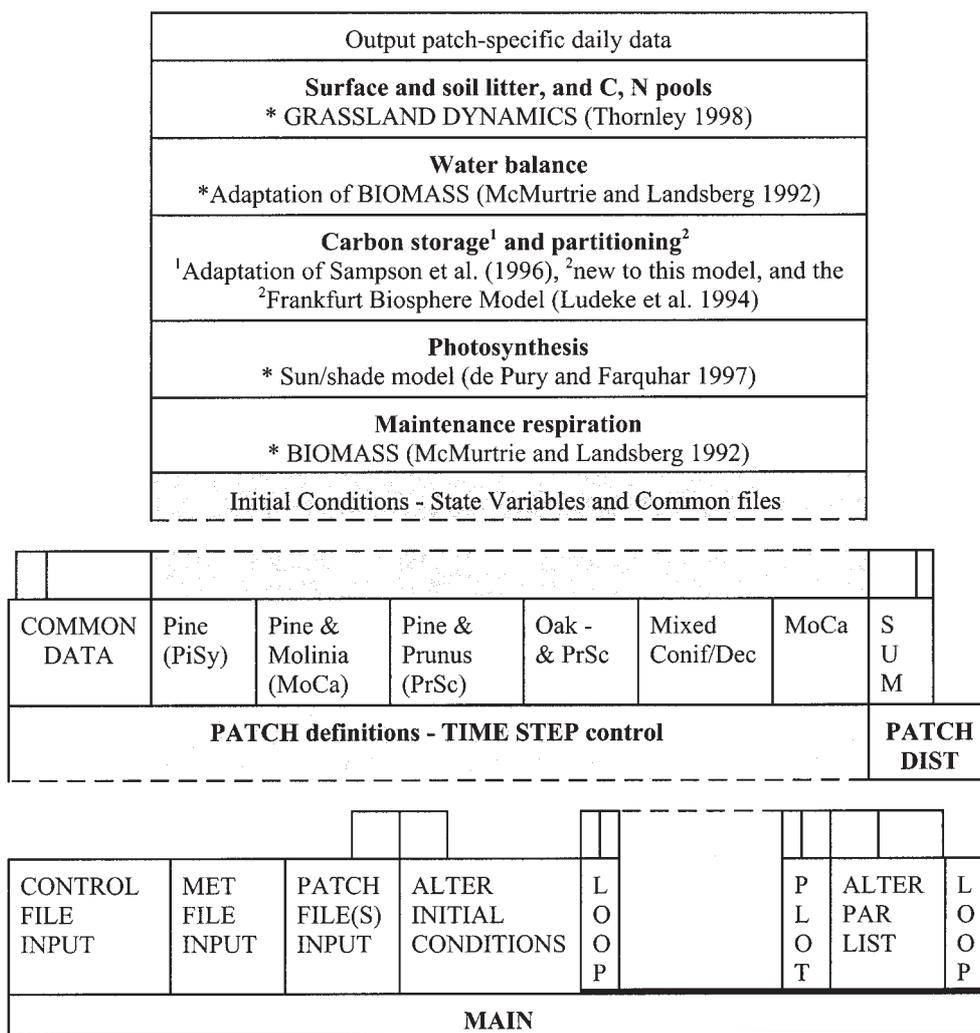


Figure 1. Schematic flow-chart with the structure and process modules of the model SECRETS. The model enables simulation of multiple patches within the run sequence, although only the pine (*Pinus sylvestris* L.) is depicted here. Process modules were either borrowed directly from the author, with permission, or coded from manuscript.

The sun/shade model was written as a simplified model of photosynthesis based on the Farquhar [8] biochemical formulation. This model (single and multi-layer simulations) compared well for wheat, against more complex, and computationally intensive, multi-layer models. An adaptation of this model was well suited for our purposes because an improved “big-leaf” model is valuable for applications where: (i) limited information on canopy structure is available, or (ii) multiple species and multiple structures are simulated.

The sun/shade model has a strong dependence on foliage nitrogen (N) concentration and, thus, canopy N content. Accordingly, V_{CMAX} (maximum rate of Rubisco activity) and J_{MAX} (potential electron transport rate) are estimated for sun and shade foliage from a canopy N profile [6]. However, a canopy analysis in 1997 from this site found no statistically significant canopy N profile [12]. Moreover, the foliage N concentrations are so high (~2.03%) as to be considered saturating. Thus, we modified the model to include V_{CMAX} as an input

variable; as currently written, V_{CMAX} is assumed constant for all canopy foliage. The parameter J_{MAX} is estimated from V_{CMAX} as originally developed in the sun/shade formulation [6].

The sun/shade model is essentially a reformulation of the principles of the big-leaf model. The model uses an adaptation of the Beer-Lambert [25] equation to estimate canopy light interception and, thus, the assumptions of a uniform, homogeneous canopy are violated. Therefore, we provide adjustments to account for the discontinuous leaf distribution found in Scots pine canopies.

In SECRETS we account for inter- and intra-crown clumping. For inter-crown clumping we introduce a factor to reduce “effective” PAR interception [c.f.r., 39]. The equation acts, in principle, to leave intact the attenuation of PAR for a continuous canopy while reducing effective light capture when the solar angle rises above the canopy plane. Specifically, hourly PAR interception is reduced by η as:

$$\eta = 1 - \phi \exp\left(\frac{-\phi \text{LAI}}{\cos(\theta)}\right) \quad (1)$$

where: η = PAR interception reduction factor (scaled from $1 - \phi$ to 1),

ϕ = gap fraction (proportional; 0 to 1),

LAI = leaf area index, and

θ = zenith solar angle (in degrees).

If solar altitude was to reach zenith, PAR interception would be reduced by canopy gap fraction. Because we simulate photosynthesis on an hourly time step, this factor varies over the course of the day and the day of year (changing solar azimuth).

We also reduce effective PAR interception as influenced by intra-crown foliage clumping. Our Phi term (Jarvis, personal communication) is a direct multiplier on LAI in the modified Beer-Lambert algorithm as found in the sun/shade model.

We estimate diffuse and direct beam PAR interception by sun and shade leaves [43]. Missing values for shortwave radiation are estimated from empirical equations [3]. Hourly PAR is read as input into the model. For those days with missing hourly PAR values, we estimate PAR using a diurnal relative PAR trend and incident shortwave.

2.2.2.2 Maintenance respiration

The original formulation for autotrophic maintenance respiration (R_A) from BIOMASS [23] was retained and adapted with two minor modifications. First, soil temperature was added as a driver variable for fine and

coarse root respiration. Second, a reference temperature of 15 °C was added to the respiration function.

Estimates of woody tissue respiration are calculated from sapwood biomass. We estimate stem sapwood biomass as 1 minus the ratio of heartwood to total tree radius. For simplification we assume that branch wood has equal proportions of heartwood to sapwood as stemwood. Fine and coarse roots are assumed to be comprised entirely of sapwood xylem tissue.

2.2.2.3 Carbon partitioning

Because we are principally interested in short term fluxes (i.e., one year), we have developed a simple carbon partitioning schema. However, we have also included into SECRETS a modification of the C partitioning scheme found in the Frankfurt Biosphere model [22]. For this exercise only the simplified approach will be discussed.

Carbon partitioning incorporates labile carbon storage (soluble sugars and starch) as well as daily net canopy assimilation (GPP minus R_A), and it follows a hierarchy starting with foliage production. We estimate foliage production from projected LAI (input). First, we assume two foliage cohorts present in the canopy at maximum LAI. Thus, foliage production for the current year is assumed to be one-half the total LAI at peak leaf area (converted to mass units). Then, using either linear (normalized to a daily production rate), or logistic (first derivative multiplied by cohort production) equations, the model calculates daily foliage production (dFoldt) between the day with minimum LAI to peak LAI. The parameters required to fit both equations are calculated at the start of the simulation period. The empirical estimate of foliage production (if present) is subtracted from the simulated estimate of daily net assimilate, along with an estimate of foliage construction respiration (foliage R_C). If daily assimilate is negative, or if the estimated foliage production plus foliage R_C is higher than available assimilate, C is removed from labile C storage in an amount necessary to meet production and foliage R_C requirements. Carbon storage is assumed proportional to standing biomass (5% for stem, and 12% for foliage and fine roots) [36]. A similar approach is used for fine roots, although fine root production is estimated from needle-litterfall [27]. Fine root mortality is assumed proportional to foliage litterfall and, although root production and root sloughing occur throughout the year, we assume an annualized steady state.

Any additional growth (beyond foliage and fine root production) is determined by the daily status of net assimilate (positive or negative C balance), the current state of the labile C storage pool, and the growth phenology (for stems, branches, and coarse roots). Within the

active growing season (as determined by phenology), any assimilate available after fine root production (if present) is treated as a generic C pool to be used for stem, branch, and coarse root (> 2 mm ; including tap root) production (SBCR). The allocation coefficients among these tissues are determined by the relative mass of each tissue at the start of the simulation cycle. We assume proportionality among these tissue components over time, an assumption that is only valid for mature trees.

We use species-specific coefficients to define the maximum, relative growth potential of combined SBCR production (daily basis). These coefficients allocate a fraction of daily net assimilate, if any is available after foliage and/or fine root production (if applicable) to labile storage. This insures that by the end of the simulation cycle the labile carbon content is near unity to the initial labile storage (adjusted to a mass basis because of growth). Coarse root production can occur independently of stem and branch production, depending the daily status of net assimilate, the current state of the labile C storage pool, and growth phenology. Tissue R_C fractions are from the literature [5].

The LAI data from Gond et al. [9] indicate senescence of the two-year-old foliage cohort during the current-year cohort production. Thus, we calculate this foliage litter-fall between minimum and peak leaf area as the difference between that estimated from half total LAI at peak leaf area and that determined from the absolute difference in LAI during this period. This too is calculated on the first time step, with a daily estimate calculated as the absolute amount divided by the number of days between minimum and peak leaf area. Foliage senescence during other times of the year is calculated as the daily difference in LAI.

2.2.2.4. Water balance

The original formulation of water balance found in BIOMASS was retained in this model. Small changes were necessary to accommodate the hourly time-step for canopy conductance, and the inclusion of multiple species and multiple patch simulations. Because this is a sequential model, water balance must follow hierarchies in the simulation time line. Obviously, it is relatively simple to establish a hierarchy in the reduction of rainfall by successive layers, via canopy interception and, subsequently, evaporation of rain water (i.e., overstory > understory > surface litter). However, once water has percolated through the surface litter, access to available soil water (from a modeling perspective) becomes more convoluted. Thus, for patches with more than one species present, the overstory species has first access to soil water (i.e., for transpiration); water lost through transpiration is subtracted from the available

water column prior to access by the accompanying patch species. Obviously, species would compete for soil water based on fine root density, rhizosphere activity by microrhizal associations, and the distribution within the soil profile. However, soil water is rarely, if ever, limiting on this site. Soil available water is estimated from the percent sand and clay fraction [38].

2.2.2.5. Soil carbon and nitrogen

The surface and soil module of the GRASSLAND DYNAMICS simulation model [45], was coded and included into SECRETS. We choose this model because it incorporates the pertinent soil biogeochemical processes found in forest ecosystems. Please consult the GRASSLAND DYNAMICS reference for details [45]. Parameterization of the surface and soil sub-module included both a re-fitting of the temperature dependence function $f(T)$ for the biochemical processes and calibration of the C and N inputs.

The parameters of $f(T)$ were estimated for our site. Namely, the temperature function was fit to soil CO_2 efflux data from the site for 1997 [13] using nonlinear least squares curve fitting ($r^2 = 0.73$, $n = 23$). A reference temperature (15 °C) and the maximum temperature (35 °C) were thus obtained. The scaling parameter, (mft), was determined by iteration in the equilibrium exercise as discussed below.

Daily C and N inputs and outputs from the surface and soil sub-module are determined by needle litter-fall (C and N), fine root turnover (C and N), root exudation (C), and nitrogen deposition with N removed for above-ground growth. Because we assume steady-state, fine root turnover is scaled linearly with production. The associated N inputs from needle litter and fine roots depend on the C to N ratios.

GRASSLAND DYNAMICS simulates root exudation into a soluble C pool. Because we lack experimental data, we estimate root exudation as a fraction of the standing fine root biomass, the C to N ratio of fine roots, and soil temperature and water availability. Namely, we assume that 20% of fine root biomass (in carbon units) is metabolically active. This substrate C is multiplied by an asymptotic scalar; $Y = a X^B$ where Y is relative (zero to one) allocation to root exudates, and X is the fine root C to N ratio. The exponent, B , was determined by assuming a scalar value of 0.5 for a C to N ratio of 50. Finally, this value is multiplied by the daily temperature and water dependence functions. The final estimate of root exudation, however, depends on daily net assimilate. If available assimilate is zero, then root exudation equals zero. If the estimate is less than 7% of daily available assimilate, then it is used. Otherwise, we assume root exudation to be 7% of daily assimilate.

While perhaps strictly a conceptual formality, root exudates are important for ecosystem function [c.f.r., 45].

Nitrogen deposition is assumed to be 60 kg N ha⁻¹ a⁻¹ [30], with equal amounts deposited daily. Nitrogen removed from the soil N pools is calculated from biomass growth and the C to N ratios of each tissue. Because the soil C and N module is very sensitive to inputs, and because we lack a clear understanding of fine root dynamics, we assume that fine root N additions and removals are in steady state; their fluxes are ignored. We have also included a quasi N retranslocation within the canopy by comparing N concentrations of living versus senescent foliage and, by calculating the difference in N content, foliage dropped as needle litter-fall is adjusted to reflect the N removed prior to senescence. Lastly, for lack of a better approach, we use the daily ratio of the NO₃ to NH₄ pools to calculate the proportion of each used in tissue production.

2.2.2.6. Added biophysical equations

We estimate hourly leaf temperature (T) and relative humidity (RH) from daily maximum and minimum meteorological input data (air temperature at 10 m). We use a cosine function to estimate leaf T and a sine function to estimate RH . We assume minimum leaf temperatures and maximum RH at dawn, and a maximum T at mid-day (average T and minimum RH at dusk).

2.3. Parameterization and inputs

A complete description of additional variables in SECRETS not addressed above may be found in their original documentation; namely, maintenance respiration and water balance [23], photosynthesis [6], and soil C and N [45]. Input parameters for the simulations conducted here may be found in *tables A-1 to A-5* (Appendix I).

Equilibrium simulations were necessary to stabilize the soil C and N state variables. Accordingly, our procedure to obtain quasi equilibrium was as follows. First, the meteorological data from 1997 were duplicated to create data sets for a 300-year simulation. Based on the work by Thornley [42] it was determined that all pools in the system would equilibrate by year 300. Second, steady state LAI was used with the seasonal pattern in LAI observed for 1997 applied in each yearly simulation. Steady state soil water, N, and C inputs/conditions were retained from the first year to be used in each subsequent year of the equilibrium runs.

Equilibrium conditions required an iterative process of finding stable initial estimates for each state variable in relation to each other and with respect to the biochem-

ical influences and C and N inputs. We had reasonably good estimates of surface and soil C, except for the soluble C pool and the microbial population (*table A-5*). And, although we had crude estimates of total soil N, there was much uncertainty. For both C and N, the relative proportion among pools (i.e., unprotected, versus protected and stable) was unknown; we used proportional states as that found in GRASSLAND DYNAMICS [45]. And, for lack of better site estimates, the rate variables were assumed comparable to those found in GRASSLAND DYNAMICS [45] when no additional information was available.

We found it necessary to modify a few parameter estimates to obtain stable, reasonable behavior [45]. First, it was necessary to reduce the maximum potential microbial biomass population to 3.5% of the total SOM pool (5%, [45]) to permit stable run simulations; the N inputs would not sustain a larger maximal population. Second, and in conjunction, we found it necessary to increase the asymptotic scaler for microbial growth dependence on soluble C; this was necessary to insure a positive, stable soluble C pool. Lastly, we decreased the temperature scaler, mentioned above, from 1, to obtain a target C accumulation after 100 years roughly comparable to literature values [11].

Equilibrium simulations were run for 300 years. We used the relative proportion among pools (e.g., surface to soil C, and protected, unprotected, and stable SOM pools – C and N) to determine the initial states (*table A-5*). And, we used the 300-year output estimates for the NH₄, NO₃, and the soluble C pools. After re-parameterization of the state variables we determined that a stable microbial population could be obtained after one year. Thus, we replicated the 1997 and 1998 meteorological files twice to use the 365 to 730 day-of-year outputs for each year for our heterotrophic respiration estimates.

2.4. Uncertainty intervals

A sensitivity analysis determined that four parameters in the model are most influential in markedly changing the magnitude of model outputs. These include V_{CMAX} , LAI, the within-canopy gap fraction, and the soil temperature reaction scaler. Equilibrium simulations provided an estimate for the soil temperature scaler.

An approach was developed to capture inherent uncertainty in the three remaining input estimates as an interval of uncertainty in the model outputs. Specifically, we arrayed these three parameters by varying each one separately in simulations while holding the other two constant and, thereby, obtained an output array of uncertainty. The V_{CMAX} parameter for Scots pine was

Table II. Parameters, parameter description, and input values used to generate the three levels of output uncertainty in net ecosystem exchange simulated in this study.

Parameter	Description	Units	Parameter values	
			base	IOU*
V_{CMAX}	Maximum carboxylation velocity	$\mu\text{mol m}^{-2} \text{proj. s}^{-1}$	73	$\pm 20.6^+$
LAI	Leaf area index	$\text{m}^2 \text{m}^{-2}$	variable	$\pm 10\%$
Phi	Within crown clumping factor	%	35	$\pm 10\%$

* Interval of uncertainty. A matrix of all combinations of these parameter values was generated, with maximum, minimum and base response outputs examined.

⁺ Represents two standard errors of the mean.

estimated as $(73 \pm 10.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1})$ (de Pury, unpublished data). Uncertainty for V_{CMAX} was evaluated using \pm two standard errors of the mean (*table II*). The seasonal pattern in LAI for 1997 was estimated using the LI-COR LAI-2000 [9], and corrected for shoot silhouette area index. Uncertainty in LAI and the canopy gap fraction was assumed $\pm 10\%$ of the “base” estimate (Sampson et al., unpublished data). Our estimate of within-crown foliage clumping was 35%. This parameter was varied by 10%. The intervals of uncertainty for the model outputs were chosen as the maximum, minimum, and base response (“best” estimate of these three parameters). Equilibrium simulations for each interval examined were conducted.

2.5. Simulations conducted

We conducted simulations for 1997 and 1998. Results focus on the fluxes of root autotrophic respiration (R_A), soil heterotrophic respiration, and net ecosystem exchange ($\text{NEE} = \text{gross primary productivity} - R_A - R_H - R_C - \text{root exudates}$). However, we also provide complete carbon budgets to verify the model predictions to empirical estimates of growth. Simulation outputs for soil respiration (R_A and R_H) are graphically presented as a negative flux.

3. RESULTS

3.1. Carbon budgets

Simulated base estimates of gross primary productivity (GPP) were 1965 and 1888 $\text{g C m}^{-2} \text{ a}^{-1}$ for 1997 and 1998, respectively (*table III*). However, uncertainty in LAI and foliage clumping, and random sampling error in the maximum carboxylation rate yielded a boundary interval ranging from, roughly, -25% to $+20\%$ differ-

ence in GPP for both years (*table III*). Simulated net canopy assimilation was about 29% of base GPP for both years. Heterotrophic respiration (R_H) accounted for about 32% of total soil C efflux (*table III*). Together, soil autotrophic and R_H averaged 32% of the net C release from this pine stand in 1997 and 1998. Net ecosystem exchange (NEE) varied from 358 $\text{g C m}^{-2} \text{ a}^{-1}$ in 1997 to 310 $\text{g C m}^{-2} \text{ a}^{-1}$ in 1998. But, uncertainty intervals for NEE indicated a reduction of -53% in the base estimate to an increase of $+42\%$ for 1997, with a slightly narrower range observed for 1998 (-55% to $+26\%$) (*table III*).

Simulated stemwood production (base estimate) was similar to our empirical estimate for 1997 (*table IV*). The 1997 estimates of soil C efflux from simulations, however, were about 60% higher than that found for the empirical data.

Annual net primary productivity (NPP), tissue component production, and tissue construction respiration were very similar between 1997 and 1998. We therefore averaged them over the two years for both intervals of uncertainty and the base estimates. These data, along with the complete carbon budget (without reproductive

Table III. Annual, simulated carbon fluxes and (interval of) uncertainty, in $\text{g C m}^{-2} \text{ a}^{-1}$, for a 70-year-old Scots pine stand in Northern Belgium using the process model SECRETS.

Parameter	1997 estimate	1998 estimate
GPP	1965 (1459–2440)	1888 (1412–2325)
Net canopy assimilation ⁽¹⁾	586 (367–727)	522 (329–633)
Soil autotrophic respiration	$376 \pm 0.3\%$	$381 \pm 0.5\%$
Heterotrophic respiration (R_H)	$119 \pm 16\%$	$124 \pm 4\%$
Net ecosystem exchange ⁽²⁾	358 (167–509)	310 (138–392)

⁽¹⁾ GPP minus autotrophic respiration.

⁽²⁾ Net canopy assimilation minus construction respiration, root exudates, and R_H .

Table IV. A comparison of carbon fluxes (g C m⁻² a⁻¹) from the empirical and simulation estimates for 1997.

Parameter	Reference	Empirical Estimate	Simulated with SECRETS
Stem growth increment	[12]	180	190
Soil release	[12]	310	495
Autotrophic	n.a.*	140	376
Heterotrophic	n.a.	170	119

* n.a. = not applicable.

structures) for this 70-year-old Scots pine stand are summarized in *table V*.

3.2. Carbon fluxes

Although root respiration accounted for 76% of the total soil C efflux, there were distinct seasonal and inter-annual variations in the relative importance of R_H to total soil CO₂ evolution (*figure 2*). As would be expected, simulated root respiration mirrored the seasonal pattern in soil temperature, while R_H responded more markedly to daily changes in soil temperature and available water (*figure 2*). Heterotrophic respiration was manifest when soil temperature reached, roughly, 5 °C and, as soil temperatures increased and soil available water began to decline, microbial activity oscillated almost daily, and often dramatically, with changes in soil environmental conditions. Heterotrophic respiration accounted for >45% of the soil CO₂ efflux for brief periods in the spring, with total soil CO₂ flux approaching 2.5 μmol m⁻² s⁻¹ by mid-summer 1997; soil CO₂ flux peaked slightly lower in the summer of 1998 (*figure 2*). Clear temperature effects on R_H are evident around day 450 (late March 1998 – designated with “T”). A reduction in soil temperature by 6 °C decreased R_H by almost one-third. Marginally more important to total soil CO₂ flux in 1998, R_H had broader diurnal fluxes with lower winter temperatures in 1998 that resulted in increased soil CO₂ efflux when compared to 1997.

The uncertainty array resulted in a pronounced difference in the seasonal trends in the upper and lower intervals of mean, daily NEE (*figure 3*). The upper interval reached 7 μmol CO₂ m⁻² s⁻¹ in 1997 during maximum radiation periods and seasonally high LAI. Peak values were essentially identical in 1998. Simulated NEE for the lower interval, in contrast, barely reached 3 μmol CO₂ m⁻² s⁻¹ in both years. Separation between these “boundary” conditions was greatest during spring and early summer, with common trends observed between

Table V. Average annual simulated carbon budgets (g C m⁻² a⁻¹) for a 70-year-old Scots pine stand in Northern Belgium using the process model SECRETS. The intervals of uncertainty (IOU) were generated by varying leaf area index by ±10%, maximum carboxylation velocity by ±2 standard errors of the mean, and the intra-canopy gap factor (Phi) by ±10% from base estimates one factor at a time, and choosing the minimum and maximum response.

Ecosystem Parameter	High IOU	Low IOU	Base estimate
Net Canopy Assimilation	680	348	554
NPP			
Stems	237	59	170
Branches	44	11	31
Coarse Roots	42	10	30
Foliage	136	111	124
Fine Roots (< 1 mm)	97	88	92
Sub-total	556	279	447
R_M			
Stems	177	173	176
Branches	33	32	32
Coarse Roots	116	113	115
Fine Roots	264	264	264
Foliage	1 112	506	786
Sub-total	1 702	1 088	1 373
R_C			
Stems	29	8	21
Branches	5	1	4
Coarse Roots	5	1	4
Fine Roots	16	14	26
Foliage	22	18	20
Sub-total	77	42	63
Root Exudates	31	25	35
Unknown	3	5	4

1997 and 1998. Both intervals of NEE exhibited negative fluxes throughout the year, however early autumn and winter net CO₂ release was higher than uptake for both intervals when compared to spring or summer periods (*figure 3*). In addition, 1998 exhibited an earlier autumnal decline in available assimilate; net CO₂ release was initiated earlier in the year, already starting in September.

4. DISCUSSION

Inherent random error in parameter estimates, and the resulting effect on the year-end C budgets for this Scots pine stand, underscores the importance of uncertainty in simulation outputs. Subtle differences in the ecophysiological inputs, all within “normal” (acceptable) random error, can yield dramatic differences in simulated NEE.

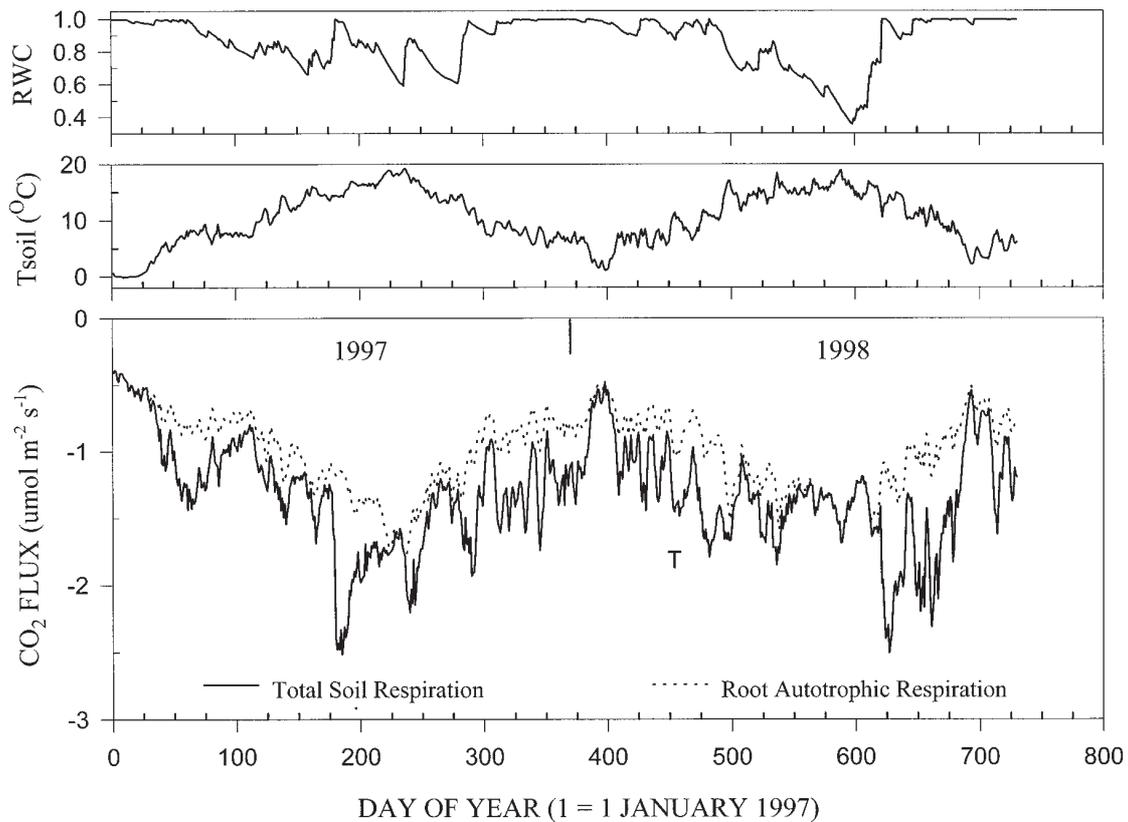


Figure 2. Soil available water (RWC) (top panel), soil temperature at 10 cm (middle panel), and simulated root autotrophic respiration (dashed line) and total soil CO_2 efflux (solid line) (bottom panel) starting in 1997 in a 70-year-old Scots pine (*Pinus sylvestris* L.) stand in the Campine region, Northern Belgium. Heterotrophic respiration represents the difference between total CO_2 efflux and root autotrophic respiration.

Our lower interval of NEE was 53% less than base simulations, either of which may be correct. When calculating the difference between two large, and nearly equivalent but opposite in sign, C fluxes (gross photosynthesis and total ecosystem respiration), relatively small changes in either estimate can result in divergent, or even opposing conclusions [10, 44]. And, upscaling processes that occur at small scales to larger spatial and temporal scales is subject to large errors due to heterogeneity and patchiness in the distribution of processes, and functional non-linearity [15]. Our results suggest that uncertainties need to be addressed formally and, in this modeling exercise, demonstrate that, indeed, conclusions regarding net ecosystem fluxes are subject to multiple interpretation depending on “base” parameterization.

Slightly higher GPP and, subsequently, higher productivity in 1997 can be explained by increased PAR

intercepted in 1997 despite lower than average rainfall (table VI). It appears that GPP was more limited by PAR than precipitation in 1997; soil available water, although at times reduced to 40% available, was adequate for reasonable growth to occur.

Table VI. Inter-annual variability in the climate drivers influencing gross primary productivity for the 1997 and 1998 simulations.

Driving variables	Units	1997	1998
Incident PAR intercepted ⁽¹⁾	$\text{MJ m}^{-2} \text{a}^{-1}$	1 032	852
Rainfall	mm a^{-1}	658	1 042

⁽¹⁾ $0.5 \times \text{incident shortwave radiation} \times (\text{fraction of absorbed PAR (fapar)}) \times (1 - \text{fraction PAR reflected})$.

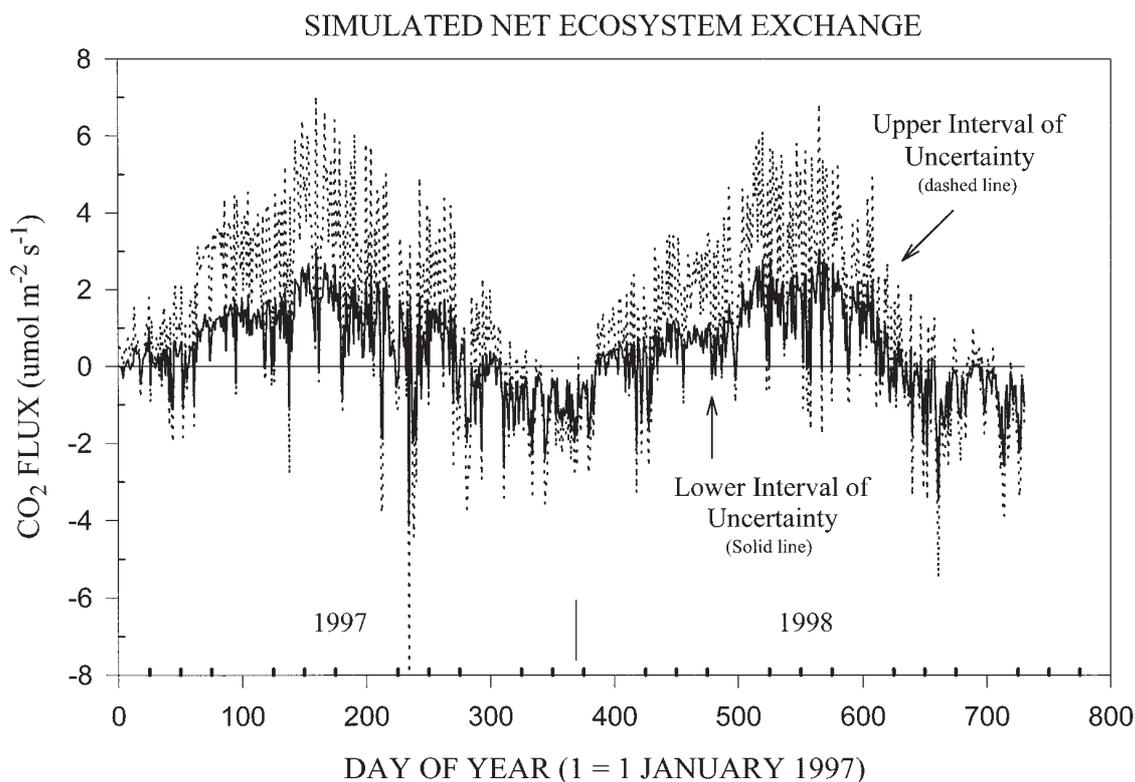


Figure 3. Simulated net ecosystem exchange (gross primary productivity minus construction, autotrophic, and heterotrophic respiration) for two levels of uncertainty starting with the 1997 calendar year in a 70-year-old Scots pine (*Pinus sylvestris* L.) stand in the Campine region, Northern Belgium. Uncertainty was estimated by varying three “sensitive” input parameters (see text) in all combinations, and choosing outputs that reflected the maximum (upper level) and minimum (lower level) response observed.

The stand-scale carbon budgets were comparable to the empirical estimates of productivity for this site. Unit conversion of the stem, branch, and coarse root production yields biomass and volume estimates similar to the empirical analyses [12, 13]. Our estimate of the ratio of net canopy assimilation to GPP, while low, was within the range found in forest ecosystems [c.f.r., 48]. The 1998 outputs (not shown) were nearly identical to the 1997 data because we used similar trends in LAI, and similar assumptions about fine root production and turnover – two important C components of this system. Slight differences in productivity resulted from reduced net canopy assimilation in 1998, however this was offset by warmer winter and early spring temperatures that enabled earlier growth in 1998.

Although simulated soil CO₂ efflux (yearly total) was 60% higher than the empirical estimates, the daily estimates were within one standard deviation of the empirical findings [14]. The year-end budgets did, however,

demonstrate differences in root R_M and the ratio of root R_M to total soil CO₂ efflux that were both higher than that found empirically [12]. However, root R_M simulated here was proportionally similar to that simulated for *P. radiata* [35]. The empirical estimates of soil CO₂ efflux for this site were relatively low and certainly considerably lower than expected [12].

Simulating heterotrophic respiration has provided a means to evaluate the relative, temporal importance of microbial activity on total soil CO₂ efflux. Simulations suggest that broad changes in soil temperature occurring on weekly time scales are important in determining microbial activity. As would be expected, microbial growth and death are sensitive to fluctuations in the soil environment and, thus, soil sampling of CO₂ release and the conclusions drawn will, obviously, be influenced by these temporal dynamics. Although these processes likely operate on much shorter time scales, results presented here indicate emergent, larger scale patterns.

Pulse events in R_H over the course of the year were sufficient to depress net C gain during otherwise nominally favorable growth periods in 1997, and in early autumn of 1998 were sufficient to shift NEE from positive to negative in these simulations (figures 2 and 3).

Our annual estimate of heterotrophic respiration for 1997 was 43% lower than that found from a soda lime study [14]. Although, this technique has been shown to underestimate soil CO_2 efflux, especially at higher fluxes [28]. It is not entirely clear why we found a lower estimate of R_H in this study, however, two possible explanations are possible. Janssens et al. [14] estimated root biomass from only two points in time during the year, and R_H was estimated as the difference between total soil CO_2 efflux and their estimate of root R_M . Thus, if they underestimated root biomass, and the soda lime estimate was low (as expected), then the simulated and empirical estimates would converge. Daily total soil CO_2 efflux was comfortably within one standard deviation of the mean throughout both years [14]. And, although the annual average proportion of total soil C efflux attributed to R_H (~24%) was only half that estimated for this site (54%) [12], the relative contribution of R_H to total soil CO_2 efflux was nearly identical to the empirical findings for brief periods during summer. Upscaling and spatial variability of these processes have large associated errors [14].

While absolute C fluxes are subject to change due to multiple factors (climate, species-specific growth physiology, stand structure, etc.), relative fluxes could be expected to be fairly consistent among similar ecosystem types [c.f.r., 19]. Simulated R_H in this analysis was 25% of net primary production (NPP) and 33% of NEE (for 1997) which are both lower than that reported for Monterrey pine (30% of NPP and 50% of NEE) in New Zealand [e.g., 1]. We suspect that our estimate of R_H is low. Nonetheless, simulated total soil CO_2 efflux was comparable to that observed for similar vegetation complexes, and that predicted for this site from regional based analyses [e.g., 31].

Global simulations have suggested that net ecosystem exchange may be positive or negative for Belgium, in this case depending on the Southern El Nino oscillation [e.g., 16]. Our findings demonstrate that slight differences in stand characterization, and the physiological parameters chosen, could result in concluding that this site is a net C sink for 1997 and 1998, but of a magnitude that could vary from a low of $138 \text{ g C m}^{-2} \text{ a}^{-1}$ to a high of $509 \text{ g C m}^{-2} \text{ a}^{-1}$ (a difference larger than that found for the base simulations) depending, in part, on inter-annual variability in climate. A European study of NEE in terrestrial forest ecosystems using automated eddy covariance measurements observed increasing carbon

uptake with decreasing latitude, apparently independent of GPP [46]. They found what appears to be an asymptotic relationship between the ratio of NEE to total ecosystem respiration and latitude. We found similar ratios (0.28 for 1997; 0.21 for 1998) as that reported by Valentini et al. [46] for our site. The processes associated with these differences, and potential shifts from positive to negative C balance are perhaps best examined in robust, extensive campaigns to examine "complete" forest C budgets. These studies serve to help focus attention on critical issues relating to total stand C balance.

Productivity in this study was relatively low, and the magnitude of our unaccounted carbon sink was negligible. Low LAI and GPP and, thus, slow growth rates would be expected for this 70-year-old Scots pine stand. However, the low growth rates observed here cannot be explained by resource availability; it seems improbable that N availability limits foliage production because N is abundant, if not saturating [32] and water does not appear to limit growth. Reduced growth in this stand may likely be caused by one or several factors related to stand age [e.g., 34], and N saturation [e.g., 42]. High maintenance respiration rates when compared to GPP (low NPP to GPP ratio) may also be attributed to age, although we suspect that Scots pine, at least at this latitude and age, exhibits an inefficient canopy architecture for effective PAR interception. We speculate that high carboxylation rates (table A-4) are necessary to off-set the relatively high foliage dark respiration (table A-4) and generally low LAI found for this species. Although somewhat surprising, our unaccounted C sink was only 0.2% of GPP in these simulations, and substantially lower than that observed in other budgets [e.g., 35].

The model and the model outputs, with the inclusion of additional forest patches, will be used for validation of flux measurements made by eddy correlation techniques. This is particularly relevant since eddy correlation yields flux measurements but lack detailed insight into the various parameters that determine these fluxes, as well as on the response of the fluxes to environmental variables. As more and more flux measuring sites become available, and as accurate techniques are developed, reliable models will be required for flux site comparison and validation. Moreover, several years of data comparisons will be required; simulated NEE in this study for 1998 was 13% lower than the 1997 estimate for base simulation (table III). Inter-annual variability in climate obviously alters the pattern in the C fluxes observed. While this analysis illustrates one potential scenario of the yearly carbon budget for a mature Scots pine stand, further analyses are warranted to examine inter-annual changes in NEE.

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APPENDIX I

Table A-1. Initial standing biomass and leaf area index for the 70-year-old Scots pine (*Pinus sylvestris* L.) stand in the Campine region, Northern Belgium beginning 1997.

Parameter	Units	1997	1998	Reference
Initial Carbon				
Stem	kg C m ⁻²	7.33	7.508	[13]
Branch	"	1.35	1.383	"
Fine roots	"	0.180	0.180	"
Coarse roots	"	1.285	1.311	"
Avg Sapwood radius (bh)	"	0.089	0.089	[4]
Minimum LAI	m ² m ⁻² proj	1.44	1.44	[9]
Peak LAI	m ² m ⁻² proj	1.91	1.91	"
SLA	cm ² g dwt ⁻¹	38.6	38.6	"
Proj to tot LAI	dimensionless	2.45	2.45	Gond (unpublished data)
C/N litter layer	"	27.2	27.2	Janssens (unpublished data)

Table A-2. Parameter inputs for maintenance respiration used in the process model SECRETS; simulations for a 70-year-old Scots pine (*Pinus sylvestris* L.) stand (1977) in the Campine region, Northern Belgium.

Tissue	Units	Basal maintenance respiration	Reference
Stem	mg CO ₂ g ⁻¹ dwt h ⁻¹ (15 °C)	0.012	[33]
Branch	"	0.012	"
Coarse Roots	"	0.048	"
Fine Roots	"	0.54	[12]
Foliage	n.a.	n.a.	[6]
Q ₁₀ stem/bra	dimensionless	2.0	[40]
roots	"	2.0	"
foliage	"	2.0	"

n.a.: Not applicable.

Table A-3. Parameter inputs for soil, litter, and canopy water budgets used in the process model SECRETS; simulations for a 70-year-old Scots pine (*Pinus sylvestris* L.) stand (1977) in the Campine region, Northern Belgium.

Parameter	Units	Estimate	Reference
Sand content 1	%	78	[24]
Clay content 1	%	10	"
Sand content 2	%	84	"
Clay content 2	%	6.7	"
Profile depth	m	1.3	Default
Depth of first layer	"	0.2	"
Day 1 available water	Proportional	0.95	"
Canopy H ₂ O interception	mm LAI ⁻¹	0.5	"
Litter H ₂ O interception	m ³ kg litter ⁻¹	0.0002	Default
Soil diffusivity to conductance	m s ⁻¹	0.4	Default
Soil aerodyn conductance	m s ⁻¹	0.5	Default

Default: Parameters retained from BIOMASS [23].

Table A-4. Parameter inputs for photosynthesis and associated parameters used in the process model SECRETS; simulations for a 70-year-old Scots pine (*Pinus sylvestris* L.) stand (1977) in the Campine region, Northern Belgium.

Parameter	Units	Estimate	Reference
V _{cmax}	μmol CO ₂ m ⁻² proj. s ⁻¹	73	de Pury (unpublished data)
J _{max} /V _{cmax}	dimensionless	2.2	"
Rd	μmol CO ₂ m ⁻² proj. s ⁻¹	4.0	"
BWBL	dimensionless	3.8	Unpublished data
gs (min) ^(A)	mol CO ₂ m ⁻² s ⁻¹	0.02	Default
sigma	dimensionless	0.08	Gond (unpublished data)
Light Extinction (G)	LAI ⁻¹	0.5	Sampson (unpublished data)
Phi ^(B)	dimensionless	0.91	Sampson (unpublished data)
Gap Fraction ^(C)	dimensionless	0.35	"
Foliage N	%	2.039	Janssens (unpublished data)
Canopy aerodyn conductance	m s ⁻¹	6.027	Default
leaf bound layer resistance	s m ⁻¹	35.0	Default

(A): Minimum cuticular stomatal conductance. (B): Within-crown gap correction factor to PAR interception (vis-a-vis Jarvis, personal communication). (C): Between crown gap fraction. Default: Parameters retained from the process model BIOMASS [23].

Table A-5. Parameters for soil carbon and nitrogen used in SECRETS; simulations for a 70-year-old Scots pine (*Pinus sylvestris* L.) stand (1997) in the Campine region, Belgium.

Parameter	Units	Initial Value	300 yr Equilibrium	Reference
Total Litter	kg C m ⁻²	2.85	2.85 ^(A)	[13]
Surface litter C	"	1.65	1.616	Iteration ⁽¹⁾
Soil litter C	"	1.2	1.234	"
Total SOM	kg C m ⁻²	11.6	11.6 ^(A)	[13]
SOM_uC	"	0.5	0.501	From [45] ⁽²⁾
SOM_pC	"	5.7	5.428	"
SOM_sC	"	5.4	5.671	"
Heterotrophic biomass	"	0.21	0.162	Iteration
Soluble C	kg C m ⁻²	0.00025	0.00037 ^(B)	From [45] ⁽²⁾
Total Soil N	kg C m ⁻²		-	[46]
NO ₃	"	0.0003	0.00086	"
NH ₄	"	0.002	0.0037	Iteration
Mft - biochemical	Dimensionless	1.0	0.6	Iteration
C/N foliage litter	Dimensionless	52.8	-	Janssens (unpublished data)
foliage	"	24.46	-	"
fine root xylem	"	38.48	-	"
dead FR	"	39.83	-	"
stem xylem	"	55.15 ^(C)	-	"
branch xylem	"	55.15	-	"
coarse root xylem	"	101.26	-	"
Total N	kg C m ⁻²	10% SOM	-	-
SOM_uN	"	0.06	0.058	Proportions
SOM_pN	"	0.65	0.618	"
SOM_sN	"	0.45	0.436	"

^(A): Day one pools retained and set proportionally to equilibrium outputs, ^(B): Day one pools changed to equilibrium conditions, ^(C): Estimated from branch data. ⁽¹⁾: Multiple runs to obtain stable starting conditions. ⁽²⁾: Reduced proportional to maximum microbe population.

