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Dynamics of soil organic matter in primary and secondary forest succession on sandy soils in The Netherlands: An application of the ROMUL model

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Abstract

We applied the simulation model ROMUL of soil organic matter dynamics in order to analyse and predict forest soil organic matter (SOM) changes following stand growth and also to identify gaps of data and modelling problems. SOM build-up was analysed (a) from bare sand to forest soil during a primary succession in Scots pine forest and (b) on mature forest soil under Douglas fir plantations as an example of secondary succession in The Netherlands. As some of the experimental data were unreliable we compiled a set of various scenarios with different soil moisture regime, initial SOM pools and amount and quality of above and below ground litter input. This allowed us to find the scenarios that reflect the SOM dynamics more realistically. In the Scots pine forest, total litter input was estimated as 0.50 kg m^{-2} $year^{-1}$. Two scenarios were defined for the test runs: (a) forest floor moisture regimes—‘dry, mesic and hydric’ and (b) augmenting a root litter pool with three ratios of needles and branches to roots: 1:1, 1:1.5 and 1:2.0. The scenario finally compiled had the following characteristics: (a) climate for dry site with summer drought and high winter moisture of forest floor; (b) a litter input of 0.25 kg m^{-2} $year^{-1}$ above ground and 0.50 kg m^{-2} $year^{-1}$ below ground; (c) a low nitrogen and ash content in all litter fall fractions. The test runs for the estimation of the initial SOM pools and the amount and proportion of above and below ground litter fall were also performed in the Douglas fir plantation. The inputs of above ground litter tested in various combinations were 0.30 and 0.60 kg m^{-2} $year^{-1}$, and below ground litter 0.30,

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0.60 and 0.90 kg m^{-2} $year^{-1}$. The scenario that fitted the experimental data had an SOM pool of 20–25 kg m^{-2}, an aboveground litter input of 0.6 kg m^{-2} $year^{-1}$and a below ground litter input of 0.9 kg m^{-2} $year^{-1}$. The long-term simulation corresponded well with the observed patterns of soil organic matter accumulation associated with the forest soil development in primary and secondary succession. During primary succession in Scots pine forest on dry sand there is a consistent accumulation of a raw humus forest floor. The soil dynamics in the Douglas fir plantation also coincide with the observed patterns of SOM changes during the secondary succession, with SOM decreasing significantly under young forest, and SOM being restored in the older stands.

Keywords: Simulation model; Primary and secondary succession; Scots pine; Douglas fir; Litter fall; Forest floor dynamics; Soil organic matter changes

1. Introduction

In the last 20 years, there have been rapid developments in the simulation modelling of soil organic matter (SOM) dynamics in relation to forest and agroecological problems, particularly in order to estimate the carbon balance in the biosphere (Powlson et al., 1996; Smith et al., 1997). Yet though there are many models now, few are forest soil models (Chertov et al., 1999). Examples include the Nakane (1978) and Goto et al. (1994) models, which take into account the processes of mineralisation and humification of organic debris for the large-scale evaluation of soil carbon dynamics in forest and other natural ecosystems, and the FORTNITE model by Aber and Melillo (1982) and the LINKAGE model by Pastor and Post (1985), which yield a close correlation of trees' debris decomposition with the actual evapotranspiration and lignin:nitrogen ratio. The LINKAGE model has subsequently been incorporated into forest ecosystem models (Kellomäki et al., 1992). The SOM dynamics model by Thornley and Cannell (1992) takes into account litter fall, SOM pools, and total biomass of all organism destroyers when calculating the nitrogen cycle in detail. The Q (for 'quality') model (Ågren and Bosatta, 1996) is an attempt to apply the authors' mathematical theory of SOM decomposition as a continuum of the loss of substrate quality for micro-organism destroyers. Walse et al. (1998) have compiled a model based on a comprehensive experimental data on the forest litter fall decomposition in Swedish boreal forests. There are also unnamed SOM submodels in most process-based models of forest ecosystems (Tiktak and Van Grinsven, 1995; Pórte and Bartelink, 2002) considering litter input from different cohorts and the mineralisation of SOM with nitrogen release for plant growth.

Two SOM models of grassland and agricultural soils have been used for the simulation of forest and other natural soils. The grassland model CENTURY (Parton et al., 1988) has been tested world-wide (Parton et al., 1993), and also adopted for forest ecosystems (Friend et al., 1997). The agricultural model ROTH-C (Jenkinson et al., 1987) is based on the Rothamsted long-term experimental datasets. Besides numerous agricultural applications, it has also been used for the evaluation of soil carbon dynamics in all biomes at global scale (Post et al., 1996). Nevertheless, we can conclude that most SOM models tend to be used as supplementary modules in the ecosystem models to calculate nutrient supply. Soil dynamics as a factor of vegetation development tends to be ignored (Powlson et al., 1996; Smith et al., 1997).

Most SOM simulators have been developed in the frame of the various ecosystem models. The main feature of these models is that they do not consider a surface organic layer, the forest floor, as an important morphological and functional horizon in all forest soils. These models mostly have various compartments of litter fall that transform to SOM. Perhaps, the first attempt to simulate this specific feature of forest soils is the model of Prusinkiewicz (1977). Yet there are models of forest floor dynamics only (Olson, 1963; Chertov, 1985; Jassal et al., 2004) that ignore the SOM of the mineral soil profile.

One of the main criteria of sustainable forestry is a positive or neutral carbon balance in forest ecosystems (Helsinki Process, 1995; Montreal Process, 1995). It is also relevant for forest protection policy. Boreal and temperate forests are the most extensive accumulators of carbon in living biomass and soil. The accumulation of carbon in soil organic matter is assumed to be a leading macro-process of soil formation in all forest ecosystems. The type of organic matter localisation in soil is a key characteristic and reflects the rate and type of SOM transformation (Wilde, 1958; Duchaufour, 1970; Chertov, 1981). The fundamental ecosystem processes are humus formation (humification) and the mineralisation of plant litter and humus. These are controlled by three main factors: the physical–chemical environment, substrate quality and the decomposer populations (Alexandrova, 1980). Therefore, the quantification of these processes in forest ecosystems is of crucial theoretical and practical importance.

Primary ('ecogenetic') forest succession is a classic example of the natural development of the tree–soil system. On bare sandy soils, it is largely determined by a soil formation process associated with the build-up of soil organic matter.

Primary succession on dry and mesic sites and humus-free sands under temperate and boreal conditions can be described by the following chronosequence (Clements, 1916; Odum, 1959; Connel and Slatyer, 1977; Chertov and Razumovsky, 1980; Razumovsky, 1981):

(a) pioneer communities of algae and cyanobacteria, lichens, mosses and grasses on young soils poor in organic matter;
(b) communities of conifer trees (pine, *Pinus* spp., on poor and dry sites) and some deciduous tree species (birch, *Betula* spp.) with accumulation of soil organic matter and increasing pools of nutrients in the soil;
(c) climax forest vegetation in a quasi-stable state: coniferous forest (with spruce, *Picea* spp., or fir, *Abies* spp.) in the boreal zone and with broad-leaved forest in temperate zone (with oak, *Quercus* spp., and beech, *Fagus* spp.), with high amounts of accumulated soil organic matter.

The importance of plant residues in soil formation processes, notably associated with organic matter accumulation under developing forest vegetation during the primary succession, has been demonstrated in many empirical studies (Olson, 1963; Wilde et al., 1965; Duchaufour, 1970; Chertov, 1981; Borman and Sidle, 1990). However, because of the long-term character of primary succession, the analysis of chronosequences of vegetation and soil development is beset with methodological problems. Therefore, spatially distributed data on forests of different age but with comparable site conditions are generally used to construct time series of the forest ecosystem development. Although this introduces uncertainty, such constructed chronosequences are valuable for the evaluation and validation of soil organic matter models. The Hulshorsterzand site in The Netherlands represents an excellent example of the recently developing primary succession in Scots pine forest on sandy dunes (Van Hees and Mettivier Meyer, 1985; Van Berghem et al., 1986; Emmer, 1995; Nierop, 1999).

The secondary succession of forest vegetation takes place after the ecosystem has been disturbed. The main type of such disturbance in managed forests is harvesting that removes the wood from the ecosystem, though mostly without seriously disturbing the soil. The features of forest soil dynamics in post-harvest succession are generally described in forest ecology (Covington, 1981; Kimmins, 1997; Krause, 1998; Yanaia et al., 2000). Usually, there is a visible decrease of the SOM pool in young stands developing after harvesting. Then, the pool of soil carbon recovers, reaching the values typical of mature forest. The processes of SOM changes in the case of afforestation of previously unforested land are close to the secondary succession because the forest plantations tend to be established on mature soils. Wilde et al. (1965) and Paul et al. (2002) analysed the SOM changes under afforestation. They reported that SOM dynamic trends strongly depend on environmental conditions and on the initial SOM pools. Under forest plantations, the SOM content usually increases on humus-poor former arable or devastated soils, while on humus-rich former pasture soils it can be stable or even decrease. The Speuld Douglas fir plantation in The Netherlands provides a good example of forest growth on mature soils for the analysis of the SOM dynamics in secondary succession.

Here, we report on an application of a simulation model of forest soil organic matter dynamics, ROMUL (Chertov et al., 2001a,b), to Dutch soils in order to reproduce soil organic matter build-up during primary succession on humus-free bare sand and secondary succession on mature humus-rich soil. The objective of this simulation was: (a) to demonstrate the dynamic nature of soil system strongly responding to the changes of vegetation through its litter production; (b) to clarify patterns of primary and secondary succession in the forests under consideration; (c) to show the advantage of the SOM model structure that has a separate compartment for the organic layer (forest floor, peat); (d) to identify which data necessary for the model runs have high uncertainty; (e) to analyse the uncertainty of the experimental data in relation to the moisture regime and litter fall.

2. Material and methods

2.1. The ROMUL model

The ROMUL model (Chertov et al., 2001a) is a refinement of the SOMM model (Chertov and Komarov, 1997a). It has been used for the theoretical analysis of nitrogen supply in forest soils (Chertov et al., 2001b), and for the regional evaluation of SOM dynamics in boreal forests (Chertov et al., 2002). Various versions of the model have been incorporated in four forest ecosystem models (Chertov, 1990; Chertov and Komarov, 1997b; Chertov et al., 2003; Komarov et al., 2003).

The model is based on a classic concept of ‘humus type’ (Humusform) as a succession stage of SOM decomposition marked by different groups of soil micro-organisms and fauna inherent to forest soils. It has the following processes: full mineralisation of every compartment, and processes of organic matter transformation by three different complexes of reducer-organisms that are responsible for the formation of the three main humus forms. It calculates the transformation (humification and mineralisation) of litter and SOM compartments, the gross carbon dioxide flow from the soil due to SOM mineralisation and the nitrogen available for plant growth. The rate of litter and SOM mineralisation and humification is dependent on the litter quality, soil temperature and moisture, and on some soil parameters obtained from published and our own data on organic debris decomposition in controlled conditions (Chertov, 1985; Nadporozhskaya, 2000; Nadporozhskaya et al., 2000).

The main specific feature of this model is that it calculates the processes of SOM transformation separately for organic layer (forest floor, peat) and mineral topsoil. The forest floor is considered in the model as a set of separate SOM pools with the specification of the decomposition for these horizons that is not taken into account in other SOM models. The other important peculiarity of the model is the use of the results of laboratory experiments on the decomposition of different organic debris in controlled conditions as the experimental data for the model compilation. However, the model does not take into account a biomass of reducer-organisms and litter biochemical composition. Neither does it calculate separately nitrate and ammonium nitrogen. The specific features mentioned above expand the applicability of the model both for forest and wetland peat soils without limitations for its use in grassland and agricultural soils as well. These are the main reason why we used the model for the simulation of the forest soil succession dynamics.

The model validation and sensitivity analyses had been performed using a set of published laboratory and field experiments (Chertov and Komarov, 1997a; Chertov et al., 2001a,b). The first version of the model showed good results for forest datasets (and satisfactory results for agricultural soils) in the comparative test of different models against the long-term experimental data from various other sites around the world (Smith et al., 1997).

The input parameters for the ROMUL model are the initial amounts of five pools of soil organic matter and corresponding nitrogen, the amount and quality of litter fall, and meteorological data. The fractions of soil organic matter are as follows:

1. *Surface litter*: aboveground fresh undecomposed litter in the forest floor (leaves, straw, wood, etc.), soil science symbols are L, O1.
2. *Root litter*: belowground fresh undecomposed litter of coarse and fine roots—has no symbol in soil science.
3. *Aboveground partially humified organic layer* (*decomposed forest floor*): surface organic layer as a complex of humus substances with undecomposed plant debris (‘CHS’ in ROMUL model), humified forest floor (‘forest litter’ in USA, ‘humus horizon’ in Scandinavian publications) or peat. Soil science symbols are sum of F and H, or O2 and O3, T, AT.
4. *Belowground CHS*: fraction of analytically determined total soil organic matter in mineral soils, representing humified material not bound to mineral matrix, that is ‘labile, active humus’ being analogous to the aboveground CHS. It is a fraction of partially decomposed roots that is usually removed when preparing a mineral soil sample for chemical analysis. The initial belowground CHS is

determined as a fixed proportion of the total SOM in mineral horizons. We suggest that the default proportion of labile fraction is equal to 0.4 (40%) in forest soils. The value can be easily changed at the model initialisation, taking into account that the natural soils in all climatic zones have a proportion between 0.5 and 0.3 (sometimes higher in humus-rich poorly drained soils, for example, in German Anmoor and French Hydromull). Degraded arable and pasture soils can have a proportion of labile fraction even less than 10%. The direct determination of this fraction is possible by a chemodestruction method for an estimation of soil organic matter quality (Popov et al., 1997).

5. *Humus*: fraction of stable SOM in mineral topsoil (as analytically determined SOM minus labile humus); represents so-called ‘true humus’ as a humified material bonded to the soil mineral matrix (clay minerals or sesquioxides).

The litter fall may be represented by different cohorts characterised by diverse ash and nitrogen contents and location on/in a soil as above or below ground litter cohorts. The model operates with pools of soil organic matter and nitrogen being expressed in kg m^{-2} in all soil genetic horizons or in layers of known thickness for a 100 cm deep soil profile.

To run the ROMUL model the following input data are necessary: the amount of litter input with an unlimited number of cohorts (which are characterised by their specific nitrogen and ash content), initial SOM pools, and climate data, air temperature, soil temperature at the 20 cm depth, forest floor moisture and soil moisture. The output parameters of the model include data on all residual litter cohorts, all SOM and nitrogen pools, and some flow parameters: gross carbon dioxide and available mineral nitrogen production from all litter and SOM pools. This structure of the model makes it possible to avoid a site-specific calibration at a wide range of environmental conditions.

2.2. *Site description*

2.2.1. *Primary succession in Scots pine forest*

The site used for the simulation is situated on recent inland dunes in the Hulshorsterzand area in the Veluwe (5°44′E, 52°20′N, 10–15 m above sea level). The dunes are characteristically about 2–4 m high, with steep slopes of up to about 30°. The highly quartzitic dune sands (with a median particle size of about 175 μm) are well sorted and contain 13–16% Na- and K-rich feldspars only. The dunes are excessively drained, with a water table at a depth of more than 10 m. The climate is temperate humid with a mean annual rainfall of about 800 mm, rather evenly distributed over the year. The mean annual temperature is 9.3 °C. The potential annual precipitation surplus is 325 mm. The mean annual atmospheric input of nitrogen (open field) is 20 kg ha^{-1} for the period 1978–1987 (Emmer, 1995).

Prior to the phase of man-induced wind erosion, the forest of birch and oak grew on the cover sand overlying older pre-glacial and fluvio-glacial deposits. The original forest altered into a heathland under a pressure of grazing, possibly combined with climate change, and then areas of the heathland were destroyed by wind erosion, which started in the 12th century and still continues at a small scale (Koster, 1978; Van Hees and Mettivier Meyer, 1985).

Since the first half of the 19th century, the area has gradually been encroached by natural colonisation or plantations of *Pinus sylvestris*. This has resulted in a complex mosaic of pioneer pine forest stands of different ages, ranging from 1 to 175 years (Fanta, 1986; Moszynska, 1991; Emmer, 1995). The succession is typical and representative of nutrient-poor and acid sands. The closed pine canopy is a crucial phase in the succession at the beginning of convergence (Prach, 1989). In young pine stands (0–20 years old with a tree density exceeding 1500 trees ha^{-1}), ground vegetation is almost absent. *Deschampsia flexuosa* appears and soon becomes dominant in 40–50 years old stands. After establishment, the pine stands have gradually self-thinned to about 650 trees ha^{-1}. In the subsequent succession stages, *D. flexuosa* slowly declines and mosses (*Pleurozium schreberi*, *Dicranum scoparium*, *Dicranum polysetum*) become more abundant. A possible development of these pine stands towards a regional broad-leaved climax forests is impeded by the browsing of red and roe deer (Fanta, 1986) and, perhaps, by frost damage (De Blois et al., 1991).

The organic matter content of the bare dune sands is low or very low. The soils exhibit the development of mor type humus forms. The ecto-organic part of these soils may be subdivided into L, F_1, F_2, Hr and Hd horizons which start to develop after approximately 1.5, 10, 30 and 50 years, respectively (Emmer, 1995).

The thickness of the ecto-organic profile correlates with the age of the stand. There is a razor-sharp boundary between the organic layer and the mineral soil. A weak organic matter accumulation in mineral soil is restricted to the EAh and Bhs horizons. The mineral part of the soil profile typically has a progressively developing micro-podzol in the upper 20 cm of the solum. However, soils of the site classified as a succession range from Haplic to Cambic Arenosols (Klinka et al., 1981; FAO-Unesco, 1988; cited by Emmer, 1995).

The basic properties of this landscape are as follows: (1) dry conditions (owing to temperate climate, excessive drainage and deep water table) though atmospheric precipitation is moderate and evenly distributed over the year; (2) nutrient-poor parent mineral substrate; (3) prevailing SOM accumulation in ecto-organic layer, or in ‘ectohumus’ as defined by Wilde (1958), which plays a decisive role in water and nutrient supply and the stabilisation of the ecosystem.

After Van Berghem et al. (1986), Emmer selected pine forest stands with age of 15, 30, 59, 95 and 124 years. The generalised data from Emmer (1995) on primary succession time series of pure Scots pine stands provided a good opportunity to test the SOM model.

2.2.2. *Secondary succession in Douglas fir forest*

The Speuld study site, also in the Veluwe area in central Netherlands, has an area of 2.5 ha and a gently undulating surface. It is about 50 m a.s.l. and is situated on top of an ice-pushed ridge comprised of pre-glacial sand deposits (Tiktak et al., 1988; Mohren, 1987) pushed up by ice during the Saalien glaciation in the Mid-Pleistocene and covered again by later tongues of the ice sheet (Drente Formation). The main deposit is a coarse sand, which alternates with layers of loam and clay. These so-called ‘Brown Sands’ have a large content of easily weatherable minerals and also contain heavy minerals of volcanic origin. The climate at this site is the same as at the Hulshorsterzand site.

The soils are well-drained Cambic podzols (FAO-Unesco, 1988; cited by Tiktak et al., 1995) on heterogeneous loamy sand. The water table is below 40 m throughout the year. The soils have a forest floor, well-developed Ah horizon, and Moder humus. They were initially forest soils, which were then used for agriculture but have recently been reafforested.

The Douglas fir (*Pseudotsuga menziesii*) was planted in 1962 as 2 years old seedlings. No fertilisers were applied. A regular thinning was carried out every 4–5 years: the boles were dragged away, but all canopy, including branches, were left to decompose. At the beginning of 1988, when the forest was 29 years old, the canopy closed. There is no ground vegetation on the site (Tiktak et al., 1988; Tiktak et al., 1995). The trees have a high needle mass and an extremely high ratio of foliage to fine root mass (6:1). Almost 90% of the fine roots are in the top 0.4 m of the mineral soil (Tiktak et al., 1995).

The basic properties of this forest plantation are as follows: (a) a mesic water regime, not as dry as on the dune sites; (b) a nutrient-rich parent mineral substrate; (c) sufficient initial SOM content before forest planting; (d) a root litter input mainly in the mineral topsoil; (e) intensive forest management of the plantation: thinning every 4–5 years for the first 25 years of the forest stand.

Note that the area where the forests lie has heavy atmospheric nitrogen deposition, so the soils are likely to exhibit signs of nitrogen saturation. However, the data on soil properties shows very high values for the C:N ratio: from 40 to 68 in the forest floor in Scots pine forest, and about 26 in the soil profile in Douglas fir plantation. Moreover, the C:N ratio in the forest floor under Sots pine forest is highest in the H layer (Emmer, 1995), as has also been observed in other extremely poor sandy soils (Vladychenskii, 1975; Chertov, 1981; Bogatyrev, 1996; Nierop, 1999). These C:N values give no evidence of nitrogen saturation. The reason could be the low clay content and cation exchange capacity of these soils, perhaps because of rapid nitrogen loss due to winter leaching and denitrification, and the consumption of nitrogen by plant roots that in these conditions are concentrated in the forest floor.

3. Simulation scenarios and evaluation of input parameters

3.1. *Initial SOM pools*

For primary succession on dune sands, the characteristics of initial mineral substrate were obtained from Emmer (1995). The soil bulk density is 1.61 g cm^{-3}. The quantity of total SOM in mineral substrate is given by Emmer as 0.046 kg m^{-2} (0–5 cm: 0.023; 5–10 cm: 0.013; 10–15 cm: 0.010). The proportion of labile

Table 1
Total SOM and nitrogen contents in the 100 cm solum used for the simulations as initial soil parameters for Douglas fir forest

Scenario	1	2	3	4	5
Total SOM (kg m^{-2})	10	15	20	25	30
Total soil N (kg m^{-2})	0.17	0.25	0.33	0.42	0.50

humus was postulated to be 0.2 (as is usual for degraded soils). Nitrogen concentrations of initial SOM were calculated assuming a C:N ratio of 30.

For the secondary succession site, we had two sources of analytical data on the soil under the Douglas fir forest in 1987–1988: Mohren (1987) and Tiktak et al. (1988). Our calculation of the total SOM and nitrogen contents and C:N ratio for the 100 cm solum shows that the soil has an SOM pool of 19.1–20.4 kg m^{-2}, and a nitrogen pool of 0.42–0.49 kg m^{-2}.

The C:N ratio of the soil horizons varied from 13 in deep soil to 34 in the forest floor, with a mean of about 26. The bulk density is 1.24–1.35 g cm^{-3} in the topsoil to 1.40–1.56 g cm^{-3} in the deep soil. The mean dry mass of the litter is 2.44 kg m^{-2}. These data refer to the 25–26 years old Douglas fir stand. No data were available for the initial soil. We compiled five scenarios with a different initial SOM in the solum (Table 1). For all soils, we used a C:N ratio of 35, a proportion of labile humus in mineral topsoil of 0.3, and a bulk density of the solum of 1.40 g cm^{-3}. The initial SOM in the forest floor was set at zero.

3.2. *Calculation of litter input*

Some uncertainty occurs due to the contribution to litter fall by different plant species. In Scots pine primary succession site, lichens dominate the ground cover in the young stands. *Deshampsia flexuosa* dominates the herb layer of 45–75 years old stands, but then its cover declines and shrubs prevail in 90–120 years old stands (Moszynska, 1991; Emmer, 1995). As Emmer (1995) showed that the dynamics of SOM accumulation are different on dunes compared with blow-outs, we composed the scenario taking into consideration the prevailing pine tree litter fall only.

We calculated litter input using the data for Scots pine forests (Rodin and Bazilevich, 1967; Persson, 1978; Flower-Ellis and Olsson, 1978; Grishina et al., 1990; Jozefaciukowa, 1990; Morozova, 1991; De Vries, 1994; Emmer, 1995). The assumptions were: (1) there is a real dominance of pine residues in total aboveground plant litter fall; (2) total root litter fall equals or exceeds aboveground litter fall; (3) the ecto-organic layer is a major rooting environment with corresponding input of root litter. We did not take into account coarse woody debris for the build-up of soil organic matter. According to Rodin and Bazilevich (1967), Staaf and Berg (1973), Vladychenskii (1975) and Flower-Ellis and Olsson (1978), a coarse litter fall fraction (bark, twigs, branches and trunks) may account for up to 50% of the total litter fall. The total amount of aboveground litter fall in the mature forest was set at 0.25 kg m^{-2} year^{-1}. Many studies have measured root production and the annual input from roots to the soil under forest (Persson, 1978; Ulrich et al., 1981; Vogt et al., 1983, 1986; Nadelhoffer and Raich, 1992). They have found root inputs double or treble the above ground litter fall obtained by separate calculations. Because the litter parameters were vague, we performed a set of model runs in which we varied the amount of litter fall input. Scenarios ‘root 1.5’ and ‘root 2.0’ contained, respectively, 1.5 and 2.0 times more roots than the 0.25 kg m^{-2} year^{-1} of the basic scenario. Root litter that reaches the ecto-organic layer may be up to 75% of total root litter production (Persson, 1978; Jozefaciukowa, 1990; De Vries, 1994); this proportion was set for the simulations.

It is well known that the nitrogen content of plant tissues varies greatly in different sites. For example, for pine needles it varies from 4.2 mg g^{-1} (Berg and Staaf, 1980) to 9.0 mg g^{-1}of nitrogen (Kazimirov et al., 1977). Kittredge (1948) reported nitrogen content in freshly fallen pine needles ranging from 5.8 to 8.4 mg g^{-1}. We had actual data on the plant tissue quality of this dune site for pine needles from the upper litter horizon in forest floor and twigs only (Emmer, 1995). The nitrogen content of these cohorts may be higher due to nitrogen imported through soil fungi and bacteria (Zeller et al., 2000); however, we used Emmer’s measured data. Data on the nitrogen and ash contents of pine roots were calculated using mean values from Morozova (1991) and De Vries (1994). The nitrogen concentration in pine root used in our study (4.0 mg g^{-1}) correlates with the data from Ruark (1993) who found that C:N values of young seedlings root averaged 148 and the C:N ratio of 35 years old

Table 2
Parameters of litter fall cohorts in Scots pine and Douglas fir forests (kg m^{-2} $year^{-1}$)

Age	Needles	Twigs, bark and cones	Roots coming to organic layer	Roots coming to mineral solum
Scots pine				
0–5	0.038	0.004	0.112	0.038
6–10	0.055	0.006	0.150	0.050
11–20	0.075	0.025	0.225	0.076
21–35	0.085	0.065	0.255	0.088
36–45	0.100	0.100	0.300	0.100
46–55	0.115	0.115	0.337	0.113
56–125	0.125	0.125	0.374	0.126
Douglas fir				
0–5	0.090	0.010	0.006	0.100
6–15	0.135	0.015	0.011	0.149
16–90	0.270	0.030	0.020	0.300

fine roots of loblolly pine stands ranged from 131 to 94.

The total nitrogen pool in aboveground litter fall of Scots pine was determined to be about 43 kg ha^{-1}; additionally, dwarf shrubs and herbs may contribute about 13–39 kg ha^{-1} of nitrogen to the soil annually (Moszinska, unpublished data; cited by Emmer, 1995). These values were found by studying pine stands on the blow-outs near the sand dunes. The estimates of nitrogen input with leaf litter fall during the forest succession were 8.6–44.0 kg (N) ha^{-1} (Rodin and Bazilevich, 1967). The nitrogen input with total litter fall during the succession was estimated to be 16–41.5 kg (N) ha^{-1} (Chertov, 1981). So we also performed a set of model runs with nitrogen concentrations in litter fall varying from 20 to 54 kg ha^{-1} $year^{-1}$. We ended up with the data for litter cohort scenarios presented in Tables 2 and 3 that met all the conditions discussed above.

For the secondary succession in the Douglas fir site, the data for the 29 years old stands are as follows: average stem diameter is 21 cm at breast height (Tiktak et al., 1988), average tree height is 19.5 m (Tiktak et al., 1995), stem density is 765–812 trees ha^{-1}, aboveground litter fall (measured by litter trap) is 0.280–0.290 kg m^{-2} $year^{-1}$ (Van der Maas and Pape, 1991; Tiktak et al., 1995). The litter fall is 89–95.5% of needles and 4.5–11% of twigs (Tiktak et al., 1988; Van der Maas and Pape, 1991). In the simulation, the litter fall was set with a ratio of needles to twigs of 9:1. The needle fall derived indirectly from the observation on a needle life span was given almost double values—the mean is about 0.68 kg m^{-2} (Tiktak et al., 1995). We used 0.3 and 0.6 kg m^{-2} $year^{-1}$ of total aboveground litter fall in the simulations (respectively, the N1 and N2 scenarios).

Root distribution in the soil profile of the Douglas fir forest was estimated using the data from Laitat et al. (1999: 6.5% of total dead roots reach the litter) and Olsthorn (1998: mean 7.6% of fine root biomass found in the forest floor). In our simulations, we took into account that 7.0% of fine root litter goes to the forest floor and the rest (93.0%) ends up in the mineral horizons. Despite data that foliage mass was 6 times greater than fine root mass (Tiktak et al., 1995), the annual root litter inputs for the Douglas fir forest of 16–90 years age we used were 0.3, 0.6 and 0.9 kg m^{-2}

Table 3
Chemical characteristics of litter fall cohorts in Scots pine and Douglas fir forest (mg g^{-1})

Cohorts	Nitrogen content	Ash content
Scots pine		
Needles	7.8	14
Twigs, bark and cones	3.1	7
Roots	4.0	8
Douglas fir		
Needles	18.4	25.0
Twigs, bark and cones	3.0	4.0
Roots fall	9.0	6.3
Fine roots after cutting	10.0	7.0
Coarse roots after cutting	3.0	4.0

(for, respectively, 'root 1'—R1, 'root 2'—R2 and 'root 3'—R3 scenarios). These values are in agreement with those found by Laitat et al. (1999), who estimated the dead root mass as 0.309 kg m^{-2} (we used 0.3 kg m^{-2} as the lower limit in R1 scenario). Olsthorn (1998) found that the difference between average fine root biomass in Douglas fir stands in wet and dry years may reach about 2.0 kg m^{-2} (the higher limit we used in our simulation for amount of root ending up in soil was equal to 0.9 kg m^{-2} in the R3 scenario). We ended up with the litter cohort parameters shown in Table 2. We assumed the mass of litter fall was 30% for young forest of 0–5 years, 50% for the 6–15 years stands and 100% for the forest of 16–90 years. We assumed annual litter input was the same from 30 to 90 years, due to the regular thinning.

As mentioned above, from 6 to 37 years the Douglas fir forest had been thinned every 4–5 years. Using the data from Bartelink (1998), we added to the litter fall input scenario a calculation of needles, branches, fine and coarse roots coming on/into the soil after thinning (Table 4). Additionally, for the period of 2 years after the thinning we reduced the total litter fall in proportion to the trees removed.

We simulated SOM transformation under Douglas fir forest for periods lasting 25 and 90 years, assuming the same annual litter fall from 37 to 90 years and thinning every 10 years. Additionally, we used the simulations of SOM development for the same forest under the thinning but with litter raking (removing of the fresh litter fall from the soil surface) for the period of 0–20, 20–40 and 40–60 years in each scenario. We also simulated the effect of different nitrogen contents in the annual litter fall for the basic (N2/R3) litter input scenario.

3.3. Climatic data

Detailed meteorological information were available for the central Netherlands. De Bilt meteorological station near the experimental area has data on monthly air temperatures for the last century (Wallen, 1970; Vaessen, 1988). Soil temperature has been measured since 1983 by the Wageningen meteorological station, which is also near the study areas, but these data are for a bare soil and for soil under a vegetation of short, mown grass. These values will be higher than the soil temperature in the forest. The spring temperature of the forest floor is about the same as the air temperature, but in summer it is about 1 °C lower (Schaap, 1996). Our observations (Chertov and Tarasov, 1997) revealed that in summer the forest soil temperature at depth of 10 cm was 1–4 °C lower than at the same depth under clear-cut area. We compiled the soil temperature data from measured air temperature and a correlation between soil temperature under grass sward and under the forest canopy (Chertov et al., 2001a,b).

For the Scots pine site, we used data on moisture content of mineral soil horizons found in research on spontaneous stabilisation of blow-outs by algae (Pluis, 1993), and moisture variability resulting from water repellence on the dune sand areas along the west coast of The Netherlands (Dekker, 1998). We also used the soil moisture data for a sand site near Wageningen as reference information (Mohren, 1987). The maximum winter moisture of bare sand in the field was about 6 mass% and might decrease almost to 0 mass% during the summer drought.

For the Douglas fir site, the air temperature in the climatic scenario was obtained from the data of Mohren and Kienast (1991). No data were available

Table 4
Thinning scheme for the Douglas fir plantations as used in simulation

Time (years)	No. of trees ha^{-1}	No. of trees removed ha^{-1}	Amount of litter coming on/into soil after thinning (kg m^{-2})			
			Needles	Branches	Fine roots	Coarse roots
0	2300	–	–	–	–	–
6	2100	200	0.044	0.040	0.012	0.040
11	1900	200	0.090	0.080	0.054	0.160
17	1500	400	0.292	0.344	0.160	0.600
22	1250	250	0.253	0.328	0.100	0.375
27	1000	250	0.290	0.300	0.110	0.470
37	800	200	0.262	0.218	0.100	0.400

Table 5
Climatic parameters for the simulation scenarios

Parameters[a]	January	February	March	April	May	June	July	August	September	October	November	December
Scots pine												
T_a	1.7	2.0	5.0	8.5	12.4	15.5	17.0	16.8	14.3	10.0	5.9	3.0
T_s	2.0	3.5	5.5	8.0	9.0	12.4	16.0	16.0	12.0	10.0	5.0	4.0
M	6.0	6.0	5.0	4.0	4.0	3.0	2.0	1.0	2.0	4.0	5.0	6.0
Douglas fir												
T_a	1.3	1.1	5.3	7.5	12.3	15.0	16.8	16.4	13.8	10.5	6.1	3.6
T_s	2.0	2.0	3.0	7.0	10.0	12.4	16.0	16.0	12.0	10.0	6.0	4.0
M_m	400	400	300	250	200	150	100	100	200	300	400	400
M_{md}	400	400	300	250	100	50	10	10	50	300	400	400
M_s	10.0	10.0	9.0	9.0	7.0	6.0	4.0	4.0	7.0	9.0	10.0	10.0

[a] T_a: air temperature; T_s: temperature of mineral topsoil; M: moisture of mineral topsoil in Scots pine forest (in mass%); M_m and M_{md}: moisture content (mass%) of ecto-organic layers in the mesic and mesic–dry scenarios in Douglas fir forest; M_s: moisture content of mineral topsoil in Douglas fir forest (mass%).

for the forest soil temperature. The soil temperature data were also composed using a simple statistical climate generator in the ROMUL model (Chertov et al., 2001a,b). Data for soil moisture were compiled from published information (Mohren, 1987; Tiktak et al., 1988; Mohren and Kienast, 1991). The final basic scenario for air and soil temperatures and solum moisture regimes is shown in Table 5. None of the simulated scenarios of soil temperature, moisture and litter input took into consideration year-to-year variation of climate and litter parameters.

The absence of data on forest floor moisture in Scots pine forest forced us to run a set of the different scenarios of moisture regimes at the simulated sites: dry, mesic and hydric (Table 6). Additionally, we simulated the soil development for a dry site with dry summer but with various winter moistures (from 60 to 150 mass%). None of the simulated scenarios of soil temperature, moisture and litter input take into consideration year-to-year variation of climate and litter parameters.

The time span of the simulation for Scots pine primary succession was 125 years. Taking into account the basic scenario of litter input for young and mature forests we ran a set of scenarios with the following input parameters: (a) different litter input with ‘dry’ moisture scenario—simulations with ratios of needles and branches to roots of 1:1.0, 1:1.5, 1:2.0, that is with increasing root litter fall input and (b) different forest floor moisture regimes—(dry, mesic and hydric) with the ratio of aboveground to below ground litter input of 1:2.

For the Douglas fir forest, we compiled a more complicated set of scenarios taking into account the basic litter input for 30 years old stands: (a) different litter input with the initial total SOM 10 kg m^{-2} with ratios of needles and branches to roots of 1:1 (N1/R1), 2:1 (N2/R1), 2:2 (N2/R2) and 2:3 (N2/R3); (b) basic litter input scenario N2/R2 with a different initial total SOM: 10, 15, 20, 25 and 30 kg m^{-2}; (c) basic litter input scenario N2/R2, initial SOM 30 kg m^{-2} and with three different nitrogen inputs with annual litter fall (10.6, 15.3 and 19.1 g m^{-2}); (d) litter input scenario N2/R3, initial SOM 10 kg m^{-2} and litter raking for the periods 0–20, 20–40 and 40–60 years of stand age. We included the litter raking inclusion to test the applicability of the

Table 6
Forest floor moisture (mass%) at dry, mesic and hydric simulation scenarios for Scots pine forest

Scenarios	Months											
	January	February	March	April	May	June	July	August	September	October	November	December
Dry	100	100	75	50	20	15	8	8	10	20	75	100
Mesic	150	150	150	100	100	75	50	20	50	75	150	150
Hydric	700	700	600	450	300	200	100	200	300	450	650	800

ROMUL model for simulating the effects of anthropogenic disturbance of soil.

4. Results of the simulations

4.1. Primary succession in Scots pine forest

4.1.1. Effects of the different litter inputs

Both the scenario with a root litter input equal to aboveground plant debris and the 1:1.5 scenario (in which aboveground plant debris was 1.5) resulted in very low organic matter accumulation. The most realistic results were from a run of the scenario with double the proportion of root litter fall (Fig. 1). These runs with variation of the proportion of root input show that root litter input might be underestimated in this Scots pine forest. We subsequently used a scenario with the doubled root litter input for all simulations.

4.1.2. Simulations of the moisture regime of forest floor

Simulation of the scenario with the mesic moisture regime demonstrates a fast organic matter decomposition by moder type: the total SOM is 5.0 kg m^{-2}, C:N 43 (Fig. 2). The same litter input under a hydric regime showed the maximum organic matter accumulation by raw humus (mor) type (total SOM 17.4, C:N 88). The results of the model run under the dry moisture regime (total SOM 11.14, C:N 43) were close to the actual organic matter accumulation under the pine forest on sandy dunes.

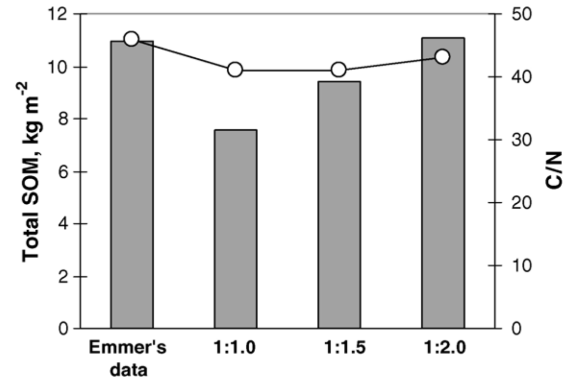

Fig. 1. Comparative data for the simulations of soil development with different amounts of root litter fall for 124 years pine forest on sandy dunes, compared with data measured by Emmer (1995). The bars show soil organic matter; the plot of the C:N ratio is also shown.

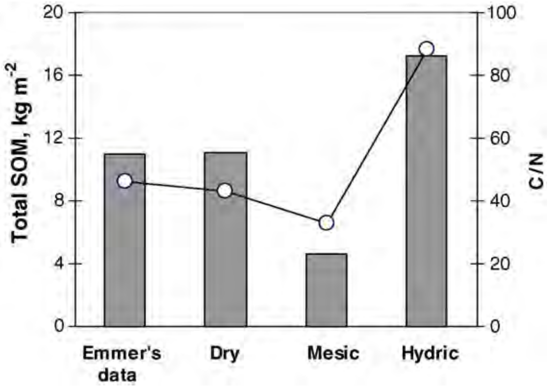

Fig. 2. Comparative data of the simulations of soil development with dry, mesic and hydric moisture regimes under 124 years old pine forest on sandy dunes, compared with data measured by Emmer (1995). The bars show soil organic matter; the plot of the C:N ratio has also been shown.

A set of runs was performed to find the importance of winter moisture for the scenarios with summer drought. We used the 'dry' scenario. Despite having a moisture content of the forest floor in winter five times higher, the results did not show so large a difference between variants (Table 7). So we selected the more realistic scenario for wet winter moisture (100 mass%) in the 'dry' scenario.

4.1.3. The general results of main scenario simulation

From the test runs described, we identified the most realistic scenario for the simulation of primary

Table 7
Results of simulation with different winter moisture of forest floor for Scots pine forest

Winter moisture of forest floor (mass%)	SOM	C:N
60	11.62	43
100	11.09	43
150	11.14	43
200	11.76	43
300	11.87	43
Measured data (Emmer, 1995)	10.97	46

The percents represent mass moisture of forest floor in three winter months.

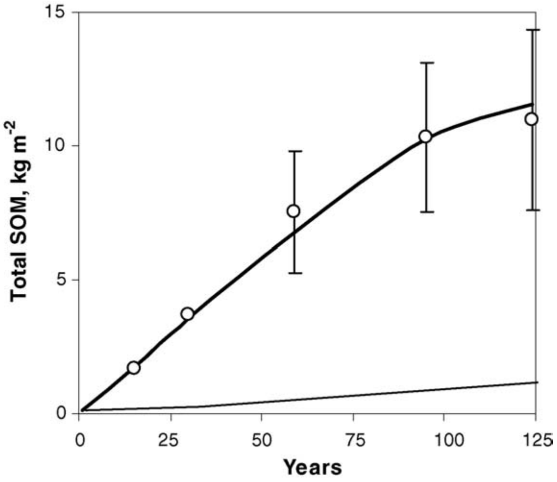

Fig. 3. The results of the ROMUL long-term simulation of soil development in the primary succession of Scots pine forests on poor sandy dunes. Points with standard error bars are Emmer's (1995) experimental data, the solid lines are ROMUL simulation: the thin line is humus in mineral topsoil, the thick line is total SOM pool.

succession of forest vegetation at poor sandy dunes (Hulshorsterzand site). It is: (a) climate for dry site with summer drought and 100% winter moisture of forest floor; (b) ratio of the mass of needles and shoots to the mass of roots in litter fall of 1:2; (c) nitrogen and ash contents in all litter fall fractions as shown in Table 1. The final results of the simulation with this scenario are presented in Fig. 3. The simulation demonstrates that the main processes of SOM accumulation were adequately modelled: (a) most SOM accumulation in the surface, partially humified, organic layer on the forest floor (F and H horizons with a pool about 10 kg m^{-2}); (b) the fast formation of a litter layer in the forest floor and its stabilisation at an input rate of 0.4 kg m^{-2}; (c) slow gradual increase of humus in the solum up to only 1.2 kg m^{-2}.

The simulated values of total SOM pool closely approximate the generalised data of Emmer (1995). The simulation also agrees satisfactorily with the total soil nitrogen pools. However, the real situation is more complex. A carbon:nitrogen ratio also plays a crucial role in the element dynamics, rate of organic matter decomposition and nitrogen availability for plant

Table 8
Comparison of Emmer's generalised data vs. ROMUL simulation for primary succession in Scots pine forest

Index	Years	Emmer (1995)	ROMUL	Error (%)
SOM (kg m^{-2})	59	7.53	8.03	6.2
	124	10.97	11.12	1.3
N (g m^{-2})	59	73.5	77.9	5.6
	124	118.0	139.3	15.3
C:N ratio	59	49	51	3.9
	124	46	40	13.0

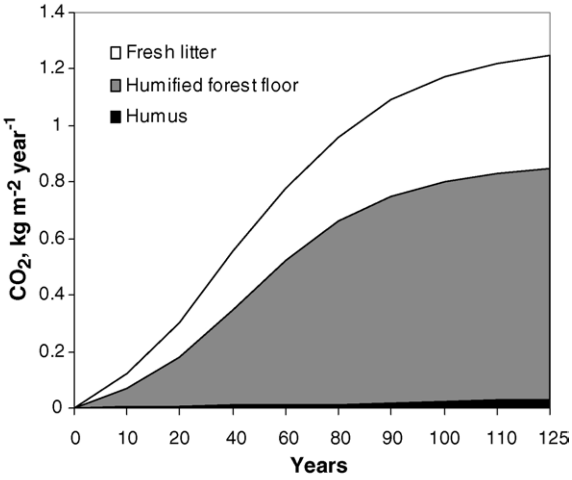

Fig. 4. Simulated CO_2 flux from the different SOM pools during the primary succession in Scots pine forest.

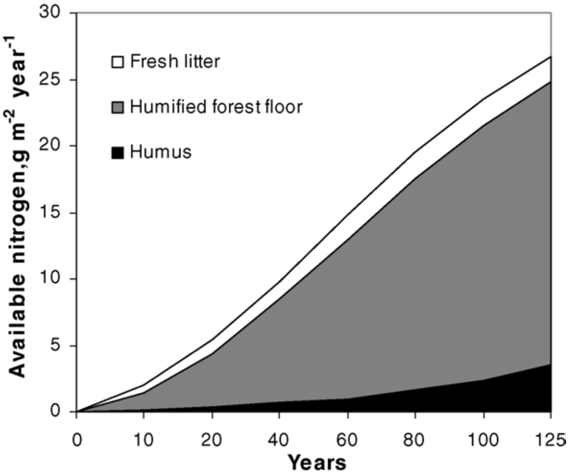

Fig. 5. Predicted role of forest floor compartments in supply of available nitrogen from the soil during primary succession in Scots pine forest.

Table 9
Comparative data of the ROMUL model runs for 25 years for the Douglas fir forest

Data	Input			Output					
	Initial SOM (kg m^{-2})	N (g m^{-2}) in annual litter fall	Moisture regime of forest floor	Organic layer			Solum		
				SOM (kg m^{-2})	N (kg m^{-2})	C:N	SOM (kg m^{-2})	N (kg m^{-2})	C:N
Simulated data									
N1/R1	10	8.1	Mesic	1.20	0.021	33.1	7.37	0.177	24.2
N2/R1	10	13.1	Mesic	1.88	0.036	30.3	8.06	0.212	22.1
N2/R2	10	16.1	Mesic	1.93	0.037	30.3	9.06	0.234	22.5
N2/R3	10	19.1	Mesic	2.00	0.039	29.7	9.90	0.258	22.3
N2/R3	15	19.1	Mesic	2.00	0.039	29.7	12.44	0.306	23.6
N2/R3	20	19.1	Mesic	2.00	0.039	29.7	14.97	0.354	24.5
N2/R3	25	19.1	Mesic	2.00	0.039	29.7	17.63	0.413	24.8
N2/R3	30	19.1	Mesic	2.00	0.039	29.7	20.08	0.459	25.3
N2/R3	30	15.3	Mesic	2.20	0.036	35.4	19.72	0.440	26.0
N2/R3	30	10.6	Mesic	2.58	0.032	46.8	19.29	0.394	28.4
N2/R2	30	16.1	Mesic–dry	2.27	0.044	29.9	19.51	0.438	25.8
N2/R3	30	19.1	Mesic–dry	2.33	0.045	30.0	20.45	0.456	26.0
N2/R3	30	15.3	Mesic–dry	2.58	0.043	34.8	20.04	0.442	26.3
Experimental data									
Mohren (1987)	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	20.38	0.49	24
Tiktak et al. (1988)	n.d.	n.d.	n.d.	2.44	0.049	29	19.13	0.42	26

Notes: n.d.: no data available. N1: aboveground litter input 0.3 kg m^{-2} $year^{-1}$; N2: aboveground litter input 0.6 kg m^{-2} $year^{-1}$; R1: root litter input 0.3 kg m^{-2} $year^{-1}$; R2: root litter input 0.6 kg m^{-2} $year^{-1}$; R3: root litter input 0.9 kg m^{-2} $year^{-1}$.

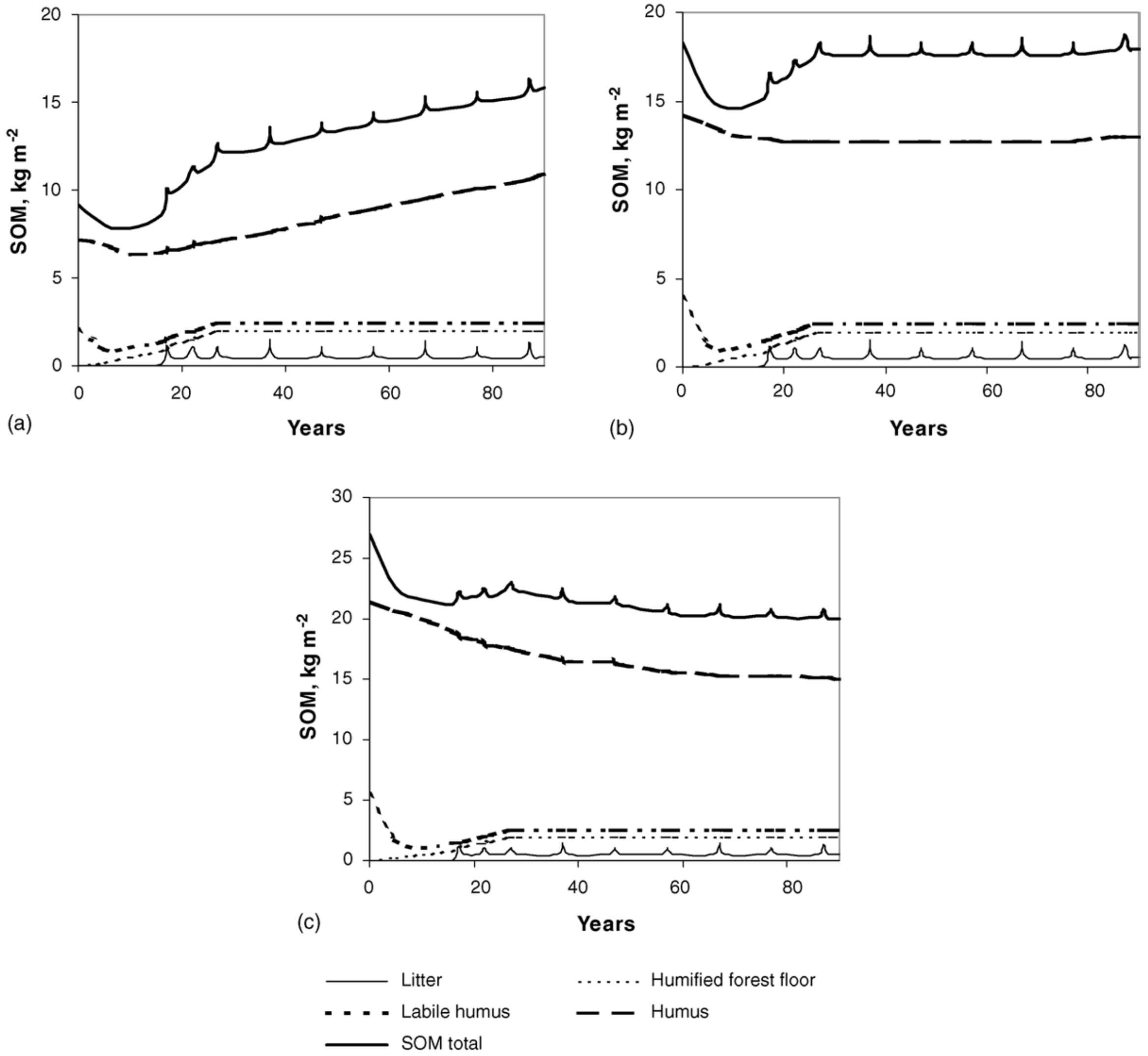

Fig. 6. Simulated data for SOM dynamics in the Douglas fir forest with thinning on the soil with initial SOM values 10 kg m^{-2} (a), 20 kg m^{-2} (b) and 30 kg m^{-2} (c). Small values of fresh litter pool are not visible on the graph.

growth. For this reason, the comparison with field data is more complex (Table 8). The simulated and experimental data on C:N ratio agreed well at age 59, but by the end of simulated period had diverged (NB the margin of error was 15%).

The controlling role of organic layer (ectohumus) in the functioning of forest soil can be seen more clearly from the data on CO_2 emission from a soil. CO_2 is a final product of litter and SOM mineralisation, which is important for plant photosynthesis. The simulation shows that the organic layer and labile humus are crucial in this process (Fig. 4). The role of easily decomposed SOM fractions is pre-dominant: about 98% of CO_2 production comes from the forest floor and labile humus. According to Emmer's (1995) data, only 2.6–4.8% of the total organic matter is in the litter sub horizon of the forest floor (L). We obtained similar results from ROMUL: the litter accounted for 3.2–5.5% of the total SOM. The ROMUL runs also confirmed the importance of litter in CO_2 production: 30–40% of the

CO_2 output was from the litter and 58–68% was from the humified forest floor (H). The CO_2 flux from stable humus was about 1–2% (Fig. 4).

The results on the role of soil horizons in nitrogen supply (Fig. 5) give a different picture. In this soil with a well-developed mor forest floor, most of the available nitrogen is produced in the organic layer: about 70% is from the humified forest floor. However, in contrast with the carbon dioxide flux, in the nitrogen flux the undecomposed litter plays a minor role by comparison with other forest floor pools. Only 5–6% of the available nitrogen comes from L. However, humus is more important in the available nitrogen supply, and the stable humus layer contributes about 20%.

4.2. Secondary succession in Douglas fir forest

4.2.1. Simulations of the different litter input and initial SOM pools

The experimental and simulated data are shown in Table 9. We first tested the different inputs of litter for the soil with initial SOM 10 kg m^{-2}. The N2/R3 scenario produced results approximating the experimental data on ectohumus, but the SOM accumulation in solum was inadequate. The best results were from the scenario with a doubled aboveground input and tripled root input (N2/R3) and an initial SOM of 30 kg m^{-2}, but time series of this simulation demonstrated a steady loss of SOM.

We then studied the best way to reproduce variations in forest floor accumulation reflecting the nitrogen amounts in the litter inputs and moisture regime of the forest floor. The closest to the experimental data were N2/R2 and N2/R3, with nitrogen inputs of 16.1 and 19.1 g m^{-2} year^{-1}, respectively, plus a moisture regime with summer drought (mesic–dry).

The litter fall scenarios assume litter input stabilises after 15 years of stand growth. The plant residues coming on/into the soil after thinning are in equal proportions (like the litter input in N1/R1 scenario) and in double proportions (N2/R2) after 17 years of forest age. This explains why simulated litter peaks after thinning (Fig. 6). The forest floor mass increases gradually from the initial situation and reaches a plateau at 30 years. In the simulations, the labile humus in mineral soil decreased for the first 5 years, but then upturned; it too levelled off after 30 years.

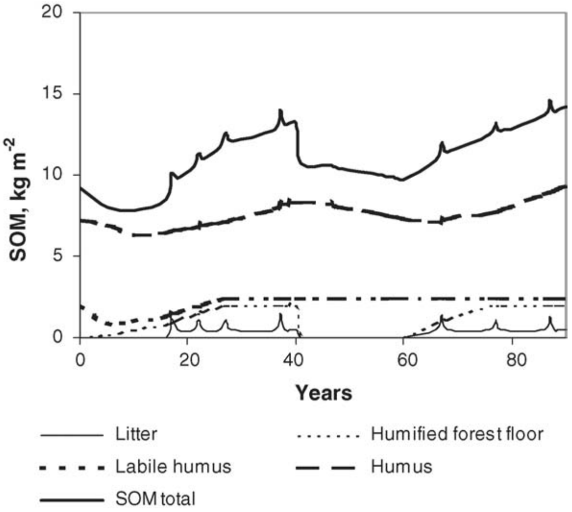

Fig. 7. Simulated data for SOM dynamics in the Douglas fir forest with thinning and litter raking during 40–60 years on the soil with initial SOM pool 10 kg m^{-2}.

Despite the large litter input, the results of our simulations show the total SOM increasing only in soils with initial SOM 10 kg m^{-2} (Fig. 6a). Soil with initial SOM 20 kg m^{-2} keeps the total SOM balance at almost the same level with a regrouping in SOM structure: more SOM is newly formed from the forest floor and less humus accumulates in the solum (Fig. 6b). Simulation of SOM alteration under the forest growth on the soil with initial SOM 30 kg m^{-2} resulted in a decrease in total SOM due to a decrease in humus (Fig. 6c). So we can conclude that the scenario with the SOM pool of 20–25 kg m^{-2}, litter inputs of 0.6 kg m^{-2} year^{-1} above ground and 0.9 kg m^{-2} year^{-1} below ground, and with nitrogen at 19.1 g m^{-2} year^{-1} best fits the experimental data.

4.2.2. Simulation of Douglas fir forest growth with litter raking

Fig. 7 shows the results of simulating total forest floor raking. The SOM of the forest floor stays at zero during the period of raking, but recovers rapidly after raking stops. The SOM of the mineral topsoil does not react so dramatically to the decrease in the forest floor litter, but the humus does not reach the level found in undisturbed systems, and the amount of humus reflects the effect of this disturbance. The litter raking at the start of forest growth does not strongly influence SOM dynamics because of the low values of forest floor mass. The maximum negative effect is the removal of the organic layer in the mature Douglas fir forest (Fig. 7).

5. Discussion and conclusion

The ROMUL model used for the simulation demonstrates some specific features in relation to the other models of soil organic matter dynamics based on differential equations. The most important differences are discussed below.

The ROMUL model includes an organic layer as a separate pool, which consists of an unrestricted number of different cohorts. Each cohort originates from different kinds of litter with their specific properties. The stable humus of mineral soil is a parallel pool, which accumulates humic substances coming from all organic cohorts. The model allows for a more accurate simulation of forest soil dynamics where numerous aboveground litters varying in quality, amount and input rates form a specific surface organic layer (forest floor). Though a single model, ROMUL considers separately the processes of SOM decomposition in the organic layer (Powlson et al., 1996); this feature makes the model particularly suitable for wetland organic soils. This structural advantage of the ROMUL model demonstrated by our model runs with a raking of soil litter that enables the simulation of the removal of the forest floor that occurred under the *plaggen* (sod stripping) agricultural practice in The Netherlands and North Germany (Pape, 1970). It is more difficult to simulate this disturbance regime using SOM models without an organic layer pool.

The rate of the processes in the model has been evaluated against laboratory experiments in controlled conditions and is treated as being dependent on litter quality, temperature and moisture. This contrasts with other SOM models, which have mostly been calibrated from field experiments (Smith et al., 1997). In such models, the rate of processes of SOM decomposition is calculated in linkage with the amount of litter cohorts estimated from the current above and below ground biomass of annual and perennial grasses and herbs, and the role of fine root litter is usually ignored. However, the fine root litter is crucially important because these roots have a high growth rate and mortality (Rodin and Bazilevich, 1967; Persson, 1978; Nadelhoffer and Raich, 1992). Therefore, models that ignore fine root litter underestimate the measured biomass of fine roots as a pattern of their productivity, and also the litter pool, the total plant debris mass, and correspondingly the rate of SOM transformation rates.

The ROMUL model is not very sensitive to random modifications of its rate coefficients (Chertov et al., 2001a,b). Simultaneous random change of all coefficients within the 50% variation leads to changes of less than 10% in the main output variables. This accuracy of the variables is comparable with the accuracy of estimation of experimental data. It makes it unnecessary to do a site-specific calibration of the model for a wide range of environmental conditions.

Generally, the results of the ROMUL model correspond to the classic concept of forest soil development in primary succession in a Scots pine forest with a water regime of dry sandy sites without impact of forest fires, insect attacks and grazing (Odum, 1959; Connel and Slatyer, 1977; Razumovsky, 1981; Emmer, 1995). This development represents a consistent accumulation of SOM, in our case in a form of raw humus forest floor. The soil dynamics in the Douglas fir plantation also match the observed patterns of SOM changes in the secondary succession, with significant SOM decrease under young forest, and SOM recovery in the older stands (Covington, 1981; Chertov, 1981; Krause, 1998; Yanaia et al., 2000). Moreover, the simulated consistent increase of forest floor mass in the Douglas fir plantation also corresponds with the SOM dynamics in afforestations of previously unforested land (Wilde et al., 1965; Paul et al., 2002). However, the application of the ROMUL model encountered problems due to uncertainty in input data for the model runs.

Because initial SOM data for the Douglas fir site were lacking, we had to perform a set of simulations to specify the initial SOM values were in balance with an observed tree growth and litter input. The estimated values of SOM, about 20 $\mathrm{kg\,m^{-2}}$, are conform with Mollisols under natural grasslands (Parton et al., 1988; Chertov and Komarov, 1997a,b). However, the agricultural brown and black *plaggen* soils of The Netherlands may also contain an SOM pool of 42–65 $\mathrm{kg\,m^{-2}}$ in the 100 cm solum (Pape, 1970). The test runs with the various initial SOM pools also demonstrated the theoretical trends of SOM dynamics in the forest if initial soil properties differ. It seems that under the intensively growing Douglas fir stand the soil will increase the SOM pool if that pool has low initial values, but if the pool is sufficiently large will deplete it until a balanced steady state is reached with the forest vegetation.

The experimental data used for the simulation did not include direct measurements of soil water regime; however, the moisture content of conifer forest floor varies in a wide range: from about 10 to100–300 mass% and more. We did the runs with the different moisture regimes in Scots pine site, and found that the extra dry and extra wet regimes more closely match Emmer's (1995) data. We also obtained a satisfactory result when we used a combination of the scenarios (wet winter and dry summer as a more realistic regime).

The estimation of a needle litter fall amount and quality was a real problem in the experimental investigations. In the Douglas fir forest, the indirect method (needle biomass divided by its life span) gave results twice as high as the direct measurements (litter trap or litter net) (Tiktak et al., 1995). We tested both values and found that the model simulations yield satisfactory results when the needle litter input is assumed to correspond to indirect measurement.

A large source of uncertainty is the pool of root litter. Its range is as great – or greater – than that of the aboveground litter fall (Laitat et al., 1999). Adjusting the proportion of needles and branches to roots resulted in a simulation that closely fitted the field data. The mass of root fall used in the simulation in the both sites is close to the data of Nadelhoffer and Raich (1992) who used a carbon budget method similar to our modelling scheme to estimate some unknown values of fine root litter production in forest ecosystems. The other specific aspect of the simulation scenario is that most of the root litter in the poor Scots pine stands goes to the organic layer. When we did runs with the root fall going to mineral soil then the total SOM dynamics reflected the formation of a Moder humus type with a sufficient SOM accumulation in mineral topsoil, as is typical for Douglas fir forest.

The experimental data for the Scots pine site did not include direct measurements of nitrogen concentration in litter fall cohorts. Most published data on nitrogen concentration in needle litter are for the living tree or forest floor (Kittredge, 1948; Staaf and Berg, 1973; Berg and Staaf, 1980; Morozova, 1991; Ågren and Bosatta, 1996). These may be higher than the actual values in real litter fall, because on poor soil the nitrogen reallocation from senescent leaves to plant is 50–75% of the content of living leaves (Aerts, 1996). To find the real amount of nitrogen, its value has to be established in the short time when the senescent leaves have reduced nitrogen concentration but are not getting additional nitrogen from the soil biota. Therefore, to estimate a more realistic nitrogen concentration in the litter fall, we ran a test simulation with a variation of nitrogen content in the litter fall scenario.

Finally, from the results of our model runs, we can conclude that the main sources of uncertainty in the model application are climate, litter input, initial distribution of litter cohorts and litter nitrogen content. It is difficult to obtain reliable measurements of these variables; and they will mostly be estimates. To overcome these problems, hypotheses on the structure and flow of unknown inputs need to be tested.

If we have good experimental data then the model runs must fit these data. If the reliability of the measured input data is questionable, then it is necessary to solve the inverse problem: we should suggest a set of possible properties of the input and then compare the model runs with the experimental data so we can use a parameter that best conforms with the experiment.

In our case, the experimental litter parameters and some climatic characteristics had been poorly measured in the field. The mass of fine root litter, most of which goes to the forest floor, had not been measured at all. The computer experiment with different scenarios allowed these variables to be estimated. Using the estimated amount of root litter and its distribution between forest floor and mineral soil, it was possible to simulate total soil dynamics that corresponded well with the experimental data.

The model's assumptions for the hypotheses about litter fall seem to be realistic; they should be further checked empirically. Based on the model results, further experiments should be done to determine the temperature and moisture regimes in the succession time series, and the patterns of litter fall.

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