Dynamics of grass–clover mixtures—An analysis of the response to management with the PROductive GRASsland Simulator (PROGRASS)

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1. Introduction

Grasslands are important agroecosystems worldwide as they provide numerous goods and services such as forage to support livestock systems. They are typically maintained as permanent or rotational grasslands, with the latter being sown every few years as part of an arable crop rotation. Although rotational grasslands are expensive to establish, they are very productive in their early life. While permanent grasslands contain a mixture of many plant species, rotational grasslands only contain a few species. In grass–legume leys, symbiotic N2-fixation is essential economically, as it may sustain high productivity in the presence of low mineral nitrogen (N) inputs (Frame and Newbould, 1986; Boller and Nösberger, 1987; Whitehead, 1995a). Amounts of N2 fixed by legumes in temperate grasslands range between 50 and 250 kg N ha−1 y−1 (Frame and Newbould, 1986; Whitehead, 1995a), which is comparable to the amount of mineral or organic N added with fertilizers.

Biological N2 fixation (BNF) in mixed swards reflects the relative abundance of the legumes (Frame and Newbould, 1986), which is determined by environmental factors, management, and by interaction with the companion grasses (Whitehead, 1995a). Therefore, managing an optimal co-existence of grasses and legumes is essential for promoting grassland productivity, but in practice the task has often proven difficult (Kessler and Nösberger, 1994). This is especially the case in the presence of white clover (Trifolium repens L.), the most important forage legume in temperate climates. Average biomass fractions of white clover range from a few to around 80% (Frame and Newbould, 1986), with strong fluctuations in the course of the growing season (Menzi and Nösberger, 1998). White clover grows well in association with a range of grasses and is tolerant to grazing (Frame and Newbould, 1986; Whitehead, 1995a), but it is often less competitive in capturing light (Schwank et al., 1986) and more sensitive to winter stress and diseases than the associated grasses.

Growth of white clover in monocultures and mixtures, in particular in association with perennial ryegrass (Lolium perenne L.), has been studied extensively (Frame and Newbould, 1986; Guckert and Hay, 2001). Experiments have been designed to examine light interception and competition (Schwank et al., 1986; Woledge et al., 1992), effects of N-fertilizers (Woledge, 1988), rates of BNF...
and N-transfer (Boller and Nößberger, 1987), effects of elevated CO₂ (Zanetti et al., 1996; Hebeisen et al., 1997; Hartwig and Sadowsky, 2006; Lüscher and Aeschlimann, 2006), and winter survival (Wachendorf et al., 2001).

Results of such experiments have been used to create multi-site statistical models (e.g. Connolly and Wachendorf, 2001). However, the understanding of the mechanisms that determine the co-existence of grasses and clover in binary or multi-species associations still remains incomplete (Thornley, 2001). For this reason, mechanistic or phenomenological models have been developed as tools for analyzing grass/clover systems. Several models have been proposed, with emphasis on the competition for light (Sinoquet et al., 1990; Sinoquet and Bonhomme, 1991; Lantinga et al., 1999; Schulte and Lantinga, 2002), the short-term dynamic response of grass–clover mixtures to changes in the environment and/or management (Ross et al., 1972; Soussana and Oliveira Machado, 2000; Thornley, 2001), the role of feedback regulation for N uptake and BNF in white clover (Soussana et al., 2002), or the long-term dynamics and/or stability of grass/clover communities (Thornley et al., 1995; Schwinning and Parsons, 1996a,b; Schwinning and Parsons, 1999; Louie et al., 2002; Schulte et al., 2003; Schulte, 2003). These models have undoubtedly helped the understanding of fundamental aspects of grass/clover interactions. On the other hand, none of them has been designed and applied to elucidate the possible role of feedback processes driven by biomass partitioning between root and shoot, despite the fact that feedback processes are essential for understanding species dominance (Thornley et al., 1995). For instance, in the Hurley Pasture Model (Thornley, 1998) or the Pasture Simulation Model (Riedo et al., 1998) the clover fraction is treated as a fixed parameter, and root competition is neglected despite the fact that it plays an important role in community dynamics.

The aim of this study was to investigate the dynamics of grass/clover co-existence, and to assess the role of root developmental mechanisms in controlling grass/clover interactions in temperate rotational grassland. A new dynamic grass–clover model PROGRASS (PR0du ctive GRASSland Simulator) was developed to extend computational schemes proposed by Thornley and Johnson (1990), Thornley et al. (1995) and Schwinning and Parsons (1996a) for selected aspects of grass–clover coexistence, and by Thornley (1998) and Riedo et al. (1998) concerning carbon assimilation and plant growth. The approach involved (i) transient simulations to constrain the key parameter values, (ii) model testing against data from a Swiss field site with sown grassland under two management regimes, and (iii) long-term simulations to study the sensitivity to N-fertilization under equilibrium conditions.

2. Methods and data

2.1. Experimental sites and field data

2.1.1. The Swiss FACE experiment

The Swiss Free Air CO₂–enrichment (FACE) experiment of the ETH Zurich (see Schneider et al., 2004) was run from 1993 to 2002 at Eschikon, Switzerland (47° 27’ N and 8° 41’ E, 550 m a.s.l.). The site is characterized by a temperate climate, with annual precipitation of 1090 mm and annual mean temperature of 8.3 °C. The soil is a clay loam, eutric cambisol with ample supply of P, K and Mg, and sand, silt and clay fractions of 0.37, 0.34 and 0.29, respectively (Hebeisen et al., 1997). Rooting depth, bulk density and soil hydraulic properties were not directly measured and had to be estimated. Based on the root distribution for temperate grassland presented by Schenk and Jackson (2002) we assumed a rooting depth of 80 cm. Values of 62 mm d⁻¹ for the saturated soil hydraulic conductivity and of 0.42, 0.26 and 0.13 m² m⁻³ for the soil water content at saturation, field capacity and permanent wilting point, respectively, were calculated from soil texture using the ROSETTA model (Schaap et al., 2001).

The aim of the Swiss FACE experiment was to quantify long-term effects of elevated CO₂ and moderate N inputs (140 kg N ha⁻¹ y⁻¹). With atmospheric deposition of 30 kg N ha⁻¹ y⁻¹ and net mineralization of 30–60 kg N ha⁻¹ y⁻¹, as estimated by Soussana and Oliveira Machado (2000) for this experiment, this amounts to a total N input of roughly 200 kg N ha⁻¹ y⁻¹, which is typical for grassland management in Switzerland. The swards were cut 5 times each year and mineral N was first applied in spring and then after each of the first four cuts in proportions of 30%, 20%, 20%, 15% and 15% of the annual total.

2.1.2. The Oensingen site

A second dataset was obtained from a field experiment running since 2001 at Oensingen, on the Swiss Central Plateau (7° 17’ N, 450 m a.s.l.) (Ammann et al., 2007). At this site, annual rainfall is 1100 mm and annual mean temperature is 9.5 °C. Prior to the experiment, the land was under arable rotation. It was ploughed in November 2000, divided in two fields, which were sown in May 2001 with standard multi-species seed mixtures for two different management regimes.

The intensively managed field (INT) was cut up to five times each year and received mineral fertilizers and liquid cattle manure in amounts of roughly 200 kg total N ha⁻¹ y⁻¹ applied in similar portions after each cut. The extensive field (EXT) received no N fertilizer, was cut three times each year with the first cut not taking place before 1 June.

The soil is classified as stagnic cambisol (eutric), with sand, silt and clay fractions of 0.25, 0.32 and 0.43, respectively, pH 7.3, SOC concentration in the layer 0–30 cm = 27 mg C g⁻¹ soil dry matter, a C:N ratio = 8, and with a high clay fraction of 0.42–0.44. As for the Swiss FACE experiment, we also assumed a rooting depth of 80 cm (Schenk and Jackson, 2002) but values for soil porosity (0.53 m³ m⁻³) and the volumetric soil water content at field capacity and permanent wilting point (0.46 and 0.31 m³ m⁻³, respectively) were available from field measurements. The only soil parameter calculated from soil texture with the help of the ROSETTA model (Schaap et al., 2001) was the saturated hydraulic conductivity. The value of 410 mm d⁻¹ seems too high at first sight, but is consistent with the observed bulk density of 1.16 Mg m⁻³.

In 2001, the organic N content in the top 20 cm was 0.87 kg m⁻² and 0.82 kg m⁻² in INT and EXT, respectively, which is higher than typical contents for temperate grasslands (Jörgabys and Jackson, 2000), suggesting that relatively high amounts of mineral N were available at the start of the experiment.

The floristic composition of the swards was estimated by a visual survey using the method of Braun-Blanquet (1964), although uncertainties of the order of ±20% must be assumed, this method allows tracking the evolution of the clover fraction over time.

The PROGRASS model

A full description of PROGRASS is given in the AppendixAppendix A, but essential features are presented here. Fig. 1 provides an overview of the model structure.

The same formulations for grass and clover are used with respect to carbon (C) assimilation and mineral N uptake, plant respiration, biomass production, allocation of assimilates to shoot and root compartments, and litter production. Plant growth is formulated following Thornley (1998), but for simplicity the shoot and root...
compartments are assumed to consist of one age category only, with parameters appearing in the growth equations modified accordingly. The response of plant processes to temperature (Fig. 2a) and soil water availability (Fig. 2b) are formulated using one and the same functional form for grass and clover, but again plant-specific responses are introduced with an appropriate choice of parameters. Distinct parameterizations are also used to account for the differential effects of water stress on shoot and roots.

Light-relations are modelled assuming a higher extinction coefficient for clover than for grass. Canopy photosynthesis is basically formulated using the equations for binary mixtures developed by Ross et al. (1972) and later used by Thornley and Johnson (1990), which rest on the hypothesis of a homogeneous distribution of the leaves of both species in the horizontal plane. PROGRASS is parameterized to represent mixtures of a tall-growing grass and short-growing white clover cultivars, which are often dominating in Swiss grasslands (see Schwank et al., 1986). Accordingly, the current version of PROGRASS only accounts for the case of grass overtopping white clover. Note, however, that the formalism could be extended to represent situations in which clover overtops the grass companion.

Thus, two cases are distinguished: the first refers to situations when leaf area indices (LAI) of both species are similar and the canopy is assumed to consist of a single mixed layer. The second case refers to situations when grass overtops clover and becomes the dominant component in the upper part of the canopy. In this upper layer, light is exclusively intercepted by the grass.

The choice of the appropriate algorithm is made solely on the basis of the difference in LAI. Grass dominance in the upper part of the sward is assumed whenever the difference in LAI between grass and clover exceeds a given threshold, i.e. LAIg − LAIc > ΔLAI. If this is the case, a leaf-area index LAIg = LAIg + LAIg − ΔLAI is assumed for the upper canopy layer, which is then used to compute the additional light interception by the grass.

To keep the model simple, canopy height is not taken into account for predicting light-relations, albeit its importance in describing the vertical structure of the sward is acknowledged (Faurie et al., 1996). In the simplest case, a diagnostic relation between canopy height and LAI, as proposed, e.g. by Riedo et al. (1998), would have been needed to derive the former from the latter. However, such relations are difficult to parameterize and make the algorithm highly sensitive to the choice of the parameter values.

A key aspect of the model formulation is the allocation of assimilates to shoot and root compartments. PROGRASS makes use of the teleonomic partitioning discussed by Thornley and Johnson (1990, p. 372) and later adopted by Thornley et al. (1995). Species-specific parameters are selected to make the algorithm more flexible. Accordingly, inter-specific differences in allocation are not only induced by differences in substrate C:N ratio, but also by specific plant traits.

Plant growth is modelled as in the Hurley Pasture Model (Thornley, 1998) accounting for the partitioning between plant structural (cell walls and proteins) and plant substrate (more labile components such as sugars and amino acids) C and N components (see Schwinnning and Parsons, 1996a), but for grass the distinction is made between reproductive and vegetative growth (Riedo et al., 1998). Following Riedo et al. (1998), the grass is assumed to be in reproductive stage from the start of the growing season until the time of ear emergence or until the first cut. During reproductive growth, an increasing fraction of substrate C is allocated to the shoot rather than to the root compartment, with a concurrent reduction in the fraction of shoot biomass allocated to lamina. During vegetative growth, the fraction of the grass biomass allocated to lamina is kept constant.

For BNF and mineral N uptake, PROGRASS makes use of the computational scheme developed by Schwinnning and Parsons (1996a) assuming saturating responses to soil mineral N availability: BNF declines but mineral N uptake increases with increasing soil mineral N availability. As opposed to the original formulation, both BNF and mineral N uptake linearly depend on root mass rather than on total structural dry matter. Moreover, the feedback regulation of clover N-uptake by BNF is driven by soil mineral N availability rather than N substrate concentration of the clover component. As seen in Fig. 2c, for the choice of parameter values given in the Appendix competitive advantages in N acquisition result for clover/grass at soil mineral N availability below/above about 10 kg ha⁻¹⁻¹.

The model also includes a minimal description of soil physics, soil N turnover and the transfer of N from clover to grass via decomposition and mineralization (Frame and Newbould, 1986), assuming that no direct transfer of N from the grass to the clover and vice versa takes place. Hence, a soil compartment is added that includes one single soil organic N pool as well as one single soil mineral N pool without separation between nitrate-N and ammonium-N. N input to the soil organic N pool is from litter, which is determined by the specific turnover rates for the shoot and root compartments of grass and clover. Mineralization is formulated as a first-order process and is modified to account for effects of temperature and soil water availability according to Paul et al. (2003). N
losses arising from leaching, emissions of reactive N gases are combined in a single loss term which is proportional to the soil mineral N content (Schwinning and Parsons, 1996a).

Management options include cutting and fertilization but no grazing. Harvest exports reduce biomass and substrate plant C and N pools, while organic and mineral N applications are directly added to the soil organic and mineral N pools. To account for losses during the application of fertilizers, only 80% of the mineral and 70% of the organic N applied effectively enters the soil pools (Dueri et al., 2007).

To ensure numerical stability, PROGRASS is run with an hourly time step, and the Euler scheme is used to integrate the prognostic equations. Initial values are required for the state variables, along with site-specific parameters, management data and hourly meteorological data (including temperature, solar radiation, air vapour pressure, rainfall rate and wind). Optionally, initial values for soil N pools could be obtained from equilibrium simulation. As a rule of thumb, 500–1000 years of integration are necessary to achieve nearly steady-state conditions. Atmospheric deposition is assumed to be evenly distributed from mid February until mid November (Zürcher et al., 2003), totalling to 30 kg N ha\(^{-1}\) y\(^{-1}\). Shoot biomass and LAI are reset to pre-defined values after cutting. Since PROGRASS does not account for winter mortality, a cut is introduced at the end of each year to ensure realistic conditions at the beginning of each growing season. Otherwise, senescence is expressed by shoot and root turnover, with specific responses to temperature and soil water availability as described in the Appendix A.

### 2.3. Model configuration

Most parameter values were simply derived from the literature (Frame and Newbould, 1986; Thornley et al., 1995; Schwinning and Parsons, 1996a; Riedo et al., 1998; Thornley, 1998) or from experimental data. However, for some key parameters the initial values thus obtained were adjusted to more realistically simulate the C and N turnover observed in the Swiss FACE experiment (Section 2.1.1). These adjustable parameters are: the specific unit growth rates, \(G_0^j\); the LAI threshold, \(\Delta_{LAI}\), determining the light relation regime; the maximum specific mineral N uptake rates, \(U_{j,max}\); the maximal BNF rate, \(U_{BNF,max}\); the scaling parameters \(e_{BNF}\) and \(f_{UC}\) defining N acquisition rates; and, the parameters determining the allocation of C to the shoot and root, \(K_{Cj}\) and \(K_{Nj}\).

To constrain these parameters, equilibrium simulations were run for grass and clover in monoculture and for grass and clover

### Table 1

Simulated and observed mean values of annual quantities for grass and clover grown in monoculture and in mixture at the Swiss FACE field site (1998–1999). Results refer to the low N treatment and ambient CO\(_2\). Annual N-input from fertilization and atmospheric N deposition was 170 kg N ha\(^{-1}\) y\(^{-1}\).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Monoculture</th>
<th>Mixture</th>
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<tbody>
<tr>
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<td>Grass</td>
<td>Clover</td>
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<td>Simulation</td>
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<td>Simulation</td>
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<td>Yield(^a) 1998</td>
<td>8.7</td>
<td>5.8–8.5</td>
<td>11.8</td>
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<tr>
<td>Yield(^a) 1999</td>
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<td>6.9–9.1</td>
<td>11.6</td>
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<tr>
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<td>2.95</td>
<td>1.2–2.7</td>
<td>0.76</td>
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<tr>
<td>Root(^b) 1999</td>
<td>2.85</td>
<td>NA</td>
<td>0.73</td>
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<tr>
<td>BNF(^c) 1999</td>
<td>–</td>
<td>–</td>
<td>127</td>
</tr>
<tr>
<td>N-uptake(^c) 1998</td>
<td>190</td>
<td>103–209</td>
<td>147</td>
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NA: Not available.

\(^a\) Annual specific yield in (t ha\(^{-1}\) y\(^{-1}\)).

\(^b\) Specific root biomass measured and simulated at November in (t ha\(^{-1}\)).

\(^c\) Annual sum of BNF and mineral N-uptake in (kg ha\(^{-1}\) y\(^{-1}\)) for control ring 1 and 3, respectively.
in mixture, using hourly meteorological data from the automatic meteorological weather station maintained by the Swiss Federal Office of Meteorology and Climatology (MeteoSwiss) at Kloten (8°32’ E, 47°29’ N, 436 m a.s.l.), a site located about 7 km from the FACE field. The results were contrasted with observed values of specific yield and LAI at each cut, the annual sum of specific soil mineral N uptake and the annual sum of BNF, and the root dry mass as observed in monoculture at the end of the season (November). A maximal departure of 15% between simulations and observations was used as the criterion for the adjustment.

Regarding $U_{j_{\text{max}}}$ and $U_{\text{BNE}_{\text{max}}}$. We initially relied on the values proposed by Schwinning and Parsons (1996a), but scaled in such a way as to account for the fact that in PROGRASS they are related to root fraction rather than total biomass. For scaling purposes, we assumed a root fraction of 0.5 and 0.2 for grass and clover, respectively. Moreover, as opposed to Schwinning and Parsons (1996a), $U_{j_{\text{max}}}$ and $U_{\text{BNE}_{\text{max}}}$ were assumed to be regulated by soil temperature, as described in the Appendix.

**Fig. 3.** Simulated LAI development of grass and clover in monoculture (a and c) and mixtures (b and d) for the low N treatment (140 kg N ha$^{-1}$ y$^{-1}$) and ambient CO2 at the Swiss FACE field trial (1998–1999). Bars indicate the range of observations in two replicate blocks.

For grass in monoculture (Fig. 3a), simulated LAI development was in good agreement with observations in both years (RMSE of 0.34 m$^2$ m$^{-2}$). The same holds true for simulated annual yields (8.7 t ha$^{-1}$ y$^{-1}$) and, to a lesser extent, for root biomass at the end of the growing season (2.95 t ha$^{-1}$ in 1998). Concerning the latter, however, there was a tendency for the simulations to be in the upper range of the observations (Table 1). Good agreement was also found with respect to mineral N uptake (190–195 kg ha$^{-1}$ y$^{-1}$, Table 1).

For clover in monoculture, the annual course of LAI was less well captured by the model (RMSE of 0.69 m$^2$ m$^{-2}$), mainly because of a significant overestimation of the observed LAI during the fourth and fifth re-growth (Fig. 3c). For the same reason, annual clover yield was overestimated by the model (Table 1).

By allowing for specific traits in the allocation of assimilates (see Section 2.1), differences in root biomass between grass (2.9 t ha$^{-1}$) and clover (0.75 t ha$^{-1}$) were realistically predicted by PROGRASS (Table 1). Due to the supply of mineral N through fertilization, mineralization and deposition, rates of soil mineral N uptake by clover (147–149 kg N ha$^{-1}$ y$^{-1}$) were comparable to rates of BNF (127–134 kg N ha$^{-1}$ y$^{-1}$). For both fluxes, simulations differed from observations by less than 5%

For LAI of mixtures, the model performed better than for monocultures (RMSE of 0.28 m$^2$ m$^{-2}$ for grass and of 0.30 m$^2$ m$^{-2}$ for the clover). Concerning N acquisition, the largest departure from the observations was less than 10% (Table 1). Here, the only exception was the rate of mineral N uptake by clover, which was underestimated by the model.

In mixtures, competition for light and soil mineral N reduced C and N acquisition rates for both species relative to the monocultures, limiting the overall growth rates (Fig. 3b and d). The greater reduction (up to 50%) was found for yield, LAI and mineral N uptake in clover, thus indicating that under this type of management the grass was more competitive than its companion. Grass dominance was further favoured by the disproportion in root mass (about 1.71–1.75 t ha$^{-1}$ for grass as compared to 0.47–0.50 t ha$^{-1}$ for clover). As a consequence, annual total mineral N uptake by the grass in mixture of 169–172 kg ha$^{-1}$ y$^{-1}$ was nearly equivalent to the rate simulated for the monoculture (190–195 kg ha$^{-1}$ y$^{-1}$, Table 1).

For clover, the smaller root biomass in mixture limited competition for soil mineral N uptake (23–25 kg N ha$^{-1}$ y$^{-1}$) and impaired BNF (95–101 kg N ha$^{-1}$ y$^{-1}$). However, as seen in Table 1 the model tends to underestimate mineral N uptake by clover grown in mixtures, while still providing an acceptable prediction of the relative difference in mineral N uptake between monoculture and mixture.

### 3. Results

#### 3.1. Transient simulations

The model was tested by comparing simulation results with independent observations at the Oensingen site covering the period between May 2001 (sowing of the swards) and December 2005. Transient simulations were run assuming that all initial seedling mass was root biomass ($W_{\text{rt},c} = 0.001$ kg m$^{-2}$ and $W_{\text{rt},g} = 0.003$ kg m$^{-2}$). Initial values for the soil organic N stocks were set at 0.87 (INT) and 0.82 kg m$^{-2}$ (EXT), and soil mineral N pool at the start of the simulations at 0.001 kg N m$^{-2}$.
The difference in aboveground (shoot) biomass between the two management regimes was well captured by the model (Fig. 4), but measurements at the times of the harvest were more accurately reproduced for INT (RMSE = 0.13 kg m⁻²) than for EXT (RMSE = 0.18 kg m⁻²). The agreement between simulations and observations was best for the first two growth periods, whereas for later growth periods the model overestimated clover and thus total shoot biomass. Nevertheless, the model correctly reproduced the patterns of the clover fraction, values of roughly 60% persisting throughout the years in EXT (Fig. 4d), but declining to about 20% in 2004 and 2005 in INT (Fig. 4c). It should be added that the higher cutting frequency on the INT field resulted in a lower yield at harvest than on the EXT field. Note, however, that the annual yield is greater on the INT than on the EXT field.

Results for root biomass in relation to soil mineral N, plant N uptake and photosynthesis were used to test the possibility that the timescale for the dynamics of the grass/clover biomass ratio depended on the development of the grass root system. For both management regimes, mineral N availability was highest during the initial months after sowing (Fig. 5a and b) due to high mineralization rates in the presence of small rates of root N-uptake (Fig. 5e and f). Later, the large difference in mineral N availability between INT and EXT was caused by the application of 200 kg N ha⁻¹ y⁻¹ on INT.

Importantly, Fig. 5 reveals a striking difference between INT and EXT in terms of the dynamics of root development. While in EXT the root system of both components was in a quasi steady-state already 1 year after sowing, in INT a steady state was observed only in 2004 and 2005 when root biomass settled to 3.2 t ha⁻¹. In INT, the difference in the N uptake between 2002 and the two following years was related to higher C:N ratios and, consequently, increased C allocation to roots (Fig. 6e).

Thus, during the reproductive growth of 2002 less leaf area (LAI) developed than in 2003 and 2004 when C allocation to roots was smaller and C:N ratios were lower (Fig. 6g). This suggests that the patterns of shoot development shown in Fig. 5g were related to feedbacks between mineral N acquisition, shoot/root allocation and root development initiated during the reproductive phase of grass growth and amplified by the first application of N fertilizer in early spring. In EXT with no N addition, limited mineral N availability consistently led to higher C:N ratios, which eventually resulted in preferential allocation to the roots in grass in all 3 years.

### 3.2. Competition and feedbacks

The mechanisms underlying the different transient patterns of grass root and shoot development in INT and EXT were further analyzed by comparing the situation during the reproductive growth period in the 3 years 2002, 2003 and 2004. As shown in Fig. 6a and b, cumulative amounts of N acquired by the grass in INT by day of the year (DOY) 140 was about 45 kg N ha⁻¹ in 2002, and 60 kg N ha⁻¹ in 2003 and 2004, which was much larger than in EXT, with only 20–30 kg N ha⁻¹ in all 3 years. In INT, the difference in the N uptake between 2002 and the two following years was related to higher C:N ratios and, consequently, increased C allocation to roots (Fig. 6e).

Conversely, in INT grass was the dominant component with respect to N acquisition. A clear competitive advantage for the grass component became apparent already in 2002 in relation to N uptake (260 kg N ha⁻¹ y⁻¹, compared to 175 kg N ha⁻¹ y⁻¹ for the sum of N uptake and BNF in clover). This was similar to the amount simulated for the following years, except 2003 when N uptake was inhibited by extremely dry soil conditions. This shows that in INT reduced N uptake in grass only occurred during the first year. Nevertheless, it was clearly in 2004 and 2005 that grass was able to significantly out-compete clover for light interception and photosynthesis, which calls for additional explanations.

### 3.3. Long-term sensitivity to N-fertilization

The response of the grass–clover system to longer term fertilization, when steady-state could be expected for the root system of both components, was tested with repeated cycles of the 1981–2005 weather, assuming five cuts annually and mineral N application rate varying from 0 to 300 kg N ha⁻¹ y⁻¹ in steps of 25 kg N ha⁻¹ y⁻¹.

Increasing N fertilization reduced the fractional biomass of clover from 75 to 20% at the highest application rate (Fig. 7a). Qualitatively, the negative impact of fertilization on the clover fraction was found in both equilibrium runs (ER) and transient runs (TR) over the same 25-year period. However, in TR the response depended on the initial soil organic N content, thus confirming the results of
Fig. 5. Simulated (2001–2005) mineral N availability (a and b), specific root biomass (c and d), cumulated total N acquisition (e and f) and cumulated photosynthesis (g and h) for the INT (left) and the EXT (right) managed fields at Oensingen. In (c)–(h) a thin black line refers to grass, whereas a bold grey line refers to clover.

the short-term transient simulations presented above. It should be noted that in PROGRASS soil organic N net turnover has a characteristic timescale of the order of $10^1$ to $10^2$ years, i.e. larger than the decadal scale of transient simulations, which in turn is larger than the characteristic timescale required for establishing the root system. This sensitivity to the initial conditions in soil organic N does not show up when plotting the clover fraction against soil mineral N content (Fig. 7b), thus indicating that in the presence of a fully developed root system the growth of grass and clover was uniquely determined by soil mineral N availability.

Aboveground grass biomass (yield) increased with fertilization rate from 2.5 to more than 12 t ha$^{-1}$ y$^{-1}$, while the fraction of C allocated to roots declined with increasing fertilization from more than 35% to 10% (Fig. 8a). Concurrently, clover yield decreased from 7 to 2.5 t ha$^{-1}$ y$^{-1}$ (Fig. 8b). Root biomass of grass increased to a maximum of 2.7 t ha$^{-1}$ for an annual fertilization rate of roughly 180 kg N ha$^{-1}$ y$^{-1}$, and decreased at higher applications (Fig. 8c). The response to N addition of C-partitioning and root biomass in clover was opposite to that in grass.

N-uptake in grass increased with N addition while BNF in clover declined (Fig. 9a). The similarity in the N-response of LAIm$^*$ and of the ratio of grass to clover photosynthesis ($P_g/P_c$) suggested that LAIm$^*$ was strongly controlled by competition for light (in Fig. 9b).

4. Discussion

4.1. Model comparison

PROGRASS was designed to realistically simulate the response of a managed, mixed grassland to observed environmental conditions. In many respects, PROGRASS is similar to previously published models by Ross et al. (1972), with which it shares the overall structure and some of the mathematical formulations, Thornley et al. (1995), Schwinning and Parsons (1996a), Riedo et al. (1998) or Thornley (1998). Plant growth is calculated according to Thornley et al. (1995) and Schwinning and Parsons (1996a). Their models, however, do not account for the effects of climate on plant development, and the latter model ignores root growth, which is essential for understanding water and nutrient uptake. Moreover, similarly to PASIM (Riedo et al., 1998), PROGRASS distinguishes between the reproductive and vegetative growth phase of the grass component, which may play an important role in relation to the seasonal evolution of the clover fraction.

More parsimonious models (Schulte et al., 2003; Louie et al., 2002) of grass/clover co-existence treat grass and clover separately but do not explicitly consider soil N pools, neglect plant respiration, and do not distinguish between substrate and structural C and N. This also applies to pure shoot population models (Acevedo and
Raventós, 2002; Segarra et al., 2005), which consider growth of multiple grass species in a mixed community exclusively in terms of shoot variables such as shoot length or the number of shoot tips. In these models, shoot growth is controlled by dynamic competition among species and by specific physiological traits such as the rate for new shoot formation or coefficients for inter-specific competition effects on growth. However, below-ground mechanisms related to growth are neglected.

Compared with other models, PROGRASS was specifically parameterized for simulating the dynamics of a productive mixture of *Lolium perenne* L. and *Trifolium repens* L. under temperate climate conditions. This parameterization is more specific than in generic ecosystem models such as DAYCENT (Parton et al., 1998). Other mechanistic grassland models such as the grassland simulator PASIM (Riedo et al., 1998) and the Hurley Pasture model HPM (Thornley, 1998) include more elaborate formulations for plant processes (including mineral N-uptake), plant variables (e.g. shoot separation between lamina, stem and ear) or soil biology (multiple soil C and N pools). But, as already mentioned, PASIM and HPM do not simulate grass and clover interactions and specify the clover fraction as a fixed parameter.

The possibility to extend the HPM to predict the seasonal dynamics of the fraction of legume was considered by Thornley (2001), but rather than being mechanistic this approach is phenomenological. In this version of the HPM, a target fraction of legume is initially assumed to asymptotically depend on the whole-plant substrate C:N ratio. The rate at which the actual legume content approaches the target content is determined by the gross specific growth rate of the pasture. Simulation results with the modified HPM suggest that the phenomenological approach captures the seasonality of the legume fraction. On the other hand, use of a phenomenological model precludes detailed investigation of particular competitive processes, as noted by Thornley (2001). This type of analysis could be important for instance for understanding the response of grassland dynamics to changes in the radiation regime.

In terms of light interception, PROGRASS makes use of the same formulation of Beer’s extinction law, which has been proven useful in applications of GEM2 (Chen et al., 1996), HPM, (Thornley, 1998) and Sim-CYCLE (Ito and Oikawa, 2002). However, PROGRASS does not calculate a vertical radiation profile in the canopy as in Lantinga et al. (1999) and Riedo et al. (1998), and competition for light does not explicitly account for changes in the vertical structure of the canopy.
Fig. 7. Response of the clover fraction to: (a) mineral N fertilization in equilibrium (ER, repeated cycles of 1981–2005) and in transient runs (TR, 1981–2005); and, (b) to soil mineral N availability. Results of the equilibrium runs (dots) are averages over the last 25-year cycle. Initial organic N conditions for the transient runs (empty symbols) are 0.00, 0.87 and 2.00 kg N m$^{-2}$.

Fig. 8. Long-term response of specific allocation to root (a), yield (b) and root biomass (c) to increasing rates of mineral N fertilization.

Fig. 9. Long-term response of (a) mineral N uptake and BNF and (b) LAI and grass/clover ratio of photosynthesis ($P_g/P_c$) to increasing rates of mineral N fertilization.

The simulations stress the importance of N acquisition and allocation in determining the co-existence of grass and clover in binary swards when grass growth is favoured by fertilization. This occurs in two ways: firstly, high N uptake rates reduces the substrate C:N ratio, entailing preferential allocation to the shoot compartment and eventually leading to the situation where grass takes advantage of the possibility to overtop clover and to assimilate C more efficiently than clover, albeit a smaller light extinction coefficient. Competitive advantages of the grass component in light interception for a management with infrequent cuts and N fertilization was found in field trials by Schwank et al. (1986). Secondly, grass can quite generally profit from a larger root biomass, while clover acquires a significant fraction of N through BNF. Grass dominance as found here for fertilization rates in excess of 200 kg N ha$^{-1}$ y$^{-1}$, with fractions of clover of less than 30%, agrees well with the experimental results of Haynes (1980), Schwank et al. (1986), and Lüscher and Aeschlimann (2006).

At high rates of fertilization, clover competition is weak due to small shoot and root biomass, and low rates of BNF and mineral N uptake. However, these differences in competition obviously depend on plant traits. Here, we considered a tall cultivar of $L$. perenne but a short cultivar for $T$. repens. This choice was based on the available experimental data (Hebeisen et al., 1997; Daepp et al., 2001; Jäggi et al., 2006). Notice that clover grown in association with short grasses would compete better because of less shading by the grass (Woleadge, 1988; Woleadge et al., 1992).

The relative differences between monoculture and mixture observed in the FACE experiment with respect to mineral N uptake by clover are nicely reproduced by the model (Table 1). Nevertheless, PROGRASS tends to underestimate mineral N uptake by clover in mixtures. Since the simulated N fluxes and root biomass in monoculture match the observations, a possible reason for this behaviour is an under-/overestimation of clover/grass root biomass. Unfortunately, this hypothesis cannot be directly tested as observations of the root biomass in mixtures are not available from the FACE experiment. In theory, the underestimation of mineral N uptake entails competitive disadvantages for clover, but this does
not appear to negatively affect the simulations of the Oensingen field trials (Fig. 4), as observed and simulated clover fractions are in good agreement for both treatments.

The introduction of a reproductive growth phase for grass in the model was important to explain the increased grass shoot biomass in spring and early summer and the ability of grass to out-compete clover in terms of photosynthesis, in agreement with field data provided by Dennis and Woldage (1985). However, this mechanism can only operate in the presence of a fully developed root system, as during the reproductive stage the biomass partitioning to roots is reduced, limiting the acquisition of soil resources.

In our simulations, the clover fraction had a seasonal peak around July (Fig. 4), in agreement with the field data of Hebeisen et al. (1997). The equilibrium response of the mixture to fertilization (Figs. 7–9) qualitatively agrees with that obtained by Soussana and Oliveira Machado (2000) for a similar cutting regime, but PROGRASS predicted lower clover fractions and a more rapid decline with increasing mineral N applications. This suggests a stronger sensitivity of the clover fraction to fertilization in PROGRASS, which is supported by observations. Note that the simulated clover fraction of 30% at a fertilization rate of 140 kg N ha$^{-1}$ y$^{-1}$ agrees well with the 29% observed as an average for the same type of mixture by Lüscher and Aeschlimann (2006). With increasing fertilization, root biomass fractions (not shown here) revealed declining trends, in agreement with Soussana and Oliveira Machado (2000), but the root fractions obtained here were higher for both components. The discrepancy may be due to the fact that here we present values averaged over all growth periods from 1981 to 2005, while Soussana and Oliveira Machado (2000) provided data only for the last regrowth period.

The simulations demonstrated the importance of root development and feedback processes in determining the co-existence of grass and clover. In the transient simulations, grass root development after sowing was more important for the grass/clover dynamics than clover root development. Only after reaching a quasi-steady-state in the root system, the grass was able to out-compete clover for light. In fact there was little preferential allocation to the grass shoot during the first 2 years because mineral N uptake in spring was either limited by soil N availability and/or small root activity. While this mechanism seems important in rotational grasslands, it may be of little relevance for permanent grassland (Davies, 1988).

From a morphological point of view, the root systems of grasses and clover differ quite markedly (Evans, 1977, 1978). In temperate, productive grasslands the root mass of grass exceeds that of clover root by up to a factor of 10 (Hebeisen et al., 1997; Castle et al., 2002); resulting root:shoot ratios are therefore only of the order of 0.1–0.2 for clover (Thomas, 1987; Singh and Sale, 2000) but as high as 0.5–1.6 for grass (Vinthor, 2006). In a 4-year-old grass/clover mixture, white clover roots amounted only to 6% of the total root weight (see Young, 1958 in Whitehead, 1995b). Here, the grass:clover ratio of root biomass varied with time and with management regime (Fig. 5). In the low-intensity management regime (EXT), the fractional clover root biomass was relatively constant at around 30%, whereas in INT the fraction declined over the years to values below 15%. This dynamics in INT has implications for above-ground biomass and competition for light, as shown by the longer term response of the mixture to increasing clover N-input.

The result in Figs. 8 and 9 suggested the existence of three regimes characterizing the co-existence of grass and clover: (1) For N applications of less than 100 kg N ha$^{-1}$ y$^{-1}$, soil mineral N scarcity limits mineral N uptake by clover but promotes BNF, thus provides competitive advantages to the clover both in relation to N acquisition (i.e., mineral N uptake plus BNF) as well as photosynthesis; (2) For N applications in the range of 100–200 kg N ha$^{-1}$ y$^{-1}$ a transient regime appears with a shift in dominance from clover to grass mainly as a result of increased C partitioning to roots in grass; (3) For N-applications exceeding 200 kg N ha$^{-1}$ y$^{-1}$ grass dominates because of higher rates of both N uptake and photosynthesis.

These patterns are generally valid, but may differ in their specific characteristics depending on initial conditions and time horizon. Our simulations suggested that the influence of the initial soil organic N content is retained for a much longer time than is necessary for establishing the root system. Quantitatively, the results show that in the short-term the clover fraction is nearly inversely proportional to the initial organic N content, decreasing from 60 to 30% in extensive systems when the soil organic N stock increases from about 1 to 2 kg N m$^{-2}$. Hence, past land use has a marked effect on the composition and also on the potential productivity of rotational grasslands.

This further suggests that soil biology is in some circumstances essential for driving the grass–clover interactions. In PROGRASS, only a simple scheme is available for keeping track of the soil mineral and organic N pools. Revisiting this approach will be necessary for examining the effects of clover on the accumulation of soil organic matter. A further limitation of the model is the lack of consideration of winter mortality and spatial root expansion, the former being the likely reason for the overestimation of clover shoot biomass in autumn. Based on the experiences made so far with PROGRASS, it is expected that this overestimation of clover shoot biomass late in the year is more pronounced in monocultures than mixtures, which are the systems of interest. The comparison of simulations and observations for both fields at the Oensingen site suggests that the overestimated clover shoot biomass in autumn has minor effects on the mixture dynamics.

In this context, we finally remark that Frankow-Lindberg (1997) found preferential allocation to the root compartment and interpreted this as a strategy to improve winter survival. In addition, Boller and Nösberger (1983) proposed that preferential allocation to the roots during autumn may reflect a response to lower temperatures and the short photoperiod. It is clear that these processes need to be included in future versions of the model in order to obtain realistic year-round simulations of the grass/clover dynamics, and to investigate longer term changes in properties such as soil organic matter.

5. Conclusions

- Interactions between grass and clover in binary mixtures after sowing are related to negative and positive feedbacks in the soil–plant system that are strongly controlled by root development of the grass component.
- Under an extensive management, clover is the dominant component because limited availability of soil mineral N and N acquisition capacity of grass roots immediately after sowing deplete the substrate C:N ratio, causing preferential allocation of assimilates to the roots. As a result, the grass is incapable of generating enough leaf area to compete with clover for light, which further limits shoot growth and eventually prevents the formation of a competitive root system, thus closing the negative feedback loop.
- Under intensive fertilization, grass rapidly becomes the dominant component due to a series of positive feedbacks. These are initiated by a preferential allocation of assimilates to roots causing rapid growth of the root system. In turn, this lowers the C:N ratio of the substrate leading to preferential allocation of assimilates to the shoot and, consequently, grass out-competes clover for light.
- With the new model PROGRASS, independent data from a field experiment could be reproduced reasonably well. The model simulations provided insights into the mechanisms responsible for species dominance in response to time and management. However, further extensions of the model will be necessary to better
account for the interaction of the influence of climatic factors and management on soil properties such as C and N stocks.

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Appendix A. Model description

In PROGRASS, the dynamics of grass (Lolium perenne L.) and clover (Trifolium repens L.) is essentially described by the same equations. These equations are given in the following appendix sections and all the used variables and parameters are listed in tables at the end of each section. To keep the model description concise, a subscript j is therefore introduced to distinguish between the grass (j = g) and clover component (j = c). Similarly, a subscript i is used to denote either the shoot (i = sh) or root (i = rt) compartment.

A.1. Biomass development (Table A1)

Assuming only one tissue category per structural component, biomass development is expressed as the rate of change in structural dry matter (W_{ij}, in kg DM m^{-2}) of one shoot and root pool, given by the difference between growth (G_{ij}), decay or litter production rate (D_{ij}) and, for shoot, loss by harvest (Y_{sh,j}):

\[
\frac{dW_{sh,j}}{dt} = G_{sh,j} - D_{sh,j} - \frac{\delta(t - t_{cut})}{\Delta t} Y_{sh,j} \tag{A1.1}
\]

\[
\frac{dW_{rt,j}}{dt} = G_{rt,j} - D_{rt,j}
\]

Here \(\delta\) is a unit impulse function, which evaluates to 1 when time \(t\) is equal to \(t_{cut}\), one of the scheduled times for harvest, and to 0 otherwise, and \(\Delta t\) is the time step of integration (1 h or 0.0416667 d, in the present model setup). The growth rate of the structural dry matter components is determined by the total growth rate (\(G_{ij}\)) and the partitioning (\(\phi_{ij}\)) to the shoot and root compartments. The total growth rate \(G_{ij}\) is calculated from the growth rate constant (\(G_{ij}^0\)), the substrate concentration of carbon (\(C_{ij}\)) and nitrogen (\(N_{ij}\)), and the available total dry matter (\(W_{sh,j} + W_{rt,j}\)), with down-regulation by species-specific response functions for temperature (\(T_{ij}^f\)) and soil water availability (\(t_{sh,j}\)):

\[
G_{ij} = G_{ij}^0 C_{ij} N_{ij} (W_{sh,j} + W_{rt,j}) T_{ij}^f \tag{A1.2}
\]

Following Thornley and Johnson (1990) and Thornley et al. (1995) the allocation of assimilates to either the shoot or root compartment is found by maximizing plant specific growth rates during balanced exponential growth. This leads to:

\[
G_{sh} = \Phi_{sh,j} G_{ij}
\]

where the partitioning functions given by

\[
\begin{align*}
\phi_{sh,j} &= \frac{\psi_j}{1 + \psi_j} \\
\phi_{rt,j} &= \frac{1}{1 + \psi_j} = 1 - \phi_{sh,j}
\end{align*}
\]  

(1.14)

with

\[
\psi_j = \frac{W_{sh,j} (k_{C,j} + C_{ij}) N_{ij}}{W_{sh,j} (k_{N,j} + N_{ij})} \tag{A1.5}
\]

and parameters \(k_{C,j}\) and \(k_{N,j}\).

During the reproductive growth stage, grass preferentially allocates the freshly synthesized structural matter to the shoot compartment. The allocation functions for grass are hence modified according to Riedo et al. (1998) as

\[
\begin{align*}
\hat{\phi}_{sh,g} &= \phi_{sh,g} + (1 - \lambda_{rep}) \phi_{rt,g} \\
\hat{\phi}_{rt,g} &= \lambda_{rep} \phi_{rt,g} = 1 - \phi_{sh,g}
\end{align*}
\]

(1.6)

where \(\lambda_{rep} < 1\) during reproductive but \(\lambda_{rep} = 1\) during vegetative growth.

Grass developmental stage (DS_g) is calculated as in Riedo et al. (1998) as a normalized temperature sum:

\[
DS_g = \frac{\sum_{t=0}^{T_{rd}} \text{MAX}(0, T_{rd} - T_{base,g})}{f_{DC2} \text{rep}_{g}} \tag{A1.7}
\]

where \(T_{rd}\) is the running mean air temperature for a period of 7 consecutive days, \(T_{base,g}\) a base temperature defining the start of the growing season (\(T_{rd} \geq T_{base,g}\)) and \(f_{DC2}\) a normalization factor. The transition from reproductive to vegetative growth takes place at \(DS_g = DS_{veg}\).

During reproductive growth, \(\lambda_{rep}\) linearly decreases with DS from 1 at start to \(\lambda_{rep,ear}\) at ear emergence (\(DS_g = DS_{veg}\)), remaining at \(\lambda_{rep} = \lambda_{rep,ear}\) thereafter:

\[
\lambda_{rep} = \lambda_{rep,ear} + (1 - \lambda_{rep,ear}) \text{MAX} (0, \left[1 - \frac{DS_g}{DS_{veg}}\right]) \tag{A1.8}
\]

The litter production rate (\(D_{ij}\)) from decomposed shoot and root structural dry matter is calculated as the product of structural dry matter (\(W_{ij}\)) and specific turnover rate (\(k_{ij}\)):

\[
D_{ij} = k_{ij} W_{ij} \tag{A1.9}
\]

The turnover rate \(k_{ij}\) is equal to \(k_{ij}^0\) at 20°C and increases with increasing temperature and decreasing soil water availability according to (Thornley, 1998):

\[
k_{ij} = k_{ij}^0 \left[1 - \left(\frac{T_{i,j}}{T_{i,j}^0}\right)\right] \tag{A1.10}
\]

As remarked by Frame and Newbould (1986) turnover rates for above-ground biomass for grass and clover are comparable. We therefore set \(k_{sh,c} = k_{sh,g}\) and likewise assume \(k_{rt,c} = k_{rt,g}\).

For both species, LAI development is calculated analogously to (A1.11) as

\[
\frac{dLAI_{i,j}}{dt} = G_{LAI_{i,j}} - D_{LAI_{i,j}} - \frac{\delta(t - t_{cut})}{\Delta t} Y_{LAI,sh} \tag{A1.11}
\]

with growth rate \(G_{LAI_{i,j}}\), decay rate \(D_{LAI_{i,j}}\) and harvest losses \(Y_{LAI,sh}\). Following Riedo et al. (1998), \(G_{LAI_{i,j}}\) is expressed as a function of the shoot growth rate (\(G_{sh,i,j}\)), the specific leaf area (SLA_{i,j}), the substrate C concentration (\(C_{i,j}\)), a specific lamina area constant (\(\zeta_{i,j}\)) and the fraction of the vegetative shoot growth allocated to the lamina (\(\phi_{lam,sh}\)):

\[
G_{LAI_{i,j}} = SLA_{i,j} (1 - \zeta_{i,j}) \phi_{lam,sh} G_{sh,i,j} \tag{A1.12}
\]

Using a similar approach as for shoot, the LAI decay is calculated as

\[
D_{LAI_{i,j}} = k_{sh,i,j} LAI_{i,j} \tag{A1.13}
\]

For grass, the fraction of shoot biomass allocated to the lamina depends on the developmental stage (Riedo et al., 1998). During vegetative growth \(\phi_{lam,sh} = \phi_{lam,veg}\). During reproductive growth,
Variables and parameters used in the formulation of biomass development.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Description</th>
<th>Values and units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C_j, N_j + g, c$</td>
<td>Carbon and nitrogen substrate concentrations</td>
<td>kg C (kg DM)$^{-1}$, kg N (kg DM)$^{-1}$</td>
</tr>
<tr>
<td>$D_{l,j} = lsh, j + g, c$</td>
<td>Litter or decomposed structural dry matter flux from the shoot and root</td>
<td>kg DM m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$D_{SE,g}$</td>
<td>Developmental stage of grass</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$G_j + g, c$</td>
<td>Total growth rate</td>
<td>kg DM m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$G_{sh,j} + g, c$</td>
<td>Growth rate of the shoot and root compartments</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$k_{i,j} = lsh, rt; j + g, c$</td>
<td>Turnover rates</td>
<td>m$^{2}$ leaves (m$^{2}$ ground)$^{-1}$ d$^{-1}$</td>
</tr>
<tr>
<td>$L_{g,j} + g, c$</td>
<td>Leaf area index</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$t_{cut}$</td>
<td>Scheduled times of harvesting</td>
<td>d</td>
</tr>
<tr>
<td>$t_{air}$</td>
<td>Air temperature at reference height</td>
<td>°C</td>
</tr>
<tr>
<td>$T_{7d}$</td>
<td>Running mean temperature of consecutive 7 days</td>
<td>°C</td>
</tr>
<tr>
<td>$W_{l,j} = lsh, rt; j + g, c$</td>
<td>Structural dry matter</td>
<td>kg DM m$^{-2}$</td>
</tr>
<tr>
<td>$Y_{l,j} + g, c$</td>
<td>Harvest loss of the leaf-area index</td>
<td>m$^{2}$ leaves (m$^{2}$ ground)$^{-1}$</td>
</tr>
<tr>
<td>$Y_{sh,j} + g, c$</td>
<td>Yield</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Volumetric soil water content</td>
<td>m$^{3}$ water (m$^{3}$ soil)$^{-1}$</td>
</tr>
<tr>
<td>$\lambda_{rep}$</td>
<td>Factor describing the preferential allocation of dry matter to shoot during the reproductive growth of grass</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\phi_{l,j}, \psi_{l,j} = lsh, rt; j + g, c$</td>
<td>Functions determining the allocation of newly synthesized dry matter to shoot and root</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\phi_{l,m}, \phi_{g,j} + g, c$</td>
<td>Fraction of the grass shoot growth allocated to lamina</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>$\phi_{h,c}, \phi_{l,c}$</td>
<td>Modified partitioning functions for grass during reproductive growth</td>
<td>Dimensionless</td>
</tr>
</tbody>
</table>

however, $\phi_{l,m,g}$ declines with $D_{SE,g}$ from a maximum $\phi_{l,m,\text{max}}$ at the start of the growing season to a minimum $\phi_{l,m,\text{min}}$ at ear emergence ($D_{SE} = D_{SE,d}$), remaining at $\phi_{l,m,g} = \phi_{l,m,\text{min}}$ for the rest of the reproductive growth phase:

$$\phi_{l,m,g} = \phi_{l,m,\text{min}} + (\phi_{l,m,\text{max}} - \phi_{l,m,\text{min}}) \text{MAX} \left[ 0, \left( 1 - \frac{D_{SE}}{D_{SE,d}} \right) \right] \quad (A1.14)$$

A.2. Plant C and N substrate pools (Table A2)

A.2.1. Balance equations

Assuming that there is only one lumped substrate C and N pool for the shoot and root compartments, the differential equations expressing the plant C and N substrate balances are given by

$$\frac{dW_{C,j}}{dt} = P_j - \frac{Y_{C,j}}{\dot{\gamma}_j} (G_{sh,j} + G_{rt,j}) - R_{m,j} - R_{u,j} - \frac{\delta(t - t_{cut})}{\Delta t} Y_{C,j} \quad (A2.1)$$

$$\frac{dW_{N,j}}{dt} = U_k - \frac{Y_{N,j}}{\dot{\gamma}_j} (G_{sh,j} + G_{rt,j}) - \frac{\delta(t - t_{cut})}{\Delta t} Y_{N,j} \quad (A2.2)$$

$$\frac{dW_{N,c}}{dt} = U_k + U_{BNF} - \frac{Y_{N,c}}{\dot{\gamma}_j} (G_{sh,j} + G_{rt,j}) - \frac{\delta(t - t_{cut})}{\Delta t} Y_{N,c} \quad (A2.3)$$

According to (A2.1), the substrate C pool ($W_{C,j}$) is fed by canopy photosynthesis ($P_j$). It is depleted by the C output for growth (second term on the right-hand side of $A2.1$), maintenance respiration ($R_{m,j}$), respiration associated with N acquisition ($R_{u,j}$), and harvest ($Y_{C,j}$). It is assumed that the fraction of substrate C utilized for growth ($Y_{C,j}$) and the growth efficiency ($\dot{\gamma}_j$) are constant.

According to (A2.2) and (A2.3), the substrate N pool ($W_{N,j}$) is fed by mineral N uptake ($U_k$) and, for clover, BNF ($U_{BNF}$). It is depleted by the N output to growth (second, respectively third term on the right-hand side of $A2.2$, respectively $A2.3$) and harvest ($Y_{N,j}$). Again, it is assumed that the fractional N content ($Y_{N,j}$) in the structural pool is constant.

The C and N substrate concentrations ($C_j$ and $N_j$) are defined as the ratio of the substrate pools and the total biomass:

$$C_j = \frac{W_{C,j}}{W_{sh,j} + W_{rt,j}} \quad (A2.4)$$

$$N_j = \frac{W_{N,j}}{W_{sh,j} + W_{rt,j}}$$

A.2.2. Canopy photosynthesis in homogeneous canopies

To calculate the photosynthetic rate of the canopy, we adopt the framework developed by Thornley and Johnson (1990) for binary mixtures. More refined algorithms exist (e.g. Faurie et al., 1996),

Table A1

<table>
<thead>
<tr>
<th>Variables</th>
<th>Description</th>
<th>Values and units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$D_{SE,d}$, $D_{SE,g}$</td>
<td>Developmental stages at ear emergence and start of the vegetative growth</td>
<td>0.55, 2.00</td>
</tr>
<tr>
<td>$G_{sh,j} + g, c$</td>
<td>Shoot turnover rates at 20 °C</td>
<td>0.012 d$^{-1}$</td>
</tr>
<tr>
<td>$G_{rt,j} + g, c$</td>
<td>Root turnover rates at 20 °C</td>
<td>0.010 d$^{-1}$</td>
</tr>
<tr>
<td>$\bar{Y}<em>{i,j}, \bar{Y}</em>{g,j}$</td>
<td>Normalization factor for grass development</td>
<td>225.0 °C d</td>
</tr>
<tr>
<td>$\bar{\xi}_j + g, c$</td>
<td>Factor controlling the effects of substrate C on leaf area expansion</td>
<td>0.0416667 d (=1 h)</td>
</tr>
<tr>
<td>$\kappa_{C,C}, \kappa_{N,C}$</td>
<td>Teleonomic partitioning constants for clover</td>
<td>1.0 kg C (kg DM)$^{-1}$, 0.005 kg N (kg DM)$^{-1}$</td>
</tr>
<tr>
<td>$\kappa_{C,G}, \kappa_{N,G}$</td>
<td>Teleonomic partitioning constants for grass</td>
<td>1.0 kg C (kg DM)$^{-1}$, 0.35 kg N (kg DM)$^{-1}$</td>
</tr>
<tr>
<td>$\lambda_{rep}$</td>
<td>Preferential allocation of dry matter to shoot during the reproductive growth of grass after ear emergence</td>
<td>0.25</td>
</tr>
<tr>
<td>$\phi_{l,m,\text{min}}, \phi_{l,m,\text{max}}$</td>
<td>Fraction of the grass shoot growth allocated to lamina</td>
<td>0.50, 0.80</td>
</tr>
<tr>
<td>$\phi_{l,m,p}$</td>
<td>Fraction of the growth shoot growth allocated to lamina during reproductive growth</td>
<td>0.70</td>
</tr>
</tbody>
</table>
but they generally exceed the level of complexity of our model. We therefore assume, in a first step, a homogeneous distribution of the leaf-area density ($\ell$) in the horizontal plane. Then, for a total irradiance $I_\text{top}$ at the top of the canopy, light interception by the individual components at a depth $\ell = \ell_g + \ell_c$ in the profile is formulated as

$$I_{\text{leaf},j}(\ell) = \frac{\kappa_j}{m_j} I_\text{top} \exp(-\kappa_c \ell)$$ (A2.5)

where $m_j$ is the leaf transmission coefficient of either component and the effective extinction coefficient $\kappa_c$ is computed as a weighted average of the individual extinction coefficients $\kappa_j$:

$$\kappa_c = \frac{\kappa_g \ell_g + \kappa_c \ell_c}{\ell} = \frac{\kappa_L \ell_g + \kappa_c \ell_c}{\ell} \text{LAI}$$ (A2.6)

with LAI = LAI_g + LAI_c.

From (A2.5) and (A2.6) and using the non-rectangular hyperbola to quantify leaf photosynthesis (Thornley and Johnson, 1990; Thornley, 1998; Riedo et al., 1998), the canopy photosynthesis rate ($P_j$) of either component becomes:

$$P_j = \frac{\text{LAI}_j C_{\text{CO}_2} - c_{\text{CO}_2}}{2 \beta_j \kappa_c} \left[ F_j[I_{\text{leaf},j}(\ell = 0)] - F_j[I_{\text{leaf},j}(\ell = \text{LAI}_j)] \right]$$ (A2.7)

where

$$F_j(x) = \alpha_j x - [(\alpha_j x)^2 + 2P_{\text{max},j}(1-2\beta_j)\alpha_j x + P_{\text{max},j}^2]^{1/2}$$

$-P_{\text{max},j} \ln \left\{ \left[ (\alpha_j x)^2 + 2P_{\text{max},j}(1-2\beta_j)\alpha_j x + P_{\text{max},j}^2 \right]^{1/2} + \alpha_j x + P_{\text{max},j}(1-2\beta_j) \right\}$

$+ 2\beta_j P_{\text{max},j} \ln \left[ (\alpha_j x)^2 + 2P_{\text{max},j}(1-2\beta_j)\alpha_j x + P_{\text{max},j}^2 \right]^{1/2} + \alpha_j x + P_{\text{max},j}(1-2\beta_j)$

and where $C_{\text{CO}_2} - c$ is a conversion factor introduced to express $P_j$ in units of kgs C m$^{-2}$ d$^{-1}$, $\beta_j$ the degree of curvature of the non-rectangular hyperbola, $\kappa_c$ the effective extinction coefficient of the canopy, $\alpha_j$ the photosynthetic efficiency, and $P_{\text{max},j}$ the light-saturated leaf photosynthetic rate. To account for differences in the growth light environment, in (A2.8) $P_{\text{max},j}$ is replaced by $\hat{P}_{\text{max},j}$ (see Thornley and Johnson, 1990, Eq. (10.7a)):

$$\hat{P}_{\text{max},j} = P_{\text{max},j} \left\{ 1 - \frac{v_j}{2} \left[ 1 - \exp(-\kappa_L \text{LAI}_j) \right] \right\}$$ (A2.9)

with parameter $v_j$.

Following Thornley (1998) and Riedo et al. (1998), the photosynthetic efficiency ($\alpha_j$) and the light-saturated leaf photosynthetic rate ($P_{\text{max},j}$) are considered as functions of the environmental conditions. The leaf photosynthetic efficiency is defined by:

$$\alpha_j = \alpha_{15} \frac{T_{\text{air}}}{T_{\text{air}, \text{ref}}} \left[ C_{\text{CO}_2}(c_a) \right]$$ (A2.10)

with reference value of $\alpha_{15}$ at 15°C and responses for temperature and atmospheric CO2 concentration ($c_a$) given by

$$f_{\alpha_{15}}(T_{\text{air}}) = \left\{ \begin{array}{ll} 1 & \text{if } T_{\text{air}} < 15°C \\ \text{MAX}(0, [1 - m_{\alpha_{15}} f(T_{\text{air}} - 15)]) & \text{if } T_{\text{air}} \geq 15°C \end{array} \right.$$ (A2.11)

and

$$f_{C_{\text{CO}_2}}(c_a) = 1 - \frac{c_a \text{ref}}{c_a}$$ (A2.12)

where $m_{\alpha_{15}}$ and $c_a \text{ref}$ are parameters.

Similarly to (A2.10), the light-saturated leaf photosynthetic rate ($P_{\text{max},j}$) depends on a reference value at 20°C ($P_{\text{20},j}$) and response functions for temperature and $c_a$:

$$P_{\text{max},j} = P_{\text{20},j} f_{P_{\text{max},j}}(T_{\text{air}}, c_a) f_{C_{\text{CO}_2}}(c_a)$$ (A2.13)

Since the growth and photosynthesis of symbiotically N$_2$-fixing species is often more strongly stimulated at elevated CO2 than in grasses (Clark et al., 1997; Lüscher et al., 1998; Ainsworth et al., 2003) and white clover leaves have a greater assimilation rate of CO2 per unit leaf area than grass (Woleadge et al., 1984; Dennis and Woleodge, 1985; Woleodge, 1988 as cited in Faurie et al., 1996) the reference value $P_{\text{20},c}$ for clover is assumed 10% higher than for grass.

Implicit in (A2.13) is the fact that elevated atmospheric CO2 concentrations not only affect photosynthesis directly through $f_{P_{\text{max},j}}(c_a)$, but also indirectly through the temperature response function $f_{P_{\text{max},j}}(T_{\text{air}}, c_a)$, with explicit argument $c_a$. The former is calculated as

$$f_{P_{\text{max},j}}(c_a) = f_{P_{\text{CO}_2}}(c_{\text{CO}_2}) + r_j [f_{P_{\text{CO}_2}}(c_a) - f_{P_{\text{CO}_2}}(c_{350})]$$ (A2.14)

where $r_j$ is a scaling parameter and

$$f_{P_{\text{CO}_2}}(c_a) = \frac{1}{1 + (\kappa_{\text{CO}_2}/c_a)}$$ (A2.15)

with parameter $\kappa_{\text{CO}_2}$ (Thornley, 1998).

The temperature response $f_{P_{\text{max},j}}(T_{\text{air}}, c_a)$ is given by Eq. (A6.1), but here the upper limit of the temperature range explicitly depends on $c_a$ (Long, 1991):

$$f_{\text{up}}^{\text{P}_{\text{max},j}} = \frac{(1 + q_j) f_{\text{up}}^{\text{P}_{\text{max},j}} - f_{\text{low}}^{\text{P}_{\text{max},j}}}{q_j}$$ (A2.16)

where

$$q_j^{\text{up}} = \frac{T_{350}^{c_a} + (T_{700}^{c_a} - T_j^{350}) c_a - C_{350}}{C_{700} - C_{350}}$$ (A2.17)

and where $C_{350}$ and $C_{700}$ are reference values for $c_a$, and $T_j^{350}$ and $T_j^{700}$ the corresponding upper temperature limits.

A.2.3. Canopy photosynthesis in canopies with dominating grass component

Eq. (A2.7), with (A2.8) through (A2.17), reasonably accounts for the photosynthetic relations of a grass/clover mixture when neither of the components dominates light interception. This is probably true in general for grazed swards and for swards undergoing frequent cutting. Depending on the varieties of ryegrass and white clover and the intensity of management, however, there are situations when the clover component is overtopped by the companion grass, as seen for instance in the profiles sampled in Switzerland by Schwank et al. (1986).

In such situations, the canopy can be assumed as consisting of two layers: (i) a top grass layer characterized by a leaf-area index LAI$_c$, where grass intercepts light and assimilates carbon as in a monoculture; and (ii) a bottom layer below clover height where the two components assimilate as in homogeneous mixtures, but with light intensity reduced by the absorption in the top layer.

Photosynthesis in the top layer is calculated as in (A2.7), but now:

$$\hat{P}_{\text{top}} = \frac{C_{\text{CO}_2} - c}{2\beta_j \kappa_c} \left[ F_{\text{top}}[I_{\text{leaf},g}(\ell_g = 0)] - F_{\text{top}}[I_{\text{leaf},g}(\ell_g = \text{LAI}_c)] \right]$$ (A2.18)
where
\[ P_{\text{leaf,g}}^\text{top} = \frac{K_g}{1 - m_g} I_0 \exp(-K_g \ell_g) \]  
(A2.19)
and
\[ P_{\text{max,g}}^\text{top} = P_{\text{max,g}} \left\{ 1 - \frac{1 - \exp(-K_g \ell_g)}{2} \right\} \]  
(A2.20)
In the bottom layer, Eq. (A2.7) remains valid as well, but now the irradiance entering the layer \( I_0^\text{bottom} \) is given by:
\[ I_0^\text{bottom} = I_0 \exp(-K_g \ell_g^\text{g}) \]  
(A2.21)
and \( F_j \) in (A2.8) is evaluated with adapted values of the leaf-area:
\[ P_j = \frac{LAI \cdot CO_2 \cdot \ell_j}{2} \left\{ F_j \left[ | \ell = \text{LAI} - \ell_g^\text{g} | - F_j \left[ | \ell = \text{LAI} | \right] \right\} \]  
(A2.22)
For simplicity, \( \ell_g^\text{g} \) is expressed as the excess by \( \Delta \text{LAI} \) of \( \text{LAI}_g \) over \( \text{LAI}_c \):
\[ \text{LAI}_g = \text{MAX}(0, \text{LAI}_g - \text{LAI}_c - \Delta \text{LAI}) \]  
(A2.23)
The choice of the algorithm for computing canopy photosynthesis is taken depending on whether \( \text{LAI}_g \leq \text{LAI}_c + \Delta \text{LAI} \) (homogeneous canopies) or \( \text{LAI}_g > \text{LAI}_c + \Delta \text{LAI} \) (dominating grass component).

A.2.4. Plant respiration
Following Riedo et al. (1998), maintenance respiration \( (R_{\text{m,j}}) \) and the respiration associated with N-acquisition \( (R_{\ell,j}) \) are given by
\[ R_{\text{m,j}} = R_{\text{m,org}}^{\ell_j} \left( T_{\text{soil}} \right) \text{W}_{\text{sh,j}} \left( \ell_j \right) + R_{\text{m,org}}^{\ell_j} \left( T_{\text{soil}} \right) \text{W}_{\text{rt,j}} \left( \ell_j \right) \]  
(A2.24)
and
\[ \begin{cases} \ell_g \rightarrow \eta_{\ell,j} U_{\ell_j} \\ \ell_c \rightarrow \eta_{\ell,j} U_c + (U_{\text{BNF}}/\eta_{\text{BNF}}) \end{cases} \]  
(A2.25)
where \( \eta_{\ell,j} \) are the respiratory costs of N acquisition. Note that in (A2.24) maintenance respiration of the shoot/root compartment is controlled by air/soil temperature. Note, moreover, that we assume the same weighting value \( (\ell_j) \) for the shoot and root compartments and the same specific value of the substrate C concentration at which the maintenance respiration is half-maximal \( (K_{\ell,j}) \). For clover, a second term is added to account for the higher costs of BNF relative to mineral N uptake.

A.2.5. Nitrogen uptake and biological nitrogen fixation
The specific mineral N uptake rates by the roots of grass \( (U_g) \) and clover \( (U_c) \) vary substantially depending on the soil mineral N \( (N_{\text{min}}) \) and soil temperature \( (T_{\text{soil}}) \). Following Schwinning and Parsons (1996a), following Paul et al. (2003) using a saturating function for the soil water content:
\[ F_{\text{BNF}} = \frac{F_{\text{BNF}}(T_{\text{soil}}) e_{\text{BNF}} U_{\text{BNF, max}} \text{W}_{\text{rt,c}} \left( 1 - f_{\ell_c} \frac{N_{\text{min}}}{N_{\text{min}} + \kappa_{\text{BNF}}} \right)}{U_{\text{BNF}} = f_{\text{BNF}}(T_{\text{soil}}) e_{\text{BNF}} U_{\text{BNF, max}} \text{W}_{\text{rt,c}} \left( 1 - f_{\ell_c} \frac{N_{\text{min}}}{N_{\text{min}} + \kappa_{\text{BNF}}} \right)} \]  
(A2.28)
where the efficiency parameter \( e_{\text{BNF}} \) reflects the higher metabolism and respiration costs associated with BNF relative to mineral N uptake, \( \kappa_{\text{BNF}} \) is the substrate N concentration at which BNF is half-maximal, and \( f_{\text{BNF}}(T_{\text{soil}}) \) is formulated using the parametrization of Wu and McGeachan (1999, Fig. 2):
\[ f_{\text{BNF}}(T_{\text{soil}}) = \begin{cases} 0 & \text{if} \ T_{\text{soil}} \leq T_{\text{BNF},1} \\ \frac{(T_{\text{soil}} - T_{\text{BNF},1})}{(T_{\text{BNF},2} - T_{\text{BNF},1})} & \text{if} \ T_{\text{BNF},1} < T_{\text{soil}} \leq T_{\text{BNF},2} \\ 1 & \text{if} \ T_{\text{BNF},2} < T_{\text{soil}} \leq T_{\text{BNF},3} \\ 1 - [(T_{\text{soil}} - T_{\text{BNF},1})/(T_{\text{BNF},4} - T_{\text{BNF},1})] & \text{if} \ T_{\text{BNF},3} < T_{\text{soil}} \leq T_{\text{BNF},4} \\ 0 & \text{if} \ T_{\text{soil}} > T_{\text{BNF},4} \end{cases} \]  
(A2.29)

A.3. Soil biology (Table A3)
Following Schwinning and Parsons (1996a) the model considers one organic \( (N_{\text{org}}) \) and one mineral \( (N_{\text{min}}) \) soil pool. The organic N pool is fed by the total N litter flux \( (F_{\text{N litter}}) \) and by organic N fertilization \( (\text{N litter}) \) is given by the fractional N content of the plant decomposition rates of both species \( (D_{\text{j},j} \) as expressed by (A1.9). Assuming the same fractional N content \( (\gamma_{\text{N}}) \) for the output of substrate N to growth, the litter flux becomes:
\[ F_{\text{N litter}} = \sum_{j=1}^{2} \gamma_{\text{N}}(D_{\text{sh},j} + D_{\text{rt},j}) \]  
(A3.2)
The net mineralization rate \( F_{\text{min}} \) is computed as the product of the organic N pool \( (N_{\text{org}}) \) and the rate constant \( (c_{\text{min}}) \) (Schwinning and Parsons, 1996a) as regulated by the response soil moisture and temperature:
\[ F_{\text{min}} = F_{\text{min}}^0 (\theta) D_{\text{min}}(T_{\text{soil}}) c_{\text{min}} \]  
(A3.3)
The effect of soil water on net mineralization is described following Paul et al. (2003) using a saturating function for the soil water content:
\[ F_{\text{min}}^0(\theta) = \left[ \gamma_{\text{min},01} + \gamma_{\text{min},02} \exp \left( \gamma_{\text{min},03} \theta - \gamma_{\text{min},04} \theta_{\text{lpw}} - \theta_{\text{lpw}} \right) \right]^{-1} \]  
(A3.4)
where \( \theta_{\text{lpw}} \) and \( \theta_{\text{lpw}} \) denoting the volumetric soil water content at field capacity and the permanent wilting point (soil type specific parameters) and \( \gamma_{\text{min},01}, \gamma_{\text{min},02} \) and \( \gamma_{\text{min},03} \) representing shape parameters. Note that although the difference \( (\theta_{\text{lpw}} - \theta_{\text{lpw}}) \) is used for convenience to scale the water content in (A3.4), as suggested by Paul et al. (2003), the function is well-behaved also for volumetric soil water contents in excess of \( \theta_{\text{lpw}} \) (see Fig. 7 in Paul et al., 2003). For this reason, no additional constraints are introduced.
The effect of soil temperature on the relative rate of mineralization is described by a function proposed by Lloyd and Taylor (1994) and further modified by Kirschbaum (2000). This function exponentially increases from close to zero but is limited to 1 for soil temperatures above 40 °C:
\[ f_{\text{min}}(T_{\text{soil}}) = \begin{cases} 1, & \text{exp} \left( \gamma_{\text{min},1} (T_{\text{soil}} - T_{\text{min},1} + T_{\text{min},2}) \right) \end{cases} \]  
(A3.5)
where \( \gamma_{\text{min},1}, T_{\text{min},1} \) and \( T_{\text{min},2} \) are parameters.
The soil mineral N balance is given by the input associated with net mineralization \( (F_{\text{min}}) \), mineral N fertilization \( (\text{N fertilizer}) \), and atmospheric N deposition \( (F_{\text{N dep}}) \) and the
Table A2

Variables and parameters used in the formulation of the plant C and N substrate pools.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$c_a$</td>
<td>Atmospheric CO$_2$ concentrations</td>
<td>ppm</td>
</tr>
<tr>
<td>$C_{N,j}$</td>
<td>N$_j$ in g, c</td>
<td>Carbon and nitrogen substrate concentrations</td>
</tr>
<tr>
<td>$G_{r,j}$</td>
<td>Growth rate of the shoot and root compartments</td>
<td>kg DM m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$l_0$</td>
<td>Total irradiance at the top of the canopy</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$I_0$</td>
<td>Reduced irradiance entering the bottom layer of the canopy in mixtures with grass dominance</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$I_{top}$</td>
<td>Solar irradiance at a depth $i$ in the canopy profile</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$m_{leaf}$</td>
<td>Leaf-area density of grass and clover</td>
<td>m$^2$ leaves (m$^2$ ground)$^{-1}$ m$^{-1}$</td>
</tr>
<tr>
<td>$P_{day}$</td>
<td>Total leaf-area density of the canopy</td>
<td>m$^2$ leaves (m$^2$ ground)$^{-1}$ m$^{-1}$</td>
</tr>
<tr>
<td>$LAI_j$</td>
<td>Total area index of the canopy</td>
<td>m$^2$ leaves (m$^2$ ground)$^{-1}$</td>
</tr>
<tr>
<td>$LAI_c$</td>
<td>Grass LAI in excess of clover LAI</td>
<td>m$^2$ leaves (m$^2$ ground)$^{-1}$</td>
</tr>
<tr>
<td>$N_{min}$</td>
<td>Soil mineral N availability</td>
<td>kg N m$^{-2}$</td>
</tr>
<tr>
<td>$P_{prop}$</td>
<td>Photosynthesis rate for grass in the top layer in a mixed sward</td>
<td>kg C m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$P_{c}$</td>
<td>Canopy photosynthesis</td>
<td>kg C m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$P_{max,c}$</td>
<td>Light-saturated leaf photosynthetic rate</td>
<td>kg CO$_2$ m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$R_{n,j}$</td>
<td>Maintenance respiration rate</td>
<td>kg C m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$R_{p,j}$</td>
<td>Respiration rate associated with N acquisition</td>
<td>kg C m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$t$</td>
<td>Time</td>
<td>d</td>
</tr>
<tr>
<td>$t_{cut}$</td>
<td>Scheduled times of harvesting</td>
<td>d</td>
</tr>
<tr>
<td>$T_{air}$</td>
<td>Air and soil temperature</td>
<td>°C</td>
</tr>
<tr>
<td>$T_{soil}$</td>
<td>Soil temperature</td>
<td>°C</td>
</tr>
<tr>
<td>$T_{max}$</td>
<td>Upper temperature limit in the temperature response function for photosynthesis</td>
<td>°C</td>
</tr>
<tr>
<td>$U_{BNF}$</td>
<td>N acquisition by clover through biological N$_2$ fixation</td>
<td>kg N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$U_{j}$</td>
<td>Soil mineral N uptake</td>
<td>kg N m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$W_{C,j}$</td>
<td>Mass of substrate C in the shoot and root compartment</td>
<td>kg C m$^{-2}$</td>
</tr>
<tr>
<td>$W_{N,j}$</td>
<td>Mass of substrate N in the shoot and root compartment</td>
<td>kg N m$^{-2}$</td>
</tr>
<tr>
<td>$Y_{j}$</td>
<td>Losses of C substrate by harvest</td>
<td>kg C m$^{-2}$</td>
</tr>
<tr>
<td>$Y_{N,j}$</td>
<td>Losses of N substrate by harvest</td>
<td>kg N m$^{-2}$</td>
</tr>
<tr>
<td>$\alpha_{j}$</td>
<td>Leaf photosynthetic efficiency</td>
<td>kg CO$_2$ m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$\beta_{j}$</td>
<td>Specific constant to scale the non-specific response functions of the maximal photosynthesis rate to CO$_2$</td>
<td>kg CO$_2$ m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$\gamma_{j}$</td>
<td>Leaf-area index of grass and clover</td>
<td>m$^2$ leaves (m$^2$ ground)$^{-1}$</td>
</tr>
<tr>
<td>$\gamma_{C,j}$</td>
<td>Leaf photosynthetic efficiency</td>
<td>kg CO$_2$ m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$\gamma_{N,j}$</td>
<td>Leaf-area density of grass and clover</td>
<td>m$^2$ leaves (m$^2$ ground)$^{-1}$</td>
</tr>
<tr>
<td>$\gamma_{BNF,j}$</td>
<td>Leaf photosynthetic efficiency</td>
<td>kg CO$_2$ m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$\gamma_{r,j}$</td>
<td>Leaf photosynthetic efficiency</td>
<td>kg CO$_2$ m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$\gamma_{BNF,j}$</td>
<td>Leaf photosynthetic efficiency</td>
<td>kg CO$_2$ m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$\delta_{j}$</td>
<td>Degree of curvature of the non-rectangular hyperbola</td>
<td>kg CO$_2$ m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$\delta_{LAI}$</td>
<td>Threshold to estimate grass LAI in excess of clover LAI</td>
<td>0.5 m$^2$ leaves (m$^2$ ground)$^{-1}$</td>
</tr>
<tr>
<td>$\delta_{W}$</td>
<td>Time step of integration</td>
<td>h</td>
</tr>
<tr>
<td>$\delta_{growth}$</td>
<td>Growth efficiency</td>
<td>0.75, 0.75</td>
</tr>
<tr>
<td>$\gamma_{C,j}$</td>
<td>Fractional C content in shoot and root dry matter</td>
<td>0.45, 0.45 kg C (kg DM)$^{-1}$</td>
</tr>
<tr>
<td>$\gamma_{N,j}$</td>
<td>Fractional N content in shoot and root dry matter</td>
<td>0.01, 0.01 kg N (kg DM)$^{-1}$</td>
</tr>
<tr>
<td>$\gamma_{N,j}$</td>
<td>Respiratory cost of mineral N acquisition</td>
<td>0.45, 0.45 kg C (kg N)$^{-1}$</td>
</tr>
<tr>
<td>$c_{BNF,j}$</td>
<td>Constant regulating BNF depending on soil mineral N</td>
<td>kg N min m$^{-2}$</td>
</tr>
<tr>
<td>$c_{BNF,j}$</td>
<td>Extinction coefficient</td>
<td>0.5, 0.8</td>
</tr>
<tr>
<td>$k_{N,j}$</td>
<td>Constant regulating mineral N uptake from the soil</td>
<td>0.002, 0.0035 kg N m$^{-2}$</td>
</tr>
<tr>
<td>$k_{CO_2}$</td>
<td>CO$_2$ concentration in the response function of light-saturated leaf photosynthesis to CO$_2$</td>
<td>700 ppm</td>
</tr>
<tr>
<td>$k_{res}$</td>
<td>Maintenance respiration constant</td>
<td>0.03, 0.03 kg C (kg DM)$^{-1}$</td>
</tr>
<tr>
<td>$v_{j}$</td>
<td>Parameter used to express light-saturated leaf photosynthesis as a function of light environment</td>
<td>0.7, 0.7</td>
</tr>
</tbody>
</table>
losses associated with mineral N uptake by the grass ($U_g$) and clover ($U_c$) component and by a general N loss term ($O_{N_{\text{min}}}$):

$$\frac{dN_{\text{min}}}{dt} = F_{\text{min}} + \frac{\delta(t-t_{\text{fert.min}})}{\Delta t} N_{\text{fert.min}} + F_{\text{dep}} - U_g - U_c - O_{N_{\text{min}}}$$

(A3.6)

where $t_{\text{fert.min}}$ denotes one of the scheduled times for mineral N fertilization. According to Thornley et al. (1995) and Schwinghamer and Parsons (1996a) we model $O_{N_{\text{min}}}$ as a linear function of the soil mineral N concentrations ($N_{\text{min}}$):

$$O_{N_{\text{min}}} = \text{closs} \cdot N_{\text{min}}$$

(A3.7)

with closs denoting indicating the loss rate.

A.4. Soil physics (Table A4)

A.4.1. Soil temperature

In PROGRASS we consider only one soil layer corresponding to the rooting depth. For simplicity, we assume that any time of the day the instantaneous hourly value of the soil temperature ($T_{\text{soil}}$) is equal to the daily mean temperature ($\bar{T}_{\text{soil},d}$). The latter is calculated from the daily average air temperature of the previous day ($\bar{T}_{\text{air},d-1}$) and corrected for the dampening effects of the soil ($\bar{T}_{\text{soil,corr}}$) without accounting for soil type and soil water conditions:

$$T_{\text{soil}} = \bar{T}_{\text{soil},d} = \bar{T}_{\text{air},d-1} - T_{\text{soil,corr}}$$

(A4.1)

A.4.2. Soil water balance

The soil is treated as one lumped homogeneous layer characterized by a mean volumetric soil water content $\theta$ equal to the soil water storage $S$ divided by the rooting depth $z_{\text{root}}$:

$$\theta = \frac{S}{z_{\text{root}}}$$

(A4.2)

with

$$dS\frac{dt}{dt} = I_{\text{inf}} - E_{\text{can}} - E_{\text{soil}} - Q_{\text{drain}} - Q_{\text{surf}}$$

(A4.3)

The soil water store is replenished by infiltration ($I_{\text{inf}}$) and depleted by plant (canopy) transpiration ($E_{\text{can}}$), soil evaporation ($E_{\text{soil}}$), drainage outflow ($Q_{\text{drain}}$) and surface runoff ($Q_{\text{surf}}$).

A.4.3. Rainfall interception

Following the overflow concept in Bronstert (1994) canopy interception is treated as the filling and depletion of an interception store $S_{\text{veg}}$:

$$\frac{dS_{\text{veg}}}{dt} = I_{\text{rain}} - I_{\text{inf}} - E_{\text{int}}$$

(A4.4)

with $I_{\text{rain}}$ denoting the rainfall rate, $I_{\text{inf}}$ the infiltration rate and $E_{\text{int}}$ the rate of interception evaporation. The maximal capacity of the interception store is given by $S_{\text{veg,max}}$. Accordingly, water infiltrates into the soil whenever in a unit time interval $\tau_{\text{inf}}$ the rainfall intensity exceeds the difference between the $S_{\text{veg,max}}$ and the actual interception store $S_{\text{veg}}$:

$$I_{\text{inf}} = \text{MAX} \left( 0, I_{\text{rain}} - \frac{S_{\text{veg,max}} - S_{\text{veg}}}{\Delta t} \right)$$

(A4.5)

Further, $E_{\text{int}}$ is assumed equal to potential evapotranspiration:

$$E_{\text{int}} = \begin{cases} E_{\text{pot}} & \text{if } S_{\text{veg}} > 0 \\ 0 & \text{if } S_{\text{veg}} = 0 \end{cases}$$

(A4.6)

where $E_{\text{pot}} = E_{\text{can,pot}} + E_{\text{soil,pot}}$, the latter being given by (A4.11). (The use of the potential evapotranspiration from a free water surface would have been more adequate in this context, but the precise definition of the potential evapotranspiration is not crucial. The present assumption allows us to keep the model concise.).

The maximal canopy storage capacity $S_{\text{veg,max}}$ varies depending on the development of LAI of the grass/clover mixture:

$$S_{\text{veg,max}} = a_{\text{veg}} \frac{\text{LAI}}{\text{LAI} + b_{\text{veg}}}$$

(A4.7)

with parameters $a_{\text{veg}}$ and $b_{\text{veg}}$ and with $\text{LAI} = \text{LAI}_g + \text{LAI}_c$, as before.

A.4.4. Transpiration and evaporation

The actual rates of transpiration ($E_{\text{can}}$) and soil evaporation ($E_{\text{soil}}$) in a mixed canopy are computed based on their respective potential rates ($E_{\text{can,pot}}$ and $E_{\text{soil,pot}}$), which are linearly down-regulated, for simplicity, by the same response function for soil water $f_E^\text{veg}(\theta)$:

\[
\begin{cases}
E_{\text{can}} = f_E^\text{veg}(\theta) E_{\text{can,pot}} \\
E_{\text{soil}} = f_E^\text{veg}(\theta) E_{\text{soil,pot}}
\end{cases}
\]

(A4.8)

### Table A3

<table>
<thead>
<tr>
<th>Variables</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F_{\text{min}}$</td>
<td>Net mineralization rate</td>
<td>kg N m^{-2} d^{-1}</td>
</tr>
<tr>
<td>$F_{\text{dep}}$</td>
<td>Atmospheric N deposition rate</td>
<td>kg N m^{-2} d^{-1}</td>
</tr>
<tr>
<td>$F_{\text{litter}}$</td>
<td>N litter from grass and clover shoot and root biomass</td>
<td>kg N m^{-2} d^{-1}</td>
</tr>
<tr>
<td>$F_{\text{fert.min}}$</td>
<td>Mineral N amount applied at the scheduled times for fertilization</td>
<td>kg N m^{-2}</td>
</tr>
<tr>
<td>$N_{\text{org}}$</td>
<td>Organic N amount applied at the scheduled times for fertilization</td>
<td>kg N m^{-2}</td>
</tr>
<tr>
<td>$N_{\text{min}}$</td>
<td>Soil mineral N amount</td>
<td>kg N m^{-2}</td>
</tr>
<tr>
<td>$N_{\text{org}}$</td>
<td>Soil organic N amount</td>
<td>kg N m^{-2}</td>
</tr>
<tr>
<td>$O_{\text{N_{\text{min}}}}$</td>
<td>General loss term for soil mineral N other than N uptake</td>
<td>kg N m^{-2} d^{-1}</td>
</tr>
<tr>
<td>$F_{\text{fert.min}}$</td>
<td>Scheduled times for the application of mineral N fertilizers</td>
<td>d</td>
</tr>
<tr>
<td>$F_{\text{fert.veg}}$</td>
<td>Scheduled times for the application of organic N fertilizers</td>
<td>d</td>
</tr>
<tr>
<td>$T_{\text{soil}}$</td>
<td>Soil temperature</td>
<td>°C</td>
</tr>
<tr>
<td>$U_g, U_c$</td>
<td>Soil mineral N uptake by grass and clover</td>
<td>kg N m^{-2} d^{-1}</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Volumetric soil water content</td>
<td>m^{3} water (m^{3} soil)^{-1}</td>
</tr>
</tbody>
</table>

### Parameters

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Description</th>
<th>Values and units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$c_{\text{loss}}$</td>
<td>Loss rate constant</td>
<td>0.005 d^{-1}</td>
</tr>
<tr>
<td>$c_{\text{min}}$</td>
<td>Net mineralization rate constant</td>
<td>0.0007 d^{-1}</td>
</tr>
<tr>
<td>$\delta_{\text{min}} T$</td>
<td>Empirical parameters describing the effect of temperature on mineralization</td>
<td>3.36</td>
</tr>
<tr>
<td>$\delta_{\text{min},1}/\delta_{\text{min},2}/\delta_{\text{min},3}$</td>
<td>Empirical parameters describing the effect of soil water on mineralization</td>
<td>1, 6.63, \ldots, 5.69</td>
</tr>
<tr>
<td>$T_{\text{min},1}, T_{\text{min},2}$</td>
<td>Empirical parameters describing the effect of soil water on mineralization</td>
<td>40.00, 31.79 °C</td>
</tr>
<tr>
<td>$\Delta t$</td>
<td>Time step of integration</td>
<td>0.0416667 d (\approx 1 h)</td>
</tr>
<tr>
<td>$\nu_{\text{g}, g, c}$</td>
<td>Fractional N content in shoot and root dry matter</td>
<td>0.01, 0.01 kg N (kg DM)^{-1}</td>
</tr>
<tr>
<td>$\theta_{\text{fc}}, \theta_{\text{wp}}$</td>
<td>Volumetric soil water content at field capacity and permanent wilting point</td>
<td>Soil specific values, m^{3} water (m^{3} soil)^{-1}</td>
</tr>
</tbody>
</table>
where

$$f_\ell^0(\theta) = \begin{cases} 1 & \text{if } \theta < \theta_{ws,e} \\ \frac{f_\ell^0}{f_\ell^0_{min}} + (1 - \frac{f_\ell^0}{f_\ell^0_{min}}) \frac{\theta - \theta_{ppw}}{\theta_{ppw} - \theta_{ws,e}} & \text{if } \theta_{ppw} < \theta \leq \theta_{ws,e} \\ \frac{f_\ell^0}{f_\ell^0_{min}} & \text{if } \theta \leq \theta_{ppw} \end{cases}$$

(A4.9)

where $f_\ell^0_{min}$ is a scaling factor and the threshold indicating incipient water stress ($\theta_{ws,e}$) is calculated as the weighted average of the corresponding thresholds for grass ($\theta_{ws,g}$) and clover ($\theta_{ws,c}$):

$$\theta_{ws,e} = \frac{LAI_g \theta_{ws,g} + LAI_c \theta_{ws,c}}{LAI}$$

(A4.10)

The characteristic values $\theta_L$ and $\theta_{ppw}$ are soil-type dependent, while $\theta_{ws,g}$ and $\theta_{ws,c}$ are plant specific values. All of them are obtained from corresponding matric potentials $\psi_L$, $\psi_{ppw}$, $\psi_{ws,g}$ and $\psi_{ws,c}$ using Eq. (A5.1).

Potential transpiration ($E_{can,pot}$) and soil evaporation ($E_{soil,pot}$) are calculated using the sparse crop combination equations of Shuttleworth and Wallace (1985) but setting all resistances that depend on soil water availability to their minimal values. In short:

$$\begin{align*}
E_{can,pot} &= \lambda^{-1} X_{can} PM_{can} \\
E_{soil,pot} &= \lambda^{-1} X_{sub} PM_{sub}
\end{align*}$$

(A4.11)

where $\lambda$ is the latent heat of vaporization, and where

$$\begin{align*}
PM_{can} &= \frac{NR \Delta + (\rho c_p D_a - \Delta r_{can} NR_{sub})(r_{air} + r_{can})^{-1}}{\Delta + \gamma [1 + r_{can} (r_{air} + r_{can})^{-1}]} \\
PM_{sub} &= \frac{NR \Delta + (\rho c_p D_a - \Delta r_{sub} (NR - NR_{sub}))(r_{air} + r_{sub})^{-1}}{\Delta + \gamma [1 + r_{sub} (r_{air} + r_{sub})^{-1}]}
\end{align*}$$

(A4.12)

and

$$\begin{align*}
X_{can} &= [1 + R_{can} R_{air} / R_{sub} (R_{can} + R_{air})]^{-1} \\
X_{sub} &= [1 + R_{sub} R_{air} / R_{can} (R_{sub} + R_{air})]^{-1}
\end{align*}$$

(A4.13)

with

$$\begin{align*}
R_{air} &= (\Delta + \gamma) r_{air} \\
R_{sub} &= (\Delta + \gamma) r_{sub} + \gamma r_{can} \\
R_{can} &= (\Delta + \gamma) r_{can} + \gamma r_{sub}
\end{align*}$$

(A4.14)

In (A4.12) through (A4.14) NR denotes net radiation flux at the top of the canopy, $NR_{sub}$ the net radiation flux at the soil substrate, $\Delta = d_{ref} / d_{bare}$ the change in saturation vapour pressure $e_s$ with temperature, $\rho$ the air density, $c_p$ the specific heat at constant pressure, $D_a$ the vapour pressure deficit at reference height, $r_{air}$ the aerodynamic resistance between canopy source height and reference level, $r_{can}$ the bulk boundary layer resistance of the canopy, $r_{sub}$ the aerodynamic resistance between the substrate and the canopy source height, $r_{can}$ the bulk stomatal resistance of the canopy, $r_{sub}$ the surface resistance of the substrate and $\gamma$ the so-called psychrometric constant. The saturation vapour pressure is further calculated as

$$e_s(T_{air}) = 6.112 \exp \left\{ 17.67 \frac{T_{air}}{T_{air} + 264.2} \right\},$$

(A4.15)

where $T_{air}$ is the air temperature, while the vapour pressure deficit at reference height $(D_a)$ is found from:

$$D_a = e_s \left( 1 - \frac{RH}{100} \right)$$

(A4.16)

with RH being the relative humidity.

To compute the psychrometric constant ($\gamma$) we use:

$$\gamma = \frac{c_p P_{atm}}{M_{water} \gamma_{air}}$$

(A4.17)

where $P_{atm}$ is the atmospheric pressure and $M_{water}$ and $M_{air}$ the molecular weights of water and air, respectively. Next, net radiation $(NR)$ is assumed a linear function of global radiation $(GR)$ (Davies, 1967; Calanca, 2004):

$$NR = a_{up} + b_{up} GR$$

(A4.18)

and the amount of net radiation entering the soil substrate $(NR_{sub})$ is computed as

$$NR_{sub} = NR \exp(-\kappa_{LAI})$$

(A4.19)

To calculate the various resistances we also follow Shuttleworth and Wallace (1985). Accordingly, the aerodynamics resistance between the substrate and canopy height is given by

$$r_{a}^{sub} (\ell = LAI) = r_{a}^{sub} (\ell = 0) + [r_{a}^{sub} (\ell = LAI_{max}) - r_{a}^{sub} (\ell = 0)] \text{MIN} \times \left( 1 - \frac{LAI}{LAI_{max}} \right)$$

(A4.20)

with

$$r_{a}^{sub} (\ell = 0) = \frac{1}{K u} \ln \left( \frac{z_{ref}}{z_{0,\text{bare}}} \right) \ln \left( \frac{d + z_{0,\text{bare}}}{d} \right) \left\{ \exp(n_e) - \exp \left[ n_e \left( 1 - \frac{d + z_{0,\text{bare}}}{h_{can}} \right) \right] \right\}$$

(A4.21)

Here, $z_{ref}$ is the reference height, $u$ is the wind speed, $z_0$ the roughness length, $d$ the zero-plane displacement, $z_{0,\text{bare}}$ roughness length of the bare substrate, $h_{can}$ the canopy height, and $n_e$ the eddy diffusivity decay constant. The value for $LAI_{max}$ refers to the highest observed LAI in the considered productive mixture at the Oensingen site. Since the canopy height is not calculated in PROGRASS, Eq. (A4.21) is evaluated by the reference canopy height which is treated as the maximum canopy height:

$$h_{can} = h_{can,ref}$$

(A4.22)

This value is also used to determine the roughness length

$$d = a_d h_{can,ref}$$

(A4.23)

and the zero-plane displacement

$$z_0 = a_z h_{can,ref}$$

(A4.24)

Similarly to (A4.20) the aerodynamic resistance between canopy source height and reference level $(r_{a}^{air})$ is assumed to linearly increase with total leaf area:

$$r_{a}^{air} (\ell = LAI) = r_{a}^{air} (\ell = 0) + r_{a}^{air} (\ell = LAI_{max}) - r_{a}^{air} (\ell = 0) \text{MIN} \times \left( 1 - \frac{LAI}{LAI_{max}} \right)$$

(A4.25)

with

$$\begin{align*}
r_{a}^{air} (\ell = 0) &= \frac{1}{K u} \ln \left( \frac{z_{ref}}{z_{0,\text{bare}}} \right) - r_{a}^{sub} (\ell = 0) \\
r_{a}^{air} (\ell = LAI_{max}) &= \frac{1}{K u} \ln \left[ \frac{z_{ref} - d}{h_{can} - d} \right] \ln \left( \frac{z_{ref} - d}{h_{can} - d} \right) \\
+ \frac{h_{can}}{n_e (h_{can} - d)} \left\{ \exp \left[ n_e \left( 1 - \frac{d + z_{0,\text{bare}}}{h_{can}} \right) \right] - 1 \right\}
\end{align*}$$

(A4.26)
Table A4

Variables and parameters used in the formulation of soil physics.

<table>
<thead>
<tr>
<th>Variables and parameters</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$c_a$</td>
<td>Atmospheric CO2 concentration</td>
<td>ppm</td>
</tr>
<tr>
<td>$D$</td>
<td>Zero plane displacement of the canopy at complete coverage</td>
<td>m</td>
</tr>
<tr>
<td>$D_v$</td>
<td>Vapour pressure deficit at reference height</td>
<td>Pa</td>
</tr>
<tr>
<td>$e(T)$</td>
<td>Saturation vapour pressure as a function of temperature</td>
<td>Pa</td>
</tr>
<tr>
<td>$E_{Can}, E_{soil}$</td>
<td>Actual transpiration, resp. soil evaporation rate</td>
<td>mm d$^{-1}$</td>
</tr>
<tr>
<td>$E_{Can, pot}, E_{soil, pot}$</td>
<td>Potential transpiration, resp. soil evaporation rate</td>
<td>mm d$^{-1}$</td>
</tr>
<tr>
<td>$E_{int}$</td>
<td>Interception evaporation</td>
<td>mm d$^{-1}$</td>
</tr>
<tr>
<td>$E_{pot}$</td>
<td>Potential evapotranspiration rate</td>
<td>mm d$^{-1}$</td>
</tr>
<tr>
<td>$GR$</td>
<td>Global radiation (direct solar radiation plus sky diffuse radiation)</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$h_{can}$</td>
<td>Canopy height</td>
<td>m</td>
</tr>
<tr>
<td>$i_{inf}$</td>
<td>Infiltration rate</td>
<td>mm d$^{-1}$</td>
</tr>
<tr>
<td>$i_{rain}$</td>
<td>Rainfall rate</td>
<td>mm d$^{-1}$</td>
</tr>
<tr>
<td>$K_a(0)$</td>
<td>Unsaturated hydraulic conductivity</td>
<td>mm d$^{-1}$</td>
</tr>
<tr>
<td>$LAI$</td>
<td>Leaf-area index</td>
<td>m$^2$ leaves (m$^2$ ground)$^{-1}$</td>
</tr>
<tr>
<td>$NR, NR_{sub}$</td>
<td>Net radiation at the canopy top and soil surface</td>
<td>W m$^{-2}$</td>
</tr>
<tr>
<td>$p_{ Atmos}$</td>
<td>Atmospheric pressure</td>
<td>Pa</td>
</tr>
<tr>
<td>$P_f, J_{g, c}$</td>
<td>Canopy photosynthesis of grass and clover</td>
<td>kg C m$^{-2}$ d$^{-1}$</td>
</tr>
<tr>
<td>$Q_{Can}$</td>
<td>Drainage flow</td>
<td>mm d$^{-1}$</td>
</tr>
<tr>
<td>$Q_{surf}$</td>
<td>Surface runoff</td>
<td>mm d$^{-1}$</td>
</tr>
<tr>
<td>$v_{air}$</td>
<td>Aerodynamic resistance between canopy source height and reference level</td>
<td>s m$^{-1}$</td>
</tr>
<tr>
<td>$v_{can}$</td>
<td>Bulk boundary layer resistance of the canopy</td>
<td>s m$^{-1}$</td>
</tr>
<tr>
<td>$v_{can}$</td>
<td>Bulk stomatal resistance of the canopy</td>
<td>s m$^{-1}$</td>
</tr>
<tr>
<td>$v_{sub}$</td>
<td>Aerodynamic resistance between substrate and canopy source height</td>
<td>s m$^{-1}$</td>
</tr>
<tr>
<td>$w_{sub}$</td>
<td>Surface resistance of the substrate</td>
<td>s m$^{-1}$</td>
</tr>
<tr>
<td>$RH$</td>
<td>Relative humidity</td>
<td>%</td>
</tr>
<tr>
<td>$S$</td>
<td>Soil water store of the rooting zone</td>
<td>mm</td>
</tr>
<tr>
<td>$S_{Veg}$</td>
<td>Actual interception storage</td>
<td>mm</td>
</tr>
<tr>
<td>$S_{Veg, max}$</td>
<td>Maximal interception storage</td>
<td>mm</td>
</tr>
<tr>
<td>$T_{air}, T_{soil}$</td>
<td>Hourly air, resp. soil temperature</td>
<td>°C</td>
</tr>
<tr>
<td>$T_{air, d}, T_{soil, d}$</td>
<td>Daily mean air, resp. soil temperature</td>
<td>°C</td>
</tr>
<tr>
<td>$u$</td>
<td>Wind speed at reference height</td>
<td>m s$^{-1}$</td>
</tr>
<tr>
<td>$z_{root}$</td>
<td>Rooting depth</td>
<td>mm</td>
</tr>
<tr>
<td>$z_0$</td>
<td>Roughness length of the canopy</td>
<td>m</td>
</tr>
<tr>
<td>$\Delta$</td>
<td>Change of saturation vapour pressure with temperature</td>
<td>Pa °C$^{-1}$</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>Psychrometric constant</td>
<td>Pa °C$^{-1}$</td>
</tr>
<tr>
<td>$k_e$</td>
<td>Effective extinction coefficient of the canopy</td>
<td>dimensionless</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Volumetric soil water content</td>
<td>m$^3$ water (m$^3$ soil)$^{-1}$</td>
</tr>
<tr>
<td>$\theta_{w, e}$</td>
<td>Effective soil water content at incipient water stress; weighted average of $\theta_{w, g}$ and $\theta_{w, c}$</td>
<td>plant specific value, m$^3$ water (m$^3$ soil)$^{-1}$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Description</th>
<th>Values and units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a_4, a_20$</td>
<td>Constants relating the zero plane displacement, resp. roughness length to the canopy height</td>
<td>0.63, 0.13</td>
</tr>
<tr>
<td>$a_{NR, b_{NR}}$</td>
<td>Coefficients defining the relation between net and global radiation</td>
<td>–20 W m$^{-2}$, 0.62</td>
</tr>
<tr>
<td>$k_{S_{Veg, max}}$</td>
<td>Parameters describing the maximal canopy interception storage based on the total leaf-area</td>
<td>3 mm, 4 m$^3$ leaves (m$^2$ ground)$^{-1}$</td>
</tr>
<tr>
<td>$B$</td>
<td>Shape parameter for the desorption curve</td>
<td>Soil specific value, dimensionless</td>
</tr>
<tr>
<td>$\epsilon_{CO2}$</td>
<td>Conversion factor for the units of the photosynthetic rate</td>
<td>23563.6 C m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$A$</td>
<td>Effect of ambient CO2 on stomatal conductivity</td>
<td>2</td>
</tr>
<tr>
<td>$C_{SO2}$</td>
<td>Reference value of the atmospheric CO2 concentration</td>
<td>350 ppm</td>
</tr>
<tr>
<td>$C_P$</td>
<td>Specific heat capacity of dry air at constant pressure</td>
<td>1005 kg$^{-1}$ °C$^{-1}$</td>
</tr>
<tr>
<td>$w_{Can}$</td>
<td>Leaf width</td>
<td>0.01 m</td>
</tr>
<tr>
<td>$f_{v, min}$</td>
<td>Fraction of potential evapotranspiration at the permanent wilting point</td>
<td>0.4</td>
</tr>
<tr>
<td>$r_{50, 51}$</td>
<td>Parameters controlling stomatal conductivity</td>
<td>2592 mol m$^{-2}$ d$^{-1}$, 12</td>
</tr>
<tr>
<td>$i_{Can, ref}$</td>
<td>Reference canopy height</td>
<td>0.5 m</td>
</tr>
<tr>
<td>$k$</td>
<td>von Kármán constant</td>
<td>0.4</td>
</tr>
<tr>
<td>$LAI_{max}$</td>
<td>Saturated hydraulic conductivity</td>
<td>Soil specific value (mm d$^{-1}$)</td>
</tr>
<tr>
<td>$M_{w, a, t, m}$</td>
<td>Maximal LAI of the total canopy for canopy resistances</td>
<td>6 m$^2$ leaves (m$^2$ ground)$^{-1}$</td>
</tr>
<tr>
<td>$e_2$</td>
<td>Molecular weight of water, resp. dry air</td>
<td>18, 28.97 g Mol$^{-1}$</td>
</tr>
<tr>
<td>$f_{air}$</td>
<td>Eddy diffusivity decay constant</td>
<td>3.5</td>
</tr>
<tr>
<td>$l_{air}$</td>
<td>Reference bulk boundary layer resistance of the canopy</td>
<td>140 s m$^{-1}$</td>
</tr>
<tr>
<td>$l_{soil}$</td>
<td>Surface resistance of the substrate</td>
<td>100 s m$^{-1}$</td>
</tr>
<tr>
<td>$L_{soil, corr}$</td>
<td>Constant accounting for the dampening of soil temperature amplitude</td>
<td>1 °C</td>
</tr>
<tr>
<td>$\beta_{Can, ref}$</td>
<td>Reference height</td>
<td>2 m</td>
</tr>
<tr>
<td>$z_{bare}$</td>
<td>Roughness length of the bare substrate</td>
<td>0.01 m</td>
</tr>
<tr>
<td>$\Delta t$</td>
<td>Time step of integration</td>
<td>0.0416667 d (1=1h)</td>
</tr>
<tr>
<td>$\theta_{f, \theta_{wpw}}$</td>
<td>Soil water content at field capacity and permanent wilting point</td>
<td>Soil specific values, m$^3$ water (m$^3$ soil)$^{-1}$</td>
</tr>
<tr>
<td>$\theta_{at}$</td>
<td>Saturated soil water content</td>
<td>Soil specific value, m$^3$ water (m$^3$ soil)$^{-1}$</td>
</tr>
<tr>
<td>$\theta_{w, e}(I_{g, c})$</td>
<td>Soil water content at incipient water stress</td>
<td>2.5 × 10$^6$ kg$^{-1}$</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>Latent heat of vaporization</td>
<td>1 kg m$^{-3}$</td>
</tr>
</tbody>
</table>
For a wet soil, the substrate surface resistance \( r_s^{sub} \) becomes:

\[
r_s^{sub} = r_s^{min}
\]  

(A4.27)

Following Riedo et al. (1998), the bulk boundary layer resistance of the canopy (\( r_a^{can} \)) is expressed as a function of the wind velocity (\( u \)) and the total canopy coverage (\( LAI \)). With \( r_a^{can} \), denoting the maximal resistance value and \( d_{leaf} \) the leaf width, one has:

\[
r_a^{can} = \frac{r_a^{can}_{a,ref}}{n_e} \sqrt{\frac{d_{leaf}(1)}{1 - \exp(-0.5n_e)}} \sqrt{2LAI}\]  

(A4.28)

The unconstrained bulk stomatal resistance is formulated according to Riedo et al. (1998) as:

\[
r_s^{can} = \left\{ f_j(c_a)g_0LAI + g_1 \frac{P_z + P_r(RH/100)}{c_{CO2} - c} - c_a \right\}^{-1}
\]  

(A4.29)

where \( g_0 \) and \( g_1 \) are stomatal conductance parameters, and the function \( f_j(c_a) \) controls the acclimation response of the stomatal conductance to atmospheric CO2 concentration. Following Thornley (1998):

\[
f_j(c_a) = \frac{1 + c_{gs}}{1 + (c_{gs}c_a/C_{350})}
\]  

(A4.30)

with parameter \( c_{gs} \).

A.4.5. Runoff production

All the water flowing out from the soil when \( \theta > \theta_{pwp} \) is assumed to be matrix flow and driven by the matric potential. The drainage rate \( Q_{drain} \) is equal to the unsaturated hydraulic conductivity (\( K_u(\theta) \)) which is modelled according to Brooks and Corey (1966) and Campbell (1985) as:

\[
Q_{drain} = K_u(\theta) = K_{sat} \left( \frac{\theta}{\theta_{sat}} \right) \]  

(A4.31)

where \( K_{sat} \) is the saturated hydraulic conductivity and the parameter \( b \) determines the shape of the retention curve, Eq. (A5.1). Surface runoff (\( Q_{surf} \)) occurs whenever the difference between infiltration, evapotranspiration and drainage (\( Q_{inf} - E_{can} - E_{soil} - Q_{drain} \)) exceeds the available pore space (\( \theta_{sat} - \theta - S \)):

\[
Q_{surf} = \max(0, [(\theta_{inf} - E_{can} - E_{soil} - Q_{drain}) - (\theta_{sat} - \theta_{root} - S)])
\]  

(A4.32)

A.5. Soil water properties (Table A5)

When not determined in the field, values of the parameters \( \theta_{anaerob}, \theta_{pwp} \) and \( \theta_{wss} \), can be estimated from the corresponding values of the matric potential (\( \psi \)). Following Campbell (1985):

\[
\theta = \theta_{sat} \left( \frac{\psi}{\psi_{wss}} \right)^{1/b}
\]  

(A5.1)

where \( \theta_{sat} \) is the volumetric soil water content at saturation, \( \psi_{wss} \) the so-called air entry potential and \( b \) is a constant (see (A4.31)), and where \( \psi_{wss} \) and \( b \) were predicted from soil texture using equations discussed in Campbell (1985, p. 45 ff.).

The thresholds in soil moisture in (A6.5) are derived from (A5.1) using the following values for the thresholds in the potentials: \( \psi_{anaerob} = -3 \) J kg\(^{-1}\); \( \psi_{pwp} = -1500 \) J kg\(^{-1}\); \( \psi_{wss} = -1000 \) J kg\(^{-1}\); and, \( \psi_{wso} = -400 \) J kg\(^{-1}\). These latter two parameters for the grass and clover are set for the following reasons: as reported by Gardner (1983) and Jones (1988) the stomatal closure of grass species under water stress starts at a leaf water potential of about \(-500 \) J kg\(^{-1}\) in average, but with large variability among species, management and field conditions. In addition, experimental field studies of Aparicio-Tejo et al. (1980), Thomas (1984), Frame and Newbould (1986), Liu and Kemp (1992), Whitehead (1995a) and Lucero et al. (2000) indicate that clover is less drought-resistant than grass. As the model does not calculate the plant water status the response functions in Eq. (A6.5) are expressed by the soil water content which is related to the soil water potential using (A5.1). Taking into account all these arguments and the large uncertainty in literature the values for \( \psi_{wss, g} \) and \( \psi_{wss, c} \) for the critical soil moisture potential for grass and clover, respectively, were chosen to obtain a measurable difference in the response of grass and clover to water stress as depicted in Fig. 2b. The same value of \( \psi_{wss} \) is adopted for the shoot and root components, but differences in the response to water stress are permitted by setting \( f_{wss, g}^{low} = f_{wss, c}^{min} \). The higher intercepts for the roots are chosen to maintain root vitality under drought as root elongation, which is not included in the model, is a postulated mechanism to improve water uptake under drought conditions (Larcher, 2003).

A.6. Response functions for temperature and soil water (Table A6)

We assume that plant processes such as growth, decomposition and respiration exhibit the same response to temperature and write the response function as:

\[
f_j(T) = \max \left\{ 0, \frac{T - T_{ref}^{low}}{T_{ref}^{low} - T_{ref}^{upp}} \frac{\psi_{wss}}{\psi_{wss}^{high}} \left( T_{ref}^{low} - T_{ref}^{upp} \right) \right\}
\]  

(A6.1)

with \( T_{low} \) and \( T_{upp} \) indicating the lower and upper boundary of the permitted temperature range, \( T_{ref} \) the reference temperature and \( q \) the shape parameter (Thornley, 1998). The same response is assumed for the shoot and root compartment, but the function is evaluated with respect to air temperature in the former, respectively, soil temperature in the latter case.

For grass, the standard parameter values \( T_{low} = 0 \) C, \( T_{upp} = 45 \) C, \( T_{ref} = 20 \) C and \( q_g = 2 \) are used as defined in Thornley (1998, Eq. (3.11a)). We set \( T_{low} = 0 \) C, \( T_{upp} = 48 \) C, \( T_{ref} = 19.5 \) C and \( q_g = 2 \) for clover to account for a higher optimum temperature (Mitchell, 1956; Wachendorf et al., 2001).

The temperature response functions in (A6.1) are used to modify the growth, decomposition and respiration rates of plants assuming that atmospheric CO2 does not affect these response functions. Photosynthesis, however, responds to elevated CO2 concentrations by increasing the optimum temperature range. For grass this is accounted for by using Eqs. (A2.16) and (A2.17) to evaluate \( T_{ref}^{max,g} \), which is then inserted in (A6.1). For clover the Eqs. (A2.16) and
Table A6
Variables and parameters used in the formulation of the response functions.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>( T )</td>
<td>Temperature</td>
<td>°C</td>
</tr>
<tr>
<td>( \phi_{\text{app}}^{\text{T}_{\text{max}}}, j \in g, c )</td>
<td>Temperature maximum depending on CO(_2) in the temperature response function of photosynthesis</td>
<td>°C</td>
</tr>
<tr>
<td>( \theta )</td>
<td>Volumetric soil water content</td>
<td>m(^3) water (m(^3) soil(^{-1}))</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Description</th>
<th>Values and units</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \theta_{\text{anaerob}} )</td>
<td>Lower boundary in the water stress function related to waterlogging effects</td>
<td>0.7</td>
</tr>
<tr>
<td>( \theta_{i,j}^{\text{max}, c} )</td>
<td>Scaling parameter for the water stress function for the shoot and root based on the soil water content</td>
<td>0.2</td>
</tr>
<tr>
<td>( m_l^{\text{T}_{\text{max}, c}} )</td>
<td>Constant to scale the temperature response function for clover photosynthesis</td>
<td>1.1</td>
</tr>
<tr>
<td>( \theta_{i,j} \in g, c )</td>
<td>Shape parameter in the temperature response functions of grass and clover</td>
<td>2.2</td>
</tr>
<tr>
<td>( T_{\text{app}}^{\text{low}, g}, T_{\text{app}}^{\text{low}, c} )</td>
<td>Parameters in the temperature response function for grass</td>
<td>0.0, 20.0, 40.0 °C</td>
</tr>
<tr>
<td>( T_{\text{app}}^{\text{low}, g}, T_{\text{app}}^{\text{low}, c} )</td>
<td>Parameters in the temperature response function for clover</td>
<td>0.0, 19.5, 48.0 °C</td>
</tr>
<tr>
<td>( \theta_{\text{anaerob}} )</td>
<td>Soil water content defining stress inception when the soil becomes waterlogged</td>
<td>Plant specific values, m(^3) water (m(^3) soil(^{-1}))</td>
</tr>
<tr>
<td>( \theta_{\text{anaerob}} )</td>
<td>Soil water content at incipient water stress for grass and clover</td>
<td>Plant specific values, m(^3) water (m(^3) soil(^{-1}))</td>
</tr>
</tbody>
</table>

(A2.17) are evaluated with the specific parameters to determine the upper temperature range \( T_{\text{max}, c} \) at elevated CO\(_2\), in the temperature response function for photosynthesis (TRFP) of the clover. This value \( T_{\text{max}, c} \) is then inserted into Eq. (A6.4) and using (A6.3) defines the TRFP of the clover at elevated CO\(_2\) (A6.2):

\[
f_{\text{T}_{\text{max}, c}}^{\text{T}}(T) = \frac{m_l^{T_{\text{max}, c}} (T_{\text{ref}} - T - \theta_{\text{low}}^g) \phi_{\text{app}}^g (T_{\text{ref}} - T - \theta_{\text{low}}^g)}{(T_{\text{ref}} - T - \theta_{\text{low}}^g) \phi_{\text{app}}^g (T_{\text{ref}} - T - \theta_{\text{low}}^g)}
\]

where \( m_l^{T_{\text{max}, c}} \) is a scaling factor, and where

\[
\Delta_T = T_{\text{app}}^{\text{low}, g} - \theta_{\text{low}}^g
\]

and

\[
\Omega_T = \frac{T_{\text{app}}^{\text{low}, g} - \theta_{\text{low}}^g}{T_{\text{app}}^{\text{low}, c} - \theta_{\text{low}}^c}
\]

Note that (A6.2)–(A6.4) are scaling equations to determine the TRFP of the clover at elevated CO\(_2\) and are introduced to keep the same relation between the TRFP for grass and clover observed at ambient CO\(_2\) also at elevated CO\(_2\).

The impact of water stress on grass and clover processes is quantified assuming a discontinuous response function of the volumetric soil water content \( f_{i,j}^{\text{T}}(\theta) \). The same function but different parameterizations are used for the grass and clover, viz.:

\[
f_{i,j}^{\text{T}}(\theta) = \begin{cases} 
1 & \text{if } \theta_{\text{anaerob}} < \theta \leq \theta_{\text{cut}} \\
1 - (1 - \theta_{\text{anaerob}} - \theta_{\text{anaerob}}) \frac{\theta}{\theta_{\text{anaerob}}} & \text{if } \theta_{\text{anaerob}} < \theta \leq \theta_{\text{anaerob}} \\
1 + (1 - \theta_{\text{anaerob}}) \frac{\theta_{\text{anaerob}}}{\theta_{\text{anaerob}}} & \text{if } \theta_{\text{anaerob}} < \theta \leq \theta_{\text{anaerob}} \\
0 & \text{if } \theta \leq \theta_{\text{anaerob}} \end{cases}
\]

In (A6.5) \( \theta_{\text{anaerob}} \) is introduced to account for the oxygen deficiency that initiates shoot and root stress if the soil becomes waterlogged (McFarlane et al., 2003), whereas \( \theta_{\text{anaerob}} \) denotes the threshold below which plant processes are affected by water scarcity. The latter is assumed equal for the shoot and root compartments.

A.7. Management (Table A7)

A.7.1. Fertilization

Mineral and organic N fertilizer applications feed pulse-wisely into the corresponding N pools according to Eqs. (A3.1) and (A3.6), assuming losses of 20, respectively, 30% during the application. Following a pre-specified fertilization schedule, it is assumed that fertilization events take place within one time step \( \Delta t \) at noon of the scheduled days.

A.7.2. Harvesting

As in the case of fertilization, the canopy is cut following a predefined schedule. The harvest is removed within one time step \( \Delta t \) and the time of harvest is assumed at noon of the scheduled day. All variables related to above-ground compartments are pulse-wise reduced. The yield \( Y_{sh,j} \) is calculated as the difference between the shoot biomass \( W_{sh,j} \) and a threshold \( W_{cut,j} \) representing the remaining standing shoot biomass:

\[
Y_{sh,j} = \text{MAX}(0, W_{sh,j} - W_{cut,j})
\]

Analogously:

\[
Y_{LAI,j} = \text{MAX}(0, LAI_j - LAI_{cut,j})
\]

where \( LAI_{cut,j} \) and \( W_{cut,j} \) are related through:

\[
LAI_{cut,j} = W_{cut,j} [S\lambda_j (1 - 0.03 \phi_{\text{lam}, j})]
\]

according to (A1.12), assuming \( C_j = 0.03 \text{ kg C} (\text{kg DM})^{-1} \) in the remaining standing biomass.

The output of substrate C and N to yield \( (Y_{C,j} \text{ and } Y_{N,j}) \) respectively is calculated from the product of the yield and the plant substrate concentrations:

\[
\begin{cases} 
Y_{C,j} = Y_{sh,j} C_j \\
Y_{N,j} = Y_{sh,j} N_j
\end{cases}
\]

As mentioned in Section 2.2, a cut is introduced at the end of each year to ensure realistic conditions at the beginning of each growing season, for PROGRASS does not account for winter mortality.

A.8. Environmental variables (Table A8)

Table A7
Variables and parameters used in the formulation of management.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>( W_{cut,j} \in g, c )</td>
<td>Shoot dry matter of the standing biomass after harvest</td>
<td>kg DM m(^{-2})</td>
</tr>
<tr>
<td>( Y_{LAI,j} \in g, c )</td>
<td>Leaf-area yield</td>
<td>m(^2) leaves (m(^2) ground(^{-1}))</td>
</tr>
<tr>
<td>( Y_{N,j}, Y_{C,j} \in g, c )</td>
<td>Loss of substrate N and C to yield</td>
<td>kg N m(^{-2}), kg C m(^{-2})</td>
</tr>
<tr>
<td>( Y_{sh,j} \in g, c )</td>
<td>Dry matter yield</td>
<td>kg DM m(^{-2})</td>
</tr>
</tbody>
</table>

Parameters | Description | Values and units |
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>( LAI_{cut,j} \in g, c )</td>
<td>Leaf-area of the standing biomass after harvest</td>
<td>0.35, 0.15 m(^2) leaves (m(^2) ground(^{-1}))</td>
</tr>
</tbody>
</table>
A9. Model initialization

Model runs are started by providing initial conditions of all state variables. For above-ground biomass, the same values as those characterizing the standing biomass after harvest can be used. Initial values for root biomass can be chosen depending on the assumed state of the vegetation. If simulations starts during winter or spring time, soil water content can be set to field capacity, and the interception store can be assumed to be empty. Further, soil temperature can be estimated from air temperature.

As seen in our results, the co-existence of grass and clover depends very much on soil mineral N availability, which in turn is related to soil organic N availability. For our simulations, initial values of the soil N pools were estimated according to field observations. However, if no information is available, initial values can also be found by running an equilibrium simulation. In this case, environmental and management data covering a long enough period of time (typically of the order of 10 years) must be provided. These are then cyclically used.

References


