

Soil carbon and nitrogen changes after clearing mulga (*Acacia aneura*) vegetation in Queensland, Australia: Observations, simulations and scenario analysis

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Abstract

In the work reported here we examine the changes in soil (organic) carbon and nitrogen that are observed after converting a stand of nitrogen-fixing mulga trees (*Acacia aneura*) to buffel-grass (*Cenchrus ciliaris*) pasture that contained no nitrogen-fixing legumes. A range of previously reported field measurements was compared against the output of CenW 3.1, a reformulated version of the CENTURY model.

The model successfully reproduced the observed patterns of soil carbon, C:N ratios and nitrogen mineralisation rates under mulga vegetation. This included relatively small changes in carbon concentration down to 1 m, C:N ratios of around 11–13 across all soil depths, substantial nitrogen mineralisation rates to a depth of 90 cm and, after clearing, an on-going decrease in soil organic carbon and nitrogen stocks.

Interpretation of experimental observations was made difficult by the addition of a large amount of ‘dead’ organic matter from killed mulga roots after clearance. This material may be excluded through sieving (to 2 mm) in measurements taken shortly after tree removal, but may be included in later-year sampling as the partly decomposed material might be able to pass through sieves. Past work has usually ignored consideration of dead coarse roots. For the site carbon budget, changes in live biomass and surface litter significantly outweighed the small changes in soil organic carbon, and changes in decaying coarse roots were quantitatively more important than changes in other organic carbon pools.

Modelled nitrogen mineralisation rates were lower under buffel-grass than those under mulga and showed significant year-to-year variations that were in line with varying rainfall. It showed no consistent trend over the first 20 years after clearing because the effect of decreasing nitrogen stocks was balanced by an increase in organic matter quality with the change from lignin-rich mulga litter to buffel-grass litter with lower lignin concentration. Nitrogen mineralisation rates gradually decreased thereafter as nitrogen stocks continued to decrease but litter quality stabilised.

A scenario analysis showed that soil carbon and nitrogen trends could be affected by changing the nitrogen budget through inclusion of legumes or cessation of nutrient removal by grazing animals. Inclusion of legumes was needed to halt the decline in soil nitrogen and to ensure the long-term maintenance, or increase, in nitrogen stocks.

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1. Introduction

With a contribution of 22% of total anthropogenic greenhouse gas emissions in 1990, land-use change was a major contributor to Australia's net emissions. Fortunately, rates of land clearing and associated greenhouse gas emissions have gradually decreased since 1990 (AGO, 2005). Nonetheless, land-use change continues to be an important contributor to Australia's total emissions, and effective management of net greenhouse gas emissions can only be accomplished if all significant sources and sinks are adequately considered. This includes consideration of changes in above and below-ground carbon stocks following land-use change.

Mulga (*Acacia aneura*) ecosystems occupy 150 million hectares of arid and semi-arid lands in Australia. Some of these lands are being converted to pasture, and the associated loss of above-ground biomass constitutes an important contribution to Australia's net greenhouse gas emissions. From 1991 to 2001, nearly 400,000 ha yr⁻¹ were cleared in Queensland alone, with 95% of cleared area used for pasture development (DNRM, 2003). Changed land use can potentially also lead to a loss of below-ground carbon and nitrogen stocks.

Australia's National Carbon Accounting System (NCAS) has devoted considerable resources to monitor land-use change in Australia and quantify associated changes in biomass carbon (AGO, 2005). An understanding of changes in soil organic carbon in response to land-use change is potentially more difficult than the quantification of changes in above-ground carbon stocks. This is because changes in soil organic carbon are less readily observable than changes above ground, and scientific understanding in terms of the dependence of trends on specific underlying driving forces is still emerging.

A number of literature surveys have shown that the conversion of forests to cultivated land uses usually leads to significant soil organic carbon losses (Mann, 1986; Dalal and Mayer, 1986; Davidson and Ackerman, 1993; Murty et al., 2002; Guo and Gifford, 2002). In contrast, soil organic carbon usually changes little, or not at all, when the new land use is uncultivated grazing land (Lugo and Brown, 1993; Fearnside and Barbosa, 1998; Murty et al., 2002; Guo and Gifford, 2002).

In a more detailed study of soil carbon changes after tree-pasture conversions in Queensland, Australia, Harms et al. (2005) measured an average 8% loss of soil carbon for the top 30 cm. An interesting pattern in the work of Harms et al. (2005) was an apparent dependence of trends in soil carbon on the characteristics of the original woody vegetation. Soils under nitrogen-fixing mulga (*A. aneura*) and brigalow (*Acacia harpophylla*) stands lost more carbon upon conversion than soils under non-fixing 'box' (*Eucalyptus populnea*) eucalypt stands although another non-fixing system, 'box-ironbark' eucalypts (*Eucalyptus*

melanophloia) lost a similar amount of carbon as the nitrogen-fixing systems.

As we are interested in understanding the general reasons for the patterns of soil carbon changes after land clearing, the differences between clearing the different vegetation types are intriguing. They lead to the interesting generic question of whether nitrogen-fixing systems are inherently vulnerable to losses of soil nitrogen and associated carbon if the vegetation is changed to one without nitrogen-fixers, such as the conversion from nitrogen-fixing trees to grass vegetation that contains few legumes.

After clearing mulga stands, and with no fertiliser application, the buffel-grass pasture depends almost entirely on the 'inherited' nitrogen capital in the soil derived from the previous nitrogen-fixing vegetation. This capital is only marginally supplemented by atmospheric inputs estimated at 5 kg nitrogen per hectare per year (kgN ha⁻¹ yr⁻¹), but subject to volatilisation losses during nitrogen mineralisation, leaching and removal by grazing stock.

A number of studies have modelled changes in soil carbon after deforestation (e.g. Falloon et al., 2000; Cerri et al., 2004; Power et al., 2004; Skjemstad et al., 2004; Grace et al., 2006), but a full understanding of the relevant factors in explaining patterns of soil carbon changes after land-use change is yet to emerge. In particular, some models, such as the CENTURY model, include a fully coupled nitrogen cycle to constrain possible changes in soil carbon after deforestation (Cerri et al., 2004), whereas other models, such as Roth-C (Falloon et al., 2000; Skjemstad et al., 2004) and SOCRATES (Grace et al., 2006) have no nitrogen-cycling constraints. It remains an unresolved question whether nitrogen-cycling constraints could and should usefully constrain carbon dynamics in disturbed or undisturbed ecosystems (Rastetter et al., 1992; Kirschbaum et al., 2003).

In the present work, we studied changes in carbon and nitrogen stocks and dynamics following clearing of a (nitrogen-fixing) mulga stand in central Queensland to better understand the key drivers that may lead to changes in soil carbon and nitrogen and to the long-term supply of mineral nitrogen. In addition to its important role for carbon storage in the context of net greenhouse gas emissions, the long-term supply of mineralised nitrogen is a key aspect of the fertility of the system and, thus, a determinant of the long-term sustainability of pasture production after land-use change.

The objectives of the present study were to simulate the observed patterns of soil carbon and nitrogen dynamics under a mulga stand and then to simulate the patterns following clearing and maintaining the land under buffel-grass pasture. The model was also used to explore the expected response of soil carbon and nitrogen to modification of key aspects of the system's nitrogen economy, such as inclusion of legumes or cessation of produce removal.

2. Materials and methods

2.1. Study site

The study site is located on the 'Mulga View' property (27°59'S; 148°33'E) near St. George in southern Queensland, Australia. The soil type is a Red Kandosol, with a clay content of 12% and soil pH 6.0 in the 0–0.1 m layer, increasing with depth to 22% clay and pH 6.2 at 0.6–1.0 m soil depth. The climate is semi-arid and sub-tropical, with a mean annual temperature of 21 °C, mean annual rainfall of 510 mm yr⁻¹ and pan evaporation of 1950 mm yr⁻¹.

The original vegetation was a mature mulga stand that had occupied the site for at least the past 100 years. A portion of the site was clearfelled, burnt, ploughed and sown to a C₄ buffel-grass pasture which has been grazed by cattle since then. Full details of the site have been described by Dalal et al. (2005a, b).

Soil organic matter measurements were taken with 50-mm soil corers and sieved to pass a 2 mm fine mesh before being prepared for analysis. That procedure removed all live or recently dead root fragments, especially coarse roots. Charcoal (inert organic carbon and nitrogen) contents were measured using mid-infra-red spectroscopy of finely ground soil samples. A Partial Least-Squares analysis was applied to each infra-red spectra to estimate soil properties using the methods of Janik et al. (1995, 1998). Further details of the soil and plant measurements have been described by Dalal et al. (2005a, b) and Mathers et al. (2006).

3. Modelling

The simulations shown in the following work used the model CenW 3.1 as described by Kirschbaum (1999, 2004) and Kirschbaum and Paul (2002). The model had originally been developed and parameterised for *Pinus radiata*, but its generic structure has allowed its application for a range of plant types and environments (Kirschbaum et al., 2003, 2007; Kirschbaum, 2004).

The model runs on a daily time step and comprehensively simulates stand characteristics, such as leaf area dynamics, stand height, basal area development and gas exchange in both the short and longer-term. These stand-level dynamics are explicitly linked through the soil via carbon transfer from plants to the soil via litter fall or plant death, with subsequent nutrient transfer back from the soil to plants.

For the present simulations, a number of additional routines had to be introduced, or existing ones modified. They included addition of carbon gain by C₄ photosynthesis, inclusion of additional pools of 'inert' organic carbon (charcoal), the effect of ploughing, modifications to the calculation of biological nitrogen fixation, immobilisation of mineral nitrogen into soil organic matter and the calculation of soil temperature. Details of these new routines are given in Appendix A.

The organic matter module of CenW is based on the CENTURY model (Parton et al., 1987), but has been reformulated to better describe the patterns found under woody vegetation (Kirschbaum and Paul, 2002). As part of this modification, explicit pools of coarse and fine woody litter were introduced to deal with litter originating from dead stems, coarse roots and fallen branches.

In addition to the pool of 'resistant' organic matter that is formed by microbial transformations, a new pool, termed 'inert', was introduced to correspond to charcoal. Material can enter this pool only through fires. It was introduced because different soils can differ substantially in the amount of charcoal and, thus total organic carbon that is present based on their respective past fire histories even if edaphic and environmental drivers are the same (Skjemstad et al., 1999; Gonzalez-Perez et al., 2004). The turn-over rate of even 'resistant' organic matter based on the parameters originally given by Parton et al. (1987) is also too fast to account for the observed age of many soils, especially deeper in the profile (Baisden et al., 2002), and the addition of inert organic matter overcomes both of those problems.

For the current work, the soil was separated into seven layers (0–5, 5–10, 10–20, 20–30, 30–60, 60–100, below 100 cm, respectively). The same soil organic matter simulations were carried out for each soil layer, with each layer having its own complement of all organic matter pools. Layers differed only through the amounts and qualities of litter entering each layer. In addition, a defined small fraction of each pool was transferred to the corresponding pool in the layer below (Baisden et al., 2002). This fraction was set to 29% per cm per year. This means that every year, 29% of all organic matter pools was transferred down by 1 cm in the soil through water movements or bioturbation by soil fauna (Bernhard-Reversat, 1987; Gallagher and Wollenhaupt, 1997; Koutika et al., 2001).

All organic matter pools were also modelled explicitly for the surface litter layer. It was assumed that some transfer occurred between the surface layer and the soil layers below. That transfer was set to 40% of organic matter per year. In the earlier version of the model which included no separation into distinct layers, active, slow and resistant pools were modelled only for the soil as a whole so that transfer did not have to be considered (Kirschbaum and Paul, 2002). Patterns of organic matter with depth in the soil were modelled by adjusting the parameter describing the transfer between layers and the depth distribution of the input of litter from decaying fine and coarse roots.

As the organic matter sampling had removed all large roots and recently dead roots greater than 2 mm, the modelled sum of 'active', 'slow', 'resistant' and 'inert' components were compared against measurements whereas 'metabolic', 'structural' and 'woody' litter pools were assumed to correspond to that fraction that had been removed through sieving samples before analysis.

The model was initialised by repeatedly simulating the growth of a mulga stand over 60 years with the weather conditions as obtained for our experimental site. Parameters for nitrogen fixation and nitrogen losses were varied until modelled biomass pools corresponded to those observed for the mulga stand at the site. This ensured that all soil organic matter pools had reached a quasi-steady state based on the site climate and the biotic influences of a mulga stand. It was assumed that the stand was then killed, followed by ground fire that removed 99% of surface litter and replaced with a *C₄* pasture without legumes that was grazed three times a year with 50% of ingested nitrogen removed off-site in either animal produce or lost in urine. Mulga roots were assumed to extend to a depth of 2 m, with access to a total of 150 mm of water. Buffel-grass was assumed to have a root system extending down to only 1.5 m, with access to a total of 115 mm of water (B. Harms, unpublished).

This modelling sequence provided data for comparison with observed soil properties under mulga and pasture. The initially used parameters, including those that quantified biological nitrogen fixation, were modified and the simulations repeated through the sequence described above to obtain the closest agreement between modelled data and observations. Data were available from a mulga stand estimated to be about 60 years old and from an adjacent site that had been cleared about 20 years ago. As the model has a large number of parameters, there were an insufficient number of observations to confidently determine the value of each parameter, but the multiple observations and embedded relationships between plant and soils processes provided strong constraints on the possible trends in each observation.

The model and its source code are available at www.kirschbaum.id.au/Welcome_Page.htm, with a full list of relevant equations available at www.kirschbaum.id.au/CenW_equations.pdf and as Supplemental Material available through Soil Biology & Biochemistry.

3.1. Weather information

The weather data to drive the model were obtained from the SILO data drill (Jeffrey et al., 2001) for the years 1940–2005. Use of these data ensured that inter and intra-annual variability of the site was reflected in the simulations. For a long-term simulation after clearing, the daily observations from 1940 were used repeatedly to avoid any confounding effects from inter-annual weather variability. It provided a clearer representation of longer-term trends as driven by the changes in system properties rather than the vagaries of inter-annual weather dynamics.

The present work used daily minimum and maximum temperatures, solar radiation, rainfall and absolute humidity. Observed absolute humidity was on average about 20% lower than absolute humidity calculated from overnight minimum temperatures. This indicated that calculating absolute humidity from overnight minimum

temperatures would have provided an insufficient substitute for actual humidity measurements in this semi-arid environment.

Radiation was compared against data calculated with the routine described by Kirschbaum et al. (2007), but there was only moderate agreement between the data sets. Detailed examination of the SILO radiation data set showed many anomalies, with radiation being quite low on some days even when there was no rain and the diurnal temperature range was large, indicating that the sky was likely to have been clear on those days. Radiation should then have approached calculated clear-sky values. On other occasions, the SILO data set repeatedly reported the same values on consecutive days, thus not indicating any of the variation that might have been expected due to natural variability.

Hence, our confidence in the radiation component of the SILO data set for the Mulga View site was low, but we had no other option for improving the estimates, especially for longer runs. Radiation is, however, quite high in this environment and in excess of plant requirements for optimal growth so that errors in estimated radiation would have caused only minor errors in estimated plant performance.

3.2. Statistical analysis

The goodness-of-fit in respective comparisons between modelled and measured data was assessed by calculating model efficiency, which is the extent of variation explained by the model (or by a 1:1 line). High model efficiency can only be achieved when modelled and measured data are consistently closely related and without any systematic bias.

Formally, model efficiency, EF, was calculated as (Nash and Sutcliffe, 1970; Soares et al., 1995)

$$EF = 1 - \frac{\sum (y_o - y_m)^2}{\sum (y_o - \bar{y})^2}, \quad (1)$$

where y_o are the individual observations, y_m the corresponding modelled values and \bar{y} the mean of all observations.

In addition to reporting model efficiencies, we also report parameters and r^2 values for a line of best fit of observed against modelled data. The parameters of that line of best fit indicate whether there is any systematic bias in the model output, and the comparison between model efficiencies and r^2 values indicates whether residual error is random or systematic.

4. Results

4.1. Mulga stand

The mulga stand was modelled as being 60 years old when it was cleared, with 9 tonnes of dry weight per hectare

(tDW ha⁻¹) of foliage and 73 tDW ha⁻¹ in total above-ground biomass (B. Harms, unpublished). The mulga stand was modelled to fix nitrogen and have high foliar nitrogen concentration of about 1.9% nitrogen (per dry weight; Jalota et al., 2006).

No detailed measurements of coarse-root biomass have been taken at the site, but other studies of coarse roots of rangeland vegetation have indicated that plants growing in these marginal and water-limited environments tend to have large root systems relative to the size of their above-ground biomass (Snowdon et al., 2000; Zerihun et al., 2006). It was, therefore assumed that the stand had a coarse-root to stem ratio of 0.5. The size of this pool had important implications for soil carbon and nitrogen dynamics after tree clearing (see below).

The pattern of soil carbon with depth under mulga vegetation is shown in Fig. 1, displaying the typical pattern of decreasing carbon concentration with depth. Soil carbon was quite low, however, and changed with depth more

gradually than in many other soils, and 0.17% carbon was found at even 80 cm depth (Fig. 1(a)). This pattern of decreasing carbon concentration with depth was very well described by the model (Fig. 1(b)). To obtain that level of agreement, it had to be assumed that fine roots were also distributed fairly evenly with depth and that there was a relatively large amount of mixing by soil fauna or transport through water movements (Baisden et al., 2002).

Cumulatively, and without including the fresh litter fraction, the soil contained about 46.0 tonnes organic carbon per hectare (tC ha⁻¹) to a depth of 1 m, a further 9.9 tC ha⁻¹ below 1 m and 6.8 tC ha⁻¹ above the soil surface (1/3 of which was fine and 2/3 woody litter—data not shown).

Carbon to nitrogen (C:N) ratios did not change much with depth, with all values around 10–13 (Fig. 2). The observations showed the lowest C:N ratios to be at the highest and lowest layers, respectively. The model gave C:N ratios similar to the observations, although it could

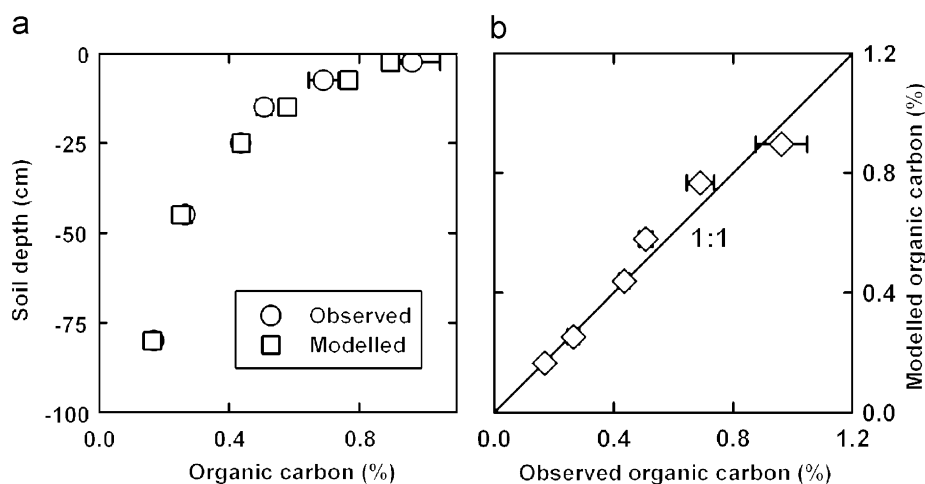


Fig. 1. Observed and modelled soil carbon concentration with soil depth (a) and modelled data plotted against observations (b). Error bars give standard errors of the means of observations. Some error bars are so small as to be masked by the size of symbols. Model efficiency, EF, was 0.963 and a regression equation to the data in (b) is given by $M = 0.973 O + 0.025$ ($r^2 = 0.964$). Observations after Dalal et al. (2005a).

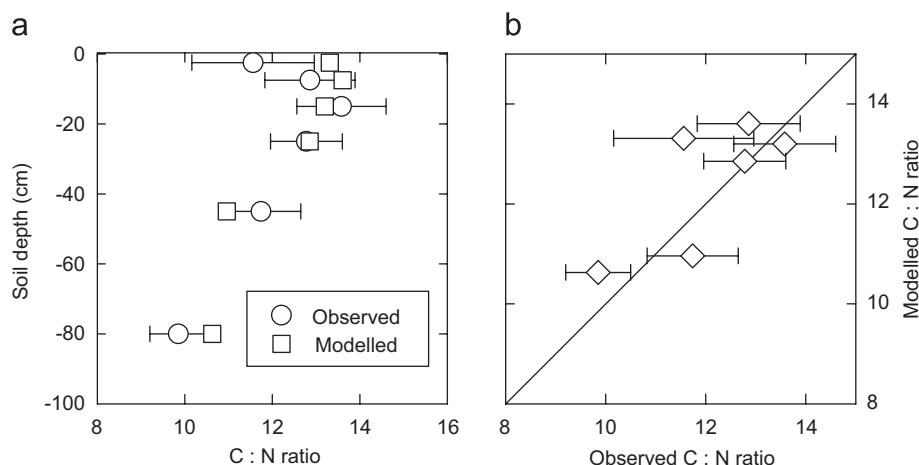


Fig. 2. Observed and modelled C:N ratios of soil organic matter with soil depth (a) and modelled data plotted against observations (b). Error bars show standard errors of the means of observations. Observations after Dalal et al. (2005b).

not replicate the apparent decrease in the C:N ratio for the upper-most soil layer because the on-going input of litter with a high C:N ratio by transfer from above the soil surface mitigated against any drop of C:N ratios to low values.

Modelled annual nitrogen mineralisation rates under mulga vegetation showed large year-to-year variation (Fig. 3), principally associated with variations in rainfall. Soil moisture is an important determinant of decomposition and nitrogen mineralisation rates so that the number of days when the soil was wet was important for determining the amount of nitrogen that could be mineralised over a year.

The highest nitrogen mineralisation rate was seen for the top layer of the soil but important contributions also came from lower layers (Fig. 4). The model overestimated the extent of decrease in mineralisation rate with depth, although there was also a large uncertainty associated with measured rates.

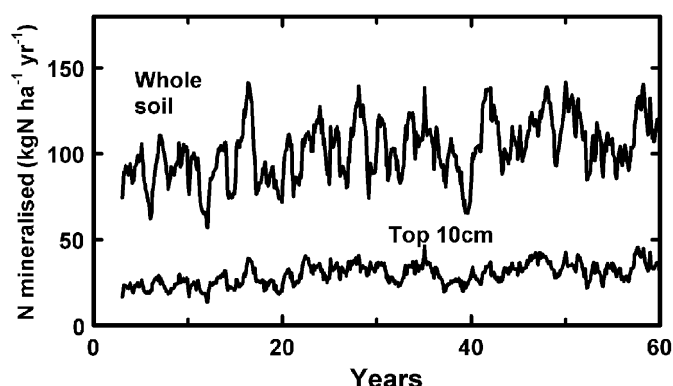


Fig. 3. Modelled nitrogen mineralisation under mulga shown either for the whole soil or for only the top 10 cm of the soil. Data show running means of the previous 12 months of simulated data.

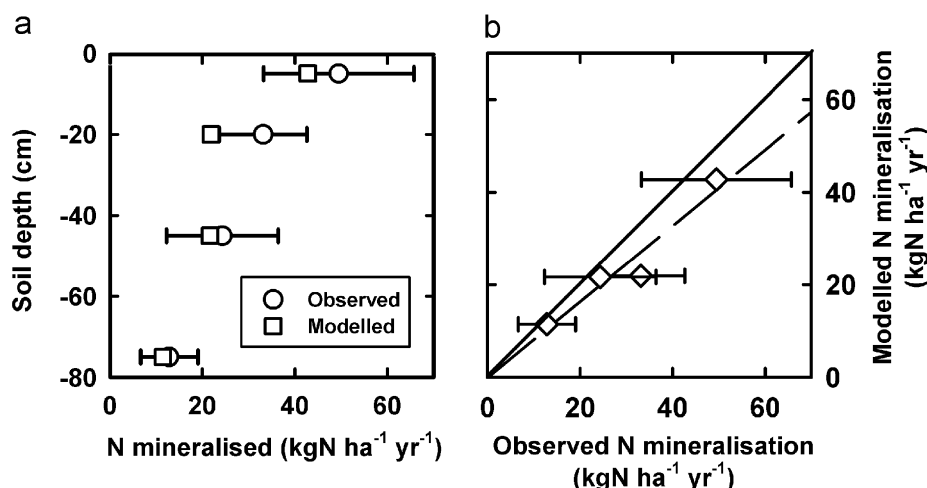


Fig. 4. Observed and modelled nitrogen mineralisation rate with depth under mulga vegetation (a) and modelled rates plotted against observations (b). Modelled nitrogen mineralised on the soil surface has been added to the nitrogen mineralisation in the uppermost soil layer. The solid line in (b) is a 1:1 line and the dashed line a line of best fit. EF = 0.749 and a regression equation in (b) is given by $M = 0.821O - 0.12$ ($r^2 = 0.930$). Observations after Mathers et al. (2006).

The rate of nitrogen mineralisation observed at depths below 40 cm is remarkable and leads to the question of how mineralisable organic nitrogen could move to those depths. Mineralisable nitrogen must originate from soil organic nitrogen that itself must originate either from dead roots or above-ground litter that is transported down the soil by water movements or bioturbation by soil fauna. Such a high nitrogen mineralisation rate at depth could be sustained only if there had either been significant transport within the soil, or through a large input from senescing fine roots at depth. To emulate these patterns in the model, it was necessary to set a fairly uniform distribution of root-litter input, and to assume a large extent of bioturbation. The soils at the study site are free-draining sandy to sandy loam soils so that considerable movement within the soil is quite feasible.

4.2. Buffel grass

Clearing was modelled as a clear fall, followed by a fire that consumed 99% of surface litter. The soil was then ploughed on a single occasion. Ploughing was assumed to incorporate all surface carbon into the soil and homogenise all soil pools other than coarse woody litter to a depth of 20 cm.

Total soil C stocks increased by more than 10 tC ha^{-1} when the mulga stand was cut (Fig. 5). This corresponded to the sudden addition of dead roots, mainly coarse roots, upon clearing the stand. It constituted no actual transfer of carbon, but simply a reclassification of formally live roots as dead roots through which that carbon became part of the pools of dead organic carbon in the soil. Other soil organic carbon pools changed little during this transition (Fig. 5(a)).

These changes in soil carbon were accompanied by corresponding trends in soil organic nitrogen (Fig. 5(b)),

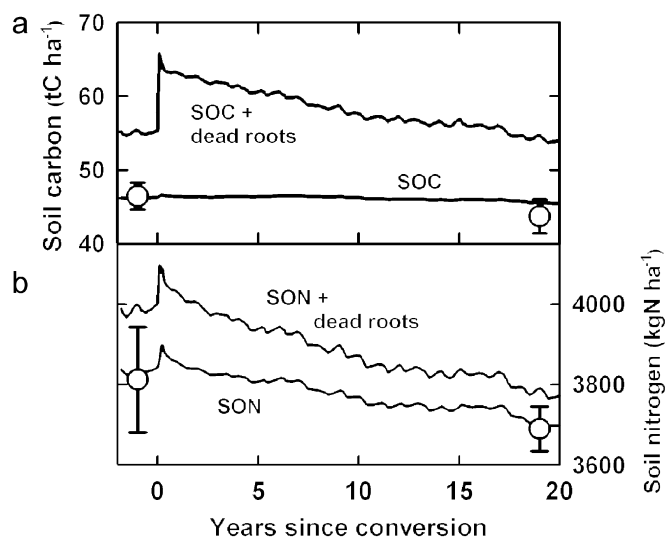


Fig. 5. Soil organic carbon (a) and nitrogen (b) stocks in the top 1 m of the soil before clearing and for 20 years after conversion. Shown are soil organic carbon (SOC) and nitrogen (SON) with and without recently dead roots. Symbols show measurements and standard errors of measurements in mulga and buffel-grass soils. Observations after Dalal et al. (2005a, b).

except that the changes were proportionately much smaller because of the low nitrogen concentration of coarse roots.

After the initial sharp increase in carbon and nitrogen upon clearing the stand, soil nitrogen stocks subsequently decreased by about 150 kgN ha^{-1} over the next 20 years (Fig. 5(b)). If one considers nitrogen in dead roots as well, then there was a total decrease by about 250 kgN ha^{-1} from the peak immediately after the inclusion of dead roots. This was accompanied by a loss of about 10 tC ha^{-1} over 20 years in dead coarse-root carbon, with only minor changes in carbon in other organic carbon pools (Fig. 5(a)). All these modelled changes conformed well to the observations of the fine fractions of soil carbon and nitrogen before and after tree clearing.

The trends in soil carbon and nitrogen were largely accounted for by changes in the upper-most soil layers, with the top 5 cm of the soil modelled to lose about 30% of carbon and nitrogen stocks (data not shown), which is consistent with observations at this site (Dalal et al., 2005a, b). Soil carbon deeper in the soil consists to a larger extent of more resistant fractions which changed little with changes in land use.

With the addition of a large amount of dead roots, the C:N ratio of the soil as a whole increased by more than two units through the input of dead roots, particularly coarse dead roots (Fig. 6). Over the following 20 years under pasture, coarse roots gradually decayed, thus reducing the C:N ratio of the soil as a whole. Some of the break-down products from the decay of coarse roots transferred to other organic matter pools, leading to a marginal increase in the C:N ratio of those pools (Fig. 6) as well.

Nitrogen mineralisation under buffel-grass (Fig. 7) showed large year-to-year variations that were similar to

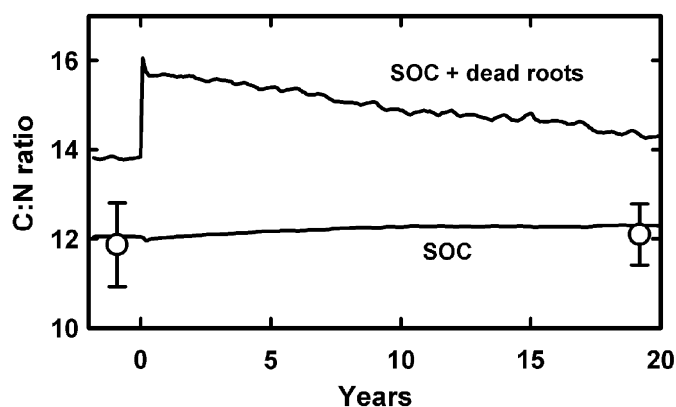


Fig. 6. C:N ratios after tree clearing, calculated with and without consideration of recently dead roots. Observations after Dalal et al. (2005b).

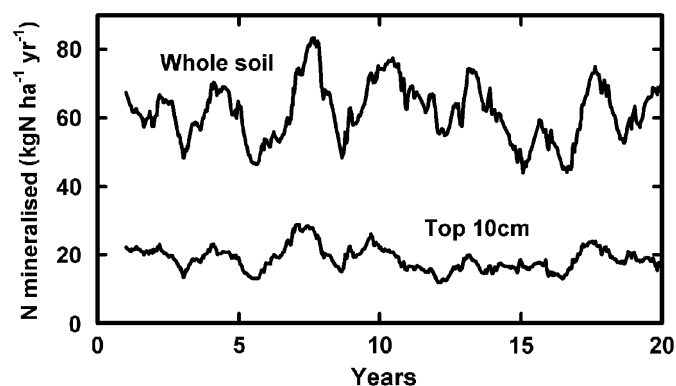


Fig. 7. Modelled annual nitrogen mineralised under buffel pasture, expressed in $\text{kgN ha}^{-1} \text{ yr}^{-1}$ either for the whole soil or for only the top 10 cm. Data show running means of modelled data over the previous 12 months.

the variability under mulga (Fig. 3). Over the 20-year modelling period, there was no apparent trend towards changing mineralisation rates despite the on-going loss of soil nitrogen under buffel-grass (Fig. 5(b)).

This relative constancy in mineralisation rates despite decreasing nitrogen stocks was mainly due to the flux of organic carbon from decaying roots which immobilised nitrogen in other soil pools. As the pool of dead roots was initially large immediately after clearing, the immobilising effect was pronounced at first, but declined over time as the remaining pool of dead roots decayed. Hence, this decreasing immobilisation effect counteracted the effect of diminishing nitrogen stocks in the system, leading to a nearly unchanged mineralisation rate over 20 years.

Structural litter also decreased after conversion from mulga to pasture (data not shown). The primary reason for that decline was that the model assumed that the decomposition rate of structural litter was inhibited by lignin in that pool. The pool started out with a high lignin concentration from the previous input of lignin-rich mulga litter, and its decomposition rate was therefore initially

inhibited. Consequently, the size of the pool was initially large. With on-going addition of low-lignin grass litter, the lignin concentration was gradually diluted so that the decomposition rate increased and the size of the pool diminished. Combined, a diminishing nitrogen capital but greater decomposability through an improved C:N ratio and lower lignin concentration in the litter pool, was responsible for the nearly unchanged nitrogen mineralisation rate over the 20 years of simulation.

However, soils under mulga were modelled to have mineralised about $50 \text{ kgN ha}^{-1} \text{ yr}^{-1}$ more nitrogen than the same soil 20 years after tree clearing (cf. Figs. 3 and 7). Once the mineralisation rate had been reduced from the higher rate under mulga to the lower rate under buffel-grass, there was no apparent further systematic decline over the length of the modelling period (Fig. 7) and variations were largely driven by year-to-year variations in weather parameters.

Experimental evidence of mineralisation rates was inconclusive, with Mathers et al. (2006) having found similar mineralisation rates under mulga and buffel-grass. Other measurements, however, showed higher mineralisation rates under mulga than buffel-grass (R.C. Dalal, unpublished) that were similar to the differences simulated by the model. We could find no apparent reason for these conflicting observations so that this specific aspect of the modelling runs could not be experimentally verified.

For a longer simulation, year-to-year weather variations were eliminated by repeatedly using the same sequence of daily weather observations for 1940 so that any temporal patterns reflected only the changing state of organic matter pools and fluxes (Fig. 8). In this longer simulation, it was apparent that carbon and nitrogen stocks together with annual mineralisation rates continued to fall over the 100-year sequence although there was little change over the first 20 years (Fig. 7). The on-going loss of the site's nitrogen capital led to a continuous reduction in nitrogen mineralisation rates. The rate of change was, however, small enough so that any long-term trends could be masked by the variations in year-to-year and multi-year weather variations.

Under standard management, the system lost carbon and nitrogen over time (Fig. 5), and we investigated whether that loss could be slowed or reversed through alternative management options (Fig. 9). We considered the inclusion of legumes, the cessation of produce removal by grazing animals and the combination of both.

Cessation of produce removal had only a relatively small effect on carbon and nitrogen stocks as it was assumed that animals did not remove a large amount of nitrogen under even standard conditions (about 10% of nitrogen in annual grass production). Without produce removal, the system retained about an additional 100 kgN ha^{-1} and 1 tC ha^{-1} over 20 years (Fig. 9).

The inclusion of legumes (assumed to fix about $15 \text{ kgN ha}^{-1} \text{ yr}^{-1}$) had a greater effect than cessation of produce removal and led to an additional nitrogen

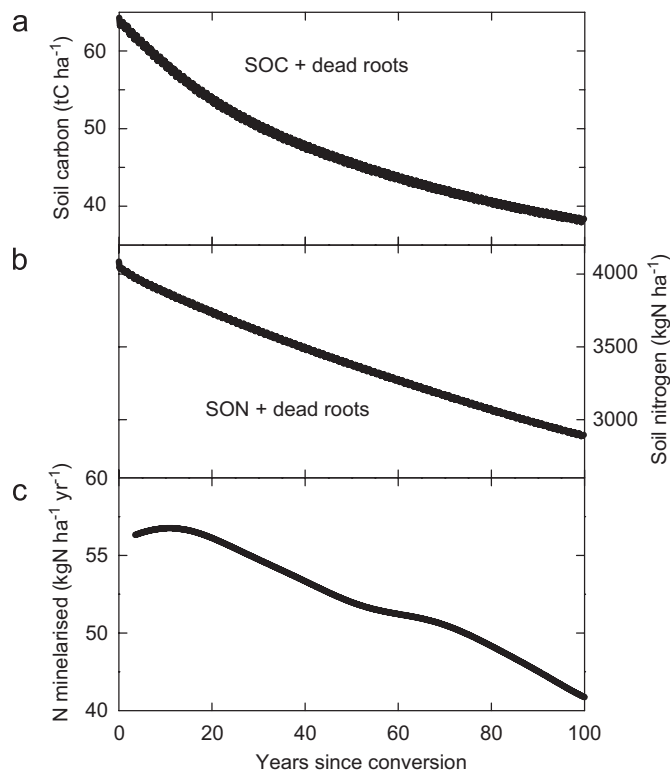


Fig. 8. Long-term trends in modelled carbon (a) and nitrogen (b) stocks including recently dead roots and annual nitrogen mineralisation rate (c) as a function of time under buffel pasture. For these simulations, the same annual weather sequence was re-used repeatedly to avoid any inter-annual variability.

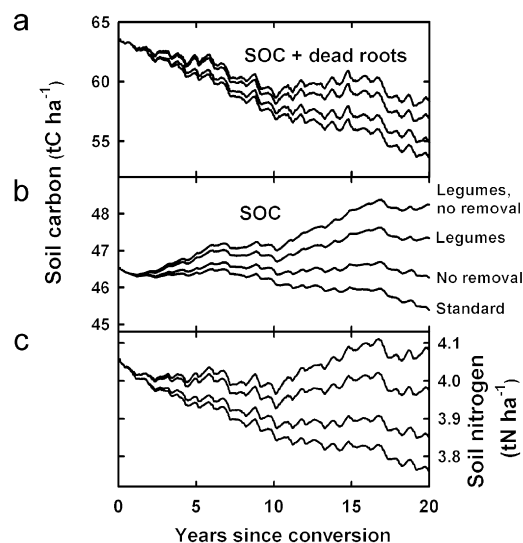


Fig. 9. Trends in soil carbon with (a) or without (b) dead roots and trends in soil nitrogen stocks including dead roots (c) under four possible management scenarios: standard management, inclusion of legumes, cessation of produce removal or both legume inclusion and cessation of produce removal as shown in the middle panel. The four scenarios appear in the same order in all panels.

retention of about 200 kgN ha^{-1} and 2 tC ha^{-1} over 20 years (Fig. 9). The extra nitrogen gain over 20 years was less than the sum of annual additions through biological

nitrogen fixation because losses from produce removal, volatilisation during nitrogen mineralisation and leaching also increased with higher nitrogen status of the system.

Inclusion of both legumes and cessation of produce removal had approximately additive effects of the individual effects of legume inclusion and produce removal on their own. Significantly, the inclusion of legumes was needed to halt the long-term decline in soil nitrogen stocks (Fig. 9(c)).

5. Discussion

The present work showed that observed soil organic carbon and nitrogen stocks as well as nitrogen mineralisation rates could be well described by CenW 3.1. Following tree clearing, the modelled subsequent trends in soil organic carbon and nitrogen largely agreed with field observations. However, measurement and conceptual problems arise with respect to coarse roots.

It is clear that a large amount of coarse roots must be present at the time of clearing (Snowdon et al., 2000; Zerihun et al., 2006), and, unless they are physically pulled out of the soil, they will remain in situ for extended periods. This can constitute a quantitatively important proportion of total carbon stocks in the soil (Bolstad and Vose, 2005) but appears to have been ignored in most past studies of trends in soil organic carbon after clearing.

Typical soil sampling regimes would encounter individual coarse roots only by chance, and typical sampling protocols, such as sieving, are likely to exclude any fragments of recently dead roots (Dalal et al., 2005 a,b; Harms et al., 2005). As roots, particularly intermediate-sized roots, gradually decay, the remnants of these former roots, however, are likely to be included in sampling in subsequent years. This may lead to apparent carbon dynamics that are related simply to the inclusion or exclusion of carbon fragments in consecutive sampling without necessarily corresponding to any changes in actual carbon stocks.

Fig. 5(a) showed that the actual amount of dead carbon decreased over time under pasture even though carbon in organic carbon pools other than dead roots remained almost unchanged. In terms of carbon accounting, this carbon is certainly present and constitutes a large and important component of overall carbon stocks (Bolstad and Vose, 2005). Despite that important role, the influence of coarse roots and their decay appears to have been rarely considered in studies of soil organic carbon trends after deforestation (see the papers cited in Murty et al., 2002; Guo and Gifford, 2002). There also appears to be very little information available about the time courses of coarse-root decay (Judas et al., 1995; Matthews, 1997), and we are not aware of any information on the decay rate of coarse roots from former mulga vegetation, in particular.

Changes in soil carbon stocks in this experimental system were small compared to the losses of above-ground biomass. The simulated mulga stand contained

73 tDW ha⁻¹ in above-ground biomass and an estimated 30 tDW ha⁻¹ in roots, with a combined stock of 103 tDW ha⁻¹ (≈ 51.5 tC ha⁻¹). Additionally, there was about 7 tC ha⁻¹ in coarse and fine surface litter. The loss of that biomass and surface litter constitutes the quantitatively significant carbon loss after conversion of mulga to pasture that dwarf any changes in soil carbon that amount to only 2–5 tC ha⁻¹ over 20 years (Fig. 5; Dalal et al., 2005a).

Biomass and surface litter carbon can be released immediately if the site is burnt. Without fire, the carbon in finer fractions such as leaves, twigs and fine roots may be released over a period of less than a year (Jalota et al., 2006) but it may take decades for carbon in dead trunks or coarse roots to decay (Matthews, 1997).

Soil organic matter contains both carbon and nitrogen at narrowly defined ratios so that any change in one element has ramification for the other element as well. An increase in carbon in the soil, such as through input of dead roots, for example, leads to the immobilisation of nitrogen in organic matter, with a subsequent reduction in mineralised nitrogen available for plant uptake. This will eventually feed back to reduce plant productivity and the input of available substrate for subsequent organic matter formation.

The present work has thus highlighted the importance of considering the nitrogen cycle in conjunction with the carbon cycle (Rastetter et al., 1992; Kirschbaum et al., 2003) and has shown that future carbon trends can be materially altered by manipulation of the site nitrogen budget (Fig. 9). Again, the fate of dead coarse roots is important, especially the extent to which they can immobilise potential nitrogen resources in the soil (Bolger et al., 2003; Devine et al., 2006).

Whether such immobilisation can occur depends critically on how closely the material in decaying roots interacts with the rest of the soil. Depending on the extent of physical, chemical and biological linkages between dead roots and the rest of the soil, this large addition of material with a high C:N ratio can potentially immobilise a large amount of available soil nitrogen and render it unavailable for plant uptake (Bolger et al., 2003; Devine et al., 2006). However, it is also possible that this large pool of carbon without matching nitrogen presents an opportunity for non-symbiotic nitrogen fixation to occur which has been observed on some coarse woody surface debris (Crawford et al., 1997).

Very large roots or the root crown of dead trees may be too far removed from the rest of the soil for significant transfer and immobilisation of nitrogen to take place. Hence, it may be that material from large chunks of dead and decaying roots essentially remains in the root channels where it forms a distinct and separate class of material that does not mix much with the rest of the soil. Alternatively, it may be that there is enough exchange and mixing through soil fauna or hyphal connections (Frey et al., 2000) so that carbon from even large roots can be distributed outside its

original root channel, or nitrogen can be transferred into root channels and become immobilised. It has been observed that some nitrogen can even be transferred into individual rotting tree stumps (Devine et al., 2006) and transfer into coarse roots would presumably be easier than any transfer into surface litter.

In the present modelling work, dead roots were kept in a separate pool, but upon the next transformation, material was mixed in with the rest of the soil's slow and active pools, which implied a greater degree of mixing than might occur in reality. Intermediate-sized roots are likely to have the greatest immobilising potential (Bolger et al., 2003), but it is very difficult to quantify the extent of this immobilisation potential, and we are not aware of any experiments or observations that tried to quantify its possible magnitude.

The present work has thus highlighted the important role of coarse roots both as a quantitatively important constituent of total site carbon stocks and as an agent to potentially significantly modify site nitrogen availability. Given those important roles, the dearth of past work on coarse roots is surprising and in urgent need to be remedied. The omission of coarse roots in past work is thus likely to have led to the wrong conclusions about soil carbon dynamics after clearing in terms of both carbon accounting and the functional relationships that operate after clearing.

Modelled and observed losses of soil organic carbon at the Mulga View site were broadly consistent with mean changes observed for tree-pasture transitions at 32 range-land sites in Queensland (Harms et al., 2005) whereas the average of all published studies (e.g. Murty et al., 2002; Guo and Gifford, 2002) that looked at the transition from forest to pasture showed no significant change in soil organic carbon at all upon this transition. While we have no specific information on the reasons for that difference, it is possible that it is due to the high nitrogen status under mulga which slowly decreased under buffel-grass owing to the absence of nitrogen fixers and the constant removal of nitrogen by grazing animals. Carbon trends are likely to be different for pasture systems that include legumes (Fig. 9) or that receive regular additions of fertiliser (Kirschbaum et al., 2003).

Exploratory modelling showed that the magnitude and even direction of change in soil carbon could be modified through changing the nitrogen budget (Fig. 9). As nitrogen dynamics are likely to differ with the management practices of different sites, soil organic carbon dynamics would be expected to also differ. This is consistent with many observations in the literature (see the examples cited in Murty et al., 2002). Fearnside and Barbosa (1998), for example, showed how carbon trends can often be related to management factors, including fertiliser addition or inclusion of nitrogen fixation by legumes, and the intensity of nitrogen removal in produce.

While there was an on-going loss of nitrogen at the experimental site, it amounted to only about 100 kgN ha^{-1}

to a depth of 1 m over 20 years (Fig. 5(b)), and led to no consistent change in the amount of nitrogen being mineralised over that period. The amount of mineralisable nitrogen remained at a similar value over that time period because the effect of a reduction in nitrogen stocks was balanced by a lesser immobilising effect by dead roots so that over the 20-year modelling horizon the system retained an almost unchanged nutrient supplying capacity (Fig. 7).

The model suggested that nitrogen mineralisation rate changed only slowly after clearing in response to the steadily diminishing nitrogen stocks but the trend was barely discernible against the influence of variations in weather patterns. In the long run, however, on-going nitrogen losses caused a reduction in mineralisation rate (Fig. 8). The system must eventually settle at a lower nitrogen status at which reduced nitrogen losses will again reach equilibrium with annual nitrogen inputs. To maintain the system's ultimate long-term sustainability, inclusion of sown legume pastures or application of fertiliser is, therefore, likely to be necessary.

The present simulations relied critically on the simulation of the effect of organic-matter quality on decomposition and nitrogen mineralisation rates. In the simulations, the effect of reducing nitrogen stocks over time was compensated by gradually increasing organic matter quality that lead to faster turn over. This quality was related to the lignin concentration in organic matter, and the lignin to nitrogen ratio in fresh litter. These dependencies have been used in the CENTURY model since its inception (Parton et al., 1987) and have found to work very well in describing the nitrogen dynamics of a wide range of litter types (Kirschbaum and Paul, 2002).

However, detailed work on the decomposition properties of the litter types found at the experimental site had shown that while lignin was a good predictor of decomposition rates, the expected inverse relationship between decomposability and nitrogen concentration was found to be weak and largely restricted to the very first phase of decomposition (Wang et al., 2004; Jalota et al., 2006).

It continues the long-standing debate of whether lignin, C:N ratios, polyphenols or other properties of fresh litter would be the strongest determinant of a litter's decomposability (Heal et al., 1997; Vanlauwe et al., 1997). The reality is probably that all these chemical constituents can play a role in terms of enhancing or retarding decomposability, and that their concentrations are generally correlated in specific litter types. Hence, in different litter types one or another constituent may show the strongest correlation with observed decomposition rates which may arise from a combination of the inherent effect of that constituent and its correlation with other constituents. As such, it is still unresolved which measure of a litter's chemical composition constitutes the best predictor of decomposability for general modelling purposes.

6. Conclusions

Simulations with CenW 3.1 successfully modelled various aspects of the studied soils, including both static carbon and nitrogen stocks and dynamic mineralisation rates. Dynamic changes in soil carbon and nitrogen stocks after conversion to buffel-grass pasture were also all consistently simulated by the model.

The treatment of coarse roots after tree removal emerged as a key issue. Dead coarse roots can constitute a large component of total site carbon stocks, yet they are usually excluded from soil carbon sampling. Over time, they may partially decompose with the residual fragments becoming included in later sampling. This can lead to apparent trends in soil carbon that are purely related to the pattern of coarse-root decay and do not necessarily reflect true trends in soil carbon.

Coarse roots tend to have high C:N ratios and can play a potentially important role by immobilising mineral nitrogen and making it unavailable for plant uptake. The extent of that immobilisation depends on the time course of coarse-root decay and the connectedness and interchange between coarse roots and the rest of the soil. Information is lacking for a full quantification of that process.

Finally, the modelling showed that trends in soil carbon could be altered through manipulation of the site nitrogen budget by either adding more nitrogen through nitrogen-fixing plants or reducing the rate of nitrogen removal by grazing animals. This suggests possible management options, such as fertiliser addition or inclusion of legumes that could be employed to maintain carbon and nitrogen stocks and ensure the long-term sustainability of pasture-production systems on cleared mulga sites.

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Appendix A. New and modified modelling routines

The following describes a number of modelling routines that have been added or modified specifically for the present work.

A.1. *C₄ photosynthesis*

C₄ photosynthesis was modelled in a simplified routine based on the work of Collatz et al. (1992) and G. Simioni (unpublished). Assimilation rate with non-limiting light, A , was calculated using a quadratic equation as

$$\beta A^2 - A(V_t + k_p p_i) + V_t k_p p_i = 0, \quad (\text{A.1})$$

where V_t is the maximum Rubisco limited rate, k_p is the phosphoenolpyruvate (PEP)-carboxylase activity (or the initial slope of the relationship of A as a function of intercellular CO_2), p_i is the intercellular CO_2 concentration and β is a curvature term in the transition from CO_2 limited to maximum-capacity limited rate.

Both V_t and k_p are given as functions of temperature so that

$$V_t = V_t(25) \frac{Q_v^{(T-25)/10}}{(1 + e^{0.3(13-T)})(1 + e^{0.3(T-36)})}, \quad (\text{A.2})$$

$$k_p = k_{p(25)} Q_k^{(T-25)/10} \quad (\text{A.3})$$

where $V_{t(25)}$ and $k_{p(25)}$ are the Rubisco-limited rate and PEP-carboxylase activity at 25 °C, Q_v and Q_k are Q_{10} functions, both set to 2 and T is average daytime temperature.

The terms $V_{t(25)}$ and $k_{p(25)}$ are linked in the present model to retain a constant proportionality irrespective of changes in nitrogen or water status or any damage by insects or extreme temperatures that are assumed to inhibit both processes equally. Hence

$$k_{p(25)} = r_{kv} V_{t(25)}, \quad (\text{A.4})$$

where r_{kv} is the proportionality ratio of PEP-carboxylase activity and the Rubisco limited rate.

The maximum rate, defined according to Eq. (1), together with the quantum yield, set to 0.06 for *C₄* plants (Ehleringer and Pearcy, 1983), and a curvature term, θ , then feed into the sward simulation model of Sands (1995) as implemented previously for *C₃* photosynthesis (Kirschbaum 1999).

A.2. Biological nitrogen fixation

Biological nitrogen fixation, N_{fix} , had previously been calculated simply as a constant proportion of daily carbon gain. As an extra safe-guard, a further negative feed-back effect was introduced so that biological nitrogen fixation scaled back with increasing nitrogen status of plants. Hence

$$N_{\text{fix}} = f_{\text{Biol}} A_d (1 - N_{\text{lim}}), \quad (\text{A.5})$$

where f_{Biol} is the proportionality term between daily carbon gain and maximum biological nitrogen fixation, A_d is daily carbon gain and N_{lim} is the calculated nitrogen limitation term.

A.3. Inert organic matter

An additional pool of inert organic matter has now been added to the model. This pool is essentially equivalent to charcoal and can therefore be formed only through fires. It is assumed to be able to decompose, but only at a very slow rate that is described relative to the rate of resistant organic matter decomposition. Decomposition of inert organic matter is accomplished by transfer of both carbon and

nitrogen to the active pool from where it is then amalgamated with other organic matter and starts to decompose like other material originating from the active pool. Inert organic matter is also mixed between layers within the soil at the same rate as other organic matter pools.

A.4. Nitrogen immobilisation

It is also assumed that there is a minor flux of nitrogen, N_r , from the pool of mineral nitrogen to the resistant or slow SOM pool. This flow had originally been introduced because of the observation that a large amount of added mineral nitrogen could be immobilised into soil organic matter. That rate of immobilisation was significantly greater than any immobilisation rate that could be due to immobilisation via the active pool (Kirschbaum and Paul, 2002).

Originally, it had been assumed that it had to be immobilised into resistant organic matter, but this assumption has now been relaxed, and a new parameter has been introduced to determine the sub-division of immobilised nitrogen between the slow and resistant pools. Hence

$$N_{r,s} = k_{\text{imm}} P_{\text{min}} r_s, \quad (\text{A.7a})$$

$$N_{r,r} = k_{\text{imm}} P_{\text{min}} (1 - r_s), \quad (\text{A.7b})$$

where $N_{r,s}$ is the amount of mineral nitrogen immobilised in the slow pool, $N_{r,r}$ the amount mineralised in the resistant pool, P_{min} the pool of mineral nitrogen, k_{imm} is the proportion of mineral nitrogen that can be immobilised and r_s is the proportion of immobilised nitrogen that is immobilised in the slow pool.

A.5. Ploughing

Ploughing is simulated simply by defining the plough depth, which is restricted by the defined soil depths in specific simulations, and then homogenising all soil pools over the total plough depth. Hence, in the present work, distinct soil layers were defined for the depths of 0–5, 5–10, 10–20, 20–30, 30–60, 60–100 and below 100 cm, and those depths were the only possible plough depths that could be used. In the present work, ploughing was assumed to homogenise the soil to a depth of 20 cm, thus involving the top three layers. Where different plough depths are to be used, the soil can be sub-divided differently into soil layers of different depth to accommodate this circumstance.

To simulate ploughing, organic matter in different layers is then summed down to the defined plough depth:

$$O_{t,j} = \sum_{i=0}^n O_{i,j}, \quad (\text{A.8})$$

where $O_{t,j}$ is the total amount of organic matter of pool type ' j ', ' i ' is a layer counter starting with 0, corresponding to the surface layer, and includes all layers to the depth of layer ' n ' that defines the depth of the plough layer.

That homogenised organic matter is then divided between the soil layers, weighted by the depth of each layer so that:

$$O_{0,j} = 0, \quad (\text{A.9a})$$

$$O_{i,j} = O_{t,j} d_i / d_p, \quad (\text{A.9b})$$

where d_i is the depth of the i th layer and d_p is the depth of the whole plough layer. This calculation is done for all layers from 1 to n . No litter is assumed to be left on the surface after ploughing.

A.6. Soil temperature

Changes in soil temperature, T_s , are calculated as

$$dT_s/dt = (T_0 - T_s)/\tau, \quad (\text{A.10})$$

where t is time in days, T_0 the temperature at the top of the soil and τ a time constant for change in soil temperature. This equation is the same as had been used before, but the temperature at the soil surface that drives changes in soil temperature had previously been taken as being equal to daily mean temperature. Following Paul et al. (2004), the effective surface temperature, T_0 , is now modulated by leaf area so that:

$$T_0 = T_m + (1be^{-Ls}), \quad (\text{A.11})$$

where T_m is daily mean temperature, b is the proportional extent by which mean soil temperature can be elevated above mean air temperature in the absence of a protective canopy, L is leaf area index and s is a term describing the sensitivity of soil temperature cooling by leaf area.

Appendix B. Supplementary materials

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.soilbio.2007.09.003](https://doi.org/10.1016/j.soilbio.2007.09.003).

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