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Modelling changes in nitrogen mineralisation following conversion of improved pasture to eucalypt plantation

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Abstract – We used a plant-soil model, G'DAY, to analyse changes in soil N supply after conversion of legume-based pasture to *Eucalyptus globulus* plantation and to forecast effects on plantation productivity over the long-term. With the model we reproduced the observed decline in net N mineralisation and amount of inorganic N in soil after one rotation of eucalypt growth in south-western Australia. The changes in soil N cycling on the short-term were mainly due to the reduced N:C ratio and reduced decomposability of tree litter. When applied for successive rotations over the long-term, the model predicted a steady decline in N mineralisation and plantation productivity. The negative balance between N inputs and outputs under plantation, mainly due to the suppression of biological N fixation, is critical for this steady decline in soil N supply. A scenario analysis indicated that retention of harvest residues has an important role to play in maintaining soil N supply under plantation, but supplementary regular application of fertiliser N would be required to ensure sustained productivity.

ecosystem modelling / eucalypt plantation / land-use change / nitrogen mineralisation / pasture

Résumé – Modélisation du changement de la minéralisation d'azote lors de la conversion d'une prairie artificielle en plantation d'eucalyptus. Nous avons utilisé le modèle plante-sol G'DAY, pour analyser les modifications d'approvisionnement du sol en azote, lors de la conversion d'une prairie à base de légumineuses en une plantation d'*Eucalyptus globulus*, afin de prévoir les effets sur la productivité de la plantation à long terme. Grâce au modèle, nous avons reproduit le déclin observé de la minéralisation nette et de la quantité de N inorganique dans le sol après une rotation d'eucalyptus au sud-ouest de l'Australie. Les changements du cycle de N dans le sol à court terme étaient principalement dus au rapport N:C réduit et à la décomposabilité réduite de la litière des arbres. Appliqué à des rotations successives à long terme, le modèle a prédit un déclin constant de la minéralisation de N et de la productivité de la plantation. L'équilibre négatif entre les entrées et les sorties de N sous la plantation, principalement due à la suppression de la fixation biologique de N, est critique pour ce déclin constant de l'approvisionnement en N du sol. Une analyse de scénarios a indiqué que la rétention de résidus de récolte a un rôle important à jouer dans le maintien de l'approvisionnement en N du sol sous une plantation, mais une application régulière supplémentaire de fertilisants azotés sera nécessaire pour assurer une productivité soutenue.

modélisation d'écosystème / plantation d'eucalyptus / changement d'utilisation des terres / minéralisation d'azote / prairie

1. INTRODUCTION

In response to a world-wide demand for pulpwood, large areas of *Eucalyptus globulus* plantations are being established in south-western Australia on former legume-based pasture land. More than 200 000 ha of *E. globulus* had been established by 2000, and the planting rate since then has been in excess of 50 000 ha·yr⁻¹ [29].

In the pasture systems soil nitrogen (N) fertility has been enhanced through biological N fixation by leguminous species. Pasture growth and N fixation are, however, suppressed after establishment of eucalypt plantations, reducing inputs of N to soil, which may result in a significant decrease in rates of soil N supply. Nitrogen fertiliser experiments have indicated that N supply limits productivity of fast growing *E. globulus* plantations at some sites [20, 33]. For optimal

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productivity of 3 to 4 year-old *E. globulus* trees in the higher (> 800 mm) rainfall zone of south-western Australia annual above-ground accumulation of N is close to 100 kg N·ha⁻¹·yr⁻¹ [33]. The extent to which such high rates of N demand by trees can be satisfied through soil N supply will largely determine whether high levels of productivity can be sustained when plantations are grown over successive rotations.

Conversion of pasture to either *Pinus radiata* [39, 41] or *E. globulus* [34] plantations usually leads to decreased rates of soil N mineralisation. However, this finding is contradicted by several studies [5, 13, 35] showing increased levels of mineralisable N under forest plantation compared to grassland. Birk [5], for example, found that soil N mineralisation decreased with increasing stand age of *P. radiata* on ex-improved pasture soils, but the pattern was less clear for the ex-unimproved pasture sites. Establishment of a balsam poplar (*Populus trichocarpa*) plantation on former grassland in northern Germany greatly increased rates of N mineralisation during the first year after afforestation [21]. These conflicting results suggest that complex processes govern changes in soil N supply with transition of pasture to forest plantation.

Changes in both quantity and quality of plant litter following afforestation may substantially alter C and N dynamics in the plant-soil system and this in turn may affect long-term site N productivity. For example, the differences in the quantity and quality of litter inputs from spruce (*Picea abies*) and ash (*Fraxinus excelsior*) compared with grass are reflected in the build-up of a relatively undecomposed phenolic fraction from lignin and hydrolysable carbohydrate compounds under these trees [42]. Above-ground litter from eucalypt plantations decomposes more slowly than litter from legume pastures because it contains higher concentrations of phenolic and lignified compounds [4, 11]. A large proportion of litter production in pasture comes from fine root turnover. This together with root exudation represents a major pool of readily decomposable C, which enhances microbial immobilisation of inorganic N – at least in the short term [3, 12].

Afforestation also induces changes in C and N cycling by altering the microclimate at the soil-litter interface. For example, temporal variation in soil temperature and humidity are generally moderated under plantation or forest due to shading by the tree canopy [25]. The transition from pasture to forest plantation also changes chemical, physical and biological properties of soil that affect organic matter decomposition [49].

Differences between the pasture and plantation system in amounts of N lost through leaching or gaseous emission may further contribute to changes in the cycles of C and N. Depending on the drainage conditions, nitrate leaching may be a significant mechanism for loss of N under legume-based pastures [16], while losses under established plantations are likely to be lower. For example, Carlyle [8] found no evidence for N leaching below 0.3 m under a 10-year old *P. radiata* plantation in southern Australia. Tight N cycling is commonly reported for closed canopy forests that have not been fertilised [48]. However, leaching losses of N may be

substantial shortly after plantation establishment, when N uptake by trees is small relative to soil N supply [19, 28, 44].

Frequent harvesting of short-rotation plantations can result in large amounts of nutrients removed from the site. For example, O'Connell and Grove [31] estimated that more than 500 kg N·ha⁻¹ was removed in harvested logs and burning of harvest residues from a highly productive site of an 8-year old *E. globulus* stand in south-western Australia. There is concern that in the longer term this removal of N will significantly decrease site fertility, resulting in lower plantation productivity.

Mathematical modelling is a powerful tool to integrate our understanding of the interacting processes that influence nutrient cycling in plant-soil systems. Models with coupled C, N and water cycles can help answer questions on how processes such as soil N supply respond to land-use changes and interact with biogeochemical mechanisms over decadal time-scales to determine long-term site productivity. With this increased understanding, models can be used to guide forest management practices such as fertiliser application and harvest residue retention to ensure sustained productivity.

The objectives of our study were to (i) quantify changes in rates of soil N mineralisation following conversion of improved legume-based pasture to short-rotation eucalypt plantation; (ii) identify, by use of a process-based simulation model, the major biogeochemical mechanisms responsible for these changes; (iii) estimate how the supply of N and plantation productivity change over a number of successive rotations; and (iv) use this information to guide management practices for sustained productivity.

2. MATERIALS AND METHODS

2.1. Field experiment and site description

The field experiment on which our model simulations were based, has been described elsewhere [34]. Briefly, two *E. globulus* first-rotation plantations (9–10 years old), with adjacent land under annual pasture (> 30 years old), were selected in south-western Australia. Sites were chosen to ensure that the pasture and plantation plots had the same soil type and history prior to plantation establishment. The region has a seasonal Mediterranean-type climate with cool, wet winters and warm to hot, dry summers. The two sites were broadly representative of the 600–1500 mm rainfall zone where *E. globulus* plantations are being established in south-western Australia. The higher productivity site (Moltoni, 34°36'S and 115°99'E; rainfall 1360 mm; summer evaporation 520 mm) had a relative fertile soil, classified as a Ferric Acrisol (FAO classification). The mean annual increment in stem volume (MAI) of the eucalypt stand at this site was 48 m³·ha⁻¹·yr⁻¹ (stem wood yield of about 290 Mg dry matter (DM)·ha⁻¹ after 10 years). The pasture site, located on adjacent farmland, received an annual fertiliser application of about 17 kg P·ha⁻¹·yr⁻¹, and was stocked with cattle. On the drier site (Gibbs, 33°50'S and 116°52'E, rainfall 630 mm;

Table I. Selected soil (0–10 cm) physico-chemical characteristics of the two sites.

Site	Land-use	Clay (0–2 µm) (%)	Silt (2–20 µm) (%)	Sand (> 20 µm) (%)	pH (H ₂ O)	Organic C (%)	Total N (%)	C:N
Moltoni	pasture	11.6	9.0	79.4	4.7	5.15	0.33	15.6
	trees	11.0	7.8	81.2	4.7	4.55	0.26	17.5
Gibbs	pasture	2.5	0.7	96.7	4.8	3.57	0.16	22.3
	trees	1.7	1.3	97.0	4.8	2.87	0.13	22.1

Table II. Amounts (Mg·ha⁻¹) of total organic C, total N and C:N ratio in soil (< 2 mm fraction) profiles at Moltoni (0–100 cm) and Gibbs (0–90 cm). Values in parentheses are the percentage in topsoil (0–20 cm).

Site	Land-use	Total organic C	Total N	C:N
Moltoni	pasture	187.0 ± 15.1 ^a (62)	8.2 ± 0.4 (64)	22.7 ± 0.7
	trees	179.5 ± 18.4 (61)	7.0 ± 1.1 (64)	26.1 ± 1.9
Gibbs	pasture	129.9 ± 3.7 (66)	4.8 ± 0.3 (79)	26.9 ± 0.8
	trees	82.4 ± 5.0 (52)	2.7 ± 0.2 (78)	30.6 ± 1.4

^a Mean ± standard error (n = 3).

Total organic C and total N were significantly different ($P < 0.05$) between land-uses at Gibbs, but not at Moltoni. At both sites, there were no significant differences in C:N ratio between land-uses (paired t-test analysis).

summer evaporation 658 mm) with a less fertile soil (Haplic Arenosol, FAO classification), MAI was 12 m³·ha⁻¹·yr⁻¹ (stem wood yield of about 60 Mg DM·ha⁻¹ after 9 years). The adjacent pasture had been fertilised with superphosphate (about 14 kg P·ha⁻¹ each year) and stocked with sheep. Selected properties of the soils at both sites are given in Table I.

At the two sites, soil moisture, inorganic N pools and rates of N mineralisation were measured in the topsoil (0–20 cm) under both land-use types from January 1997 to February 1998 using a sequential in situ core technique [38], with an incubation period of 28 days. Inorganic N was extracted with 1 M KCl after end-on-end shaking for 1 hour and determined by automated colorimetry using a LachatTM flow injection analyser. NH₄-N and NO₃-N were measured using the indophenol blue method and the Griess-Ilosvay reaction, respectively.

At each site three soil profiles were sampled to a depth of 90 (Gibbs) or 100 (Moltoni) cm to estimate total organic C and total N stocks (Tab. II). Organic C was determined using the Walkley-Black dichromate oxidation technique and total N was measured by automated colorimetry as above following digestion of soil in H₂SO₄/H₂O₂ at 360 °C.

2.2. Model description

We used the G'DAY (Generic Decomposition And Yield) model [9] that links a plant production model to an organic matter decomposition model. G'DAY simulates flows and standing pools of C and N among plant biomass, litter and soil organic matter (SOM) (Fig. 1). In this study, we used

G'DAY with a revised decomposition model [10] (Fig. 2) replacing the CENTURY model [36] to better describe the interactions between C and N dynamics in decomposing litter. The key differences between this revised decomposition model and CENTURY are: (1) microbial biomass succession is simulated and microbial biomass is the driving factor for N mineralisation-immobilisation turnover; (2) depending on soil N availability and the N requirements of microbial biomass, decomposition of litter can be N limited; (3) the N:C ratio of microbial biomass is a function of litter quality and N availability; and (4) 'quality' of leaf and fine root litter is expressed in terms of biochemically measurable pools. As a result, in this new decomposition model, the N:C ratios of the SOM pools (excluding the microbial biomass pool) are not prescribed as in CENTURY, but simulated output variables that are defined by litter characteristics and soil N availability. This makes the model more suitable to explore effects of land-use change on dynamics of soil C and N.

Detailed descriptions of G'DAY with the CENTURY decomposition model are given elsewhere [9, 26]. Here, we will only give a general review of the basic mechanisms in G'DAY with the revised decomposition model [10] including the adaptations to simulate grazed pasture. The plant production model assumes that net primary production (NPP) is proportional to intercepted photosynthetically active radiation adjusted by soil water and nitrogen stress. The forest version of G'DAY has four pools of plant biomass: foliage, branches (including coarse roots), stems and fine roots. We assume that 30% of the branch pool was belowground representing the coarse roots. The pasture version has only foliage

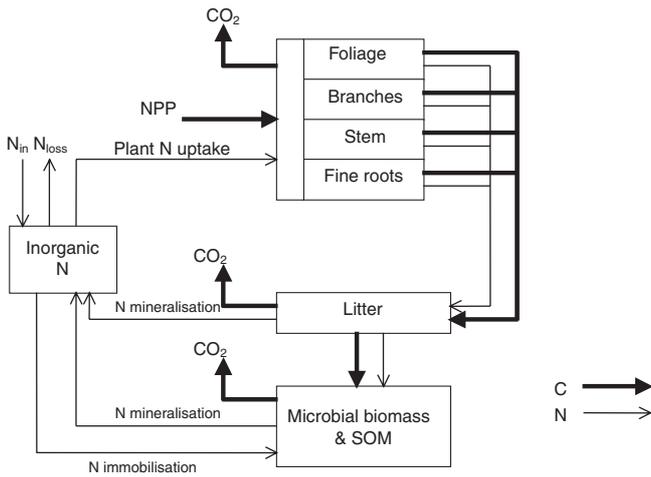
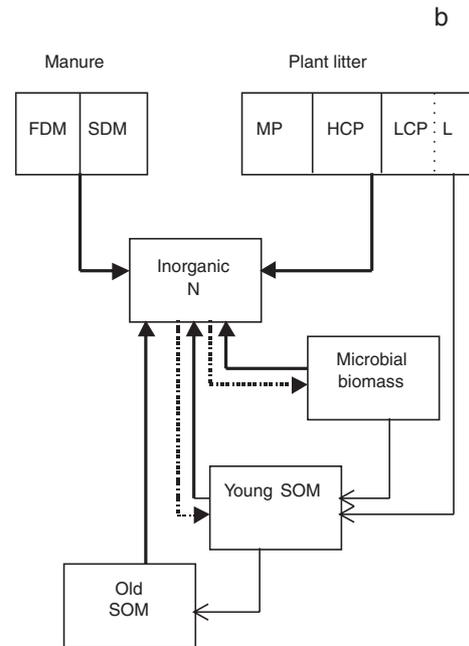
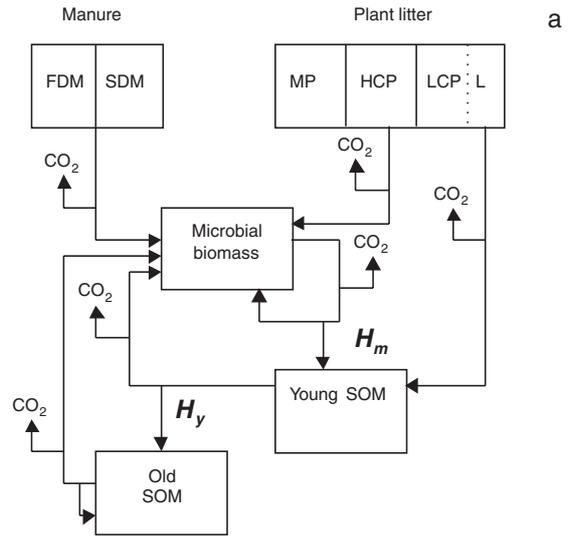


Figure 1. Pools and fluxes of carbon (C) and nitrogen (N) in the G'DAY model. NPP: net primary productivity; SOM: soil organic matter.

and fine root pools. Plant biomass pools receive C through allocation of NPP, and N through allocation of N uptake and N retranslocation. Tissue senescence is represented by assigning a constant turnover rate to each plant biomass pool, senesced plant material being transferred to litter pools. For all plant biomass pools, with the exception of fine roots [17], we assume that a proportion of N is retranslocated prior to senescence. A fraction of C and N from the pasture foliage production is lost due to consumption by grazers and part of it is returned to the litter pools through faeces and to the inorganic N pool through urine [18]. The decomposition model consists of nine organic matter pools: four plant litter pools (metabolic – including storage – compounds, holocellulose, ligno-cellulose, and woody material), two animal litter pools (a fast and slowly decomposable fraction) and three SOM pools (microbial biomass, “young” and “old” SOM) (Fig. 2a). Each plant litter pool is subdivided into above- and below-ground components. Decomposing foliar and fine root litter is divided among the first three of the above plant litter pools based on a proximate fractionation analysis [1] for holocellulose and lignin. Branch, stem and coarse root litter enter the woody litter pool. When ligno-cellulosic or woody material is decomposed, lignin (in the ligno-cellulosic or woody pool) is not incorporated into microbial biomass, but is instead transferred directly into the “young” SOM pool. This simulates the 'humus' formation by phenolic compounds formed from degradation of lignins. Simulated rates of litter (including animal faeces) decomposition are controlled by the initial composition, modified by temperature, moisture and N availability. Pools and fluxes of N are linked to C, including the pool of inorganic N (Fig. 2b). For foliar and fine root litter, it is assumed that N is associated with the metabolic and ligno-cellulosic pools, with no N in the holocellulosic pool. The proportional allocation of plant litter N to the metabolic and ligno-cellulosic pools is critical in



Inorganic flows
 → Mineralisation
 - - - - - Immobilisation
 Organic flow
 → Humification

Figure 2. Pools and fluxes of (a) carbon (C) and (b) nitrogen (N) in the decomposition sub-model of G'DAY. FDM: fast decomposing manure; SDM slowly decomposing manure; MP: metabolic plant litter; HCP: holocellulosic plant litter; LCP: ligno-cellulosic plant litter; L: lignin; SOM: soil organic matter; H_m : humification coefficient for microbial biomass; H_y : humification coefficient for “young” SOM.

predicting N mineralisation fluxes. The model assumes that the ligno-cellulosic litter pool has a N:C ratio which is half of the N:C of the total litter, and the remaining N is allocated to the metabolic litter pool. The N:C ratio of the decomposing microbial biomass is a function of N availability and the metabolic C fraction of the incoming litter, with higher values for litter with a larger fraction of metabolic compounds. As litter decomposes, N is mineralised to, or immobilised from, the inorganic N pool to maintain the N:C ratio of decomposing microbial biomass at the specified level. Depending on the soil inorganic N content, lignin humification (transformation to “young” SOM in the model) may promote additional N immobilisation into the “young” SOM pool, which simulates the process of chemical N immobilisation. Inorganic N availability is further determined by N inputs from biological fixation, fertilisation or atmospheric deposition and by N outputs via plant uptake and losses through gaseous emission or leaching. The maximum rates of microbial and plant N uptake and the rate of N loss are proportional to soil inorganic N content. Balancing potential microbial N demand or immobilisation associated with litter decomposition against inorganic N availability will determine whether the activity of decomposers is limited by N. If so, simulated decomposition fluxes are reduced to match the microbial N demand to total amount of N available.

A simple water balance model calculates daily evaporation, transpiration and soil water content of the litter layer, topsoil layer (0–20 cm) and rooting zone. For simplicity, the daily average temperature of the litter and topsoil (0–20 cm) layer are equal to the daily average air temperature.

2.3. Model parameterisation and simulations

G'DAY was parameterised to simulate land-use change from pasture to eucalypt plantation at the Moltoni and Gibbs paired sites, using measured site-specific parameters. Non site-specific parameters for the eucalypt plantation were drawn from a recent application of G'DAY to an intensively monitored *E. globulus* stand at Mumballup (950 mm rainfall) in south-western Australia [10]. Where parameters were not available from measurements in the pasture systems, data from the literature were used. The list of parameter values is given in Table III. The values of decomposition related parameters were set by fitting the model to decomposition data from ¹⁴C-labelled medic (*Medicago littoralis*) [22] and mass loss of C and N from *E. globulus* leaf and branch harvest residues in litterbags [33]. The model was further calibrated so that about 40% of faeces-N was mineralised at 25 °C (and at optimal moisture conditions) within the first 4 months of decomposition [45].

All simulations were run with a daily time step using daily long-term (44 years) average meteorological data for each site. The long-term historic data for each site were generated from interpolation of actual recorded data from nearby weather stations (SILO Datadrill; <http://www.dnr.qld.gov.au/silo>, verified on August 2002).

2.3.1. Pasture system

We initialised the model for grazed annual legume-based pasture using information on climate, soils, and management practices specific for the sites. To estimate the steady-state amounts of soil C and N under the pasture system, we ran the model to equilibrium with the “old” SOM pool kept constant using the set of parameters defined in Table III for the pasture system. The annual rate of biological N fixation and grazing intensity are two crucial model parameters as they have a direct influence on the N input and output fluxes of the plant-soil system. The sensitivity of net N mineralisation at equilibrium to these parameters was explored by performing several model runs with varying rates of biologically fixed N and grazing intensities (see below). For these ‘equilibrium simulations’, we assumed that the growing season for pasture extended from early April until late November (235 days) at Moltoni and started about 2 weeks later at Gibbs (Tab. III). On both sites, grazing was assumed for the whole year. We further assumed that, on average, 40% of grazed C returns to soil in faeces [40] and that 80% of the grazed N returns to soil in faeces (N:C = 0.022) and urine [16]. Nitrogen input through atmospheric deposition was set at 5 kg N ha⁻¹·yr⁻¹ [30]. Assumed rates of N loss (λ_i) and maximal plant (λ_p) and microbial (λ_m) N uptake from the inorganic N pool under pasture were defined for each site (Tab. III). The actual N uptake by plant and microorganisms is calculated as the smaller of the maximal N uptake and N demand. Nitrogen demand by plants and microorganisms is determined by the size and N:C ratio of the plant and microbial pools, respectively. The N loss rate at Gibbs was set at a higher value compared to Moltoni to account for the coarser soil texture at this site (Tab. III).

2.3.2. Transition from pasture to plantation

The steady-state amounts of soil C and N under pasture defined the initial soil conditions for the plantations. With the transition from pasture to plantation, grazing and N fixation ceased, and all standing pasture biomass entered the litter pools.

We assumed that eucalypt litter (leaves and fine roots) was more recalcitrant than litter from pasture, based on holocellulose and lignin concentrations determined from a proximate fractionation analysis (Tab. III). Eucalypt litter also contains proportionally more N in recalcitrant form (the ligno-cellulosic pool) than pasture plant material. Laboratory studies indicate that eucalypt leaf litter has lower N mineralisation potential than legume plant material [11]. In simulations with G'DAY, two decomposition parameters (see Tab. III) were altered with the transition from pasture to eucalypt plantation to fit mass loss data for legume residues [22] and *E. globulus* foliar harvest residues [33] decomposing in the field. Firstly, we assumed that the specific decay rate of the metabolic litter fraction was less for residues of eucalypt than pasture (Tab. III) because eucalypt leaf material has higher concentration of soluble tannins [11]. Secondly, the control by lignin on decomposition of the ligno-cellulosic pool was lowered for the plantation on the

assumption that the decomposers community in forest plantations is better adapted to decompose lignified material than in pasture. In particular, the occurrence of basidiomycete white rot fungi in the forest floor will enhance lignin decomposition. This lignin control is expressed in the model according to an exponential function [36]:

$$r_L = \exp(-\beta_{li}C_{li}/(C_{cel} + C_{li-cel})) \quad (1)$$

where r_L is the decomposition rate modifier for lignin with a value between 0 and 1, β_{li} is an empirical factor and C_{li} , C_{cel} and C_{li-cel} are the lignin, holocellulosic and ligno-cellulosic litter C pools, respectively. Thus, the parameter, β_{li} has a lower value for plantations compared to pasture (Tab. III).

To account for the differences in rooting depth between pasture and trees, it was further assumed that the plantation trees had access to a larger volume of available water compared to pasture and that the rate constant of N loss (λ_l) under plantation was half of that under pasture (Tab. III). Allocation coefficients for NPP to the different tree biomass pools were obtained by fitting field-estimated values of stem productivity and leaf area index (LAI) of the eucalypt plantations at each site.

The values of parameters λ_v , λ_u and λ_m (Tab. III) are uncertain in the model runs. Consequently, we performed a sensitivity analysis assessing how changes in these 3 parameters

Table III. Parameter values for improved pasture to *E. globulus* plantation land-use change simulations. Abbreviations: NA: not applicable.

Symbol	Definition	Pasture value	Source	Plantation value	Source
S	Growing season length (days)	235 (Moltoni) 221 (Gibbs)	Donald G. (pers. comm.)	365	
ϵ	Light use efficiency (g DM·MJ ⁻¹)	1.1	[18, 43]	1.35	[10, 23]
v_{critf}	Critical leaf N/C ratio for no production loss	0.1	[18]	0.025	O'Connell A.M., unpubl. data
σ	Specific leaf area (m ² ·kg DM ⁻¹)	25	[18, 43]	20 decrease to 4	Hingston F.J., unpubl. data; O'Connell A.M., unpubl. data
η_f	Carbon allocation to foliage	0.6	[12]	function of leaf N:C	based on O'Connell A.M., unpub. data
η_r	Carbon allocation to fine roots	0.4	[12]	function of leaf N:C	based on O'Connell A.M., unpub. data
B_a	Above-ground fraction of branches	NA		0.7	estimated
t_f	Fraction of leaf nitrogen retranslocated before senescence	0.4	estimated from [47], [18]	0.4	estimated from Hingston F.J., unpubl. data; [10]
t_r	Fraction of root nitrogen retranslocated before senescence	0	[17]	0	[17]
t_b	Fraction of branch nitrogen retranslocated before senescence	NA		0.5	estimated from Hingston F.J., unpubl. data
v_{maxf}	Maximum N:C ratio of foliage	0.1	estimated from [47]	function of age 0.066 decreasing to 0.022	estimated from Hingston F.J., unpubl. data; O'Connell A.M., unpubl. data
v_{maxr}	Maximum N:C ratio of roots	0.08	estimated	0.03	estimated from Hingston F.J., unpubl. data; O'Connell A.M., unpubl. data
v_{maxb}	Maximum N:C ratio of branches	NA		0.0035	estimated from Hingston F.J., unpubl. data; O'Connell A.M., unpubl. data; [31]
v_{maxw}	Maximum N:C ratio of wood (including bark)	NA		0.0015	estimated from Hingston F.J., unpubl. data; O'Connell A.M., unpubl. data; [31]
s_f	Foliage senescence rate (yr ⁻¹)	2.0	estimated from [7], [18]	0.3	Hingston F.J., unpubl. data; [10]
s_r	Root senescence rate (yr ⁻¹)	2.0	estimated, [18]	2.0	[10, 15]
s_b	Branch senescence rate (yr ⁻¹)	NA		0.03	Hingston F.J., unpubl. data; [10]
s_w	Wood senescence rate (yr ⁻¹)	NA		0.	
L_{fl}	Lignin fraction in foliage litter	0.08	experimentally determined	0.22	experimentally determined
L_{fh}	Lignin fraction in foliage harvest residues	NA	experimentally determined	0.17	experimentally determined
L_{rl}	Lignin fraction in root litter	0.10	experimentally determined	0.30	experimentally determined
C_{el}	Cellulose fraction in foliage litter	0.30	experimentally determined	0.35	experimentally determined

Table III. (continued)

Cel_{fh}	Cellulose fraction in foliage harvest residues	NA	experimentally determined	0.27	experimentally determined
Cel_{rl}	Cellulose fraction in root litter	0.45	experimentally determined	0.45	experimentally determined
G	Grazing intensity: fraction foliar production removed	0.55 (Moltoni) 0.40 (Gibbs)	estimated, see text	NA	
R_C	Fraction of grazed C that is returned to soil in faeces	0.4	[16]	NA	
R_N	Fraction of grazed N that is returned to soil in faeces+urine	0.8	[16]	NA	
L_{faeces}	Lignin/biomass ratio in faeces	0.25	estimated from [45]	NA	
v_{faeces}	Faeces N:C ratio	0.022	estimated from [46] and [16]	NA	
N_{dep}	Atmospheric N deposition ($kg\ N\cdot ha^{-1}\cdot yr^{-1}$)	5	[30]	5	[30]
N_{fix}	Biological N fixation ($kg\ N\cdot ha^{-1}\cdot yr^{-1}$)	120 (Moltoni) 50 (Gibbs)	estimated, see text	0	assumed, see text
λ_u	Maximum rate of plant N uptake from inorganic pool (yr^{-1})	10.2	estimated, see Appendix	10.2	estimated
λ_l	Rate of N loss from inorganic pool (yr^{-1})	0.8 (Moltoni) 2.0 (Gibbs)	estimated, see Appendix	0.4 (Moltoni) 1.0 (Gibbs)	estimated
λ_m	Maximum rate of microbial N uptake from inorganic pool (yr^{-1})	15	estimated, see Appendix	15	estimated
k_{met}	Specific decomposition rate of metabolic litter pool (yr^{-1})	180	[10]	29.2	estimated from [33] (see text)
β_{li}	Lignin control on decomposition of ligno-cellulosic pool	3.0	[36]	1.2	estimated from [33] (see text)
WHC	Available water holding capacity of soil (mm)	400 (Moltoni) 300 (Gibbs)	estimated from [6]	1600 (Moltoni) 600 (Gibbs)	estimated on basis of site productivity

for the plantation system affect NPP and net N mineralisation (see Appendix, Tab. AI).

2.3.3. Multiple rotations

With the altered parameters for plantation (Tab. III), the model was run from the equilibrium state under pasture for a number of successive 10-year rotations. In these simulations, we assumed two scenarios of harvest residue management: “no residues”, i.e. all harvest residues removed from site; and “with residues”, i.e. all harvest residues retained on site. In the “with residues” scenario, all foliage and branch C and N (above-ground parts) were transferred to the litter pools at each harvest, with distribution of leaf residues to the litter pools being based on the biochemical quality of green, fresh leaves (see Tab. III) and the branches transferred to the woody litter pool. In both scenarios of residue management, the standing pools of fine and coarse roots (below-ground parts) entered their respective litter pools at harvest. We assumed for simplicity the same specific decomposition rate for branches and coarse roots, although roots have a different biochemical composition than branches.

As values of several parameters are uncertain, simulation results presented below should only be regarded as a preliminary guide of G'DAY's capacity to simulate responses to land-use change, and not as a rigorous prediction of long-term productivity of eucalypt plantations.

3. RESULTS AND DISCUSSION

3.1. Field observations

On both sites, measured rates of net N mineralisation in the field were generally less under plantation than pasture, being threefold greater under pasture ($329\ kg\ N\cdot ha^{-1}$) than plantation ($107\ kg\ N\cdot ha^{-1}$) at Moltoni, and twice under pasture ($111\ kg\ N\cdot ha^{-1}$) than plantation ($67\ kg\ N\cdot ha^{-1}$) at Gibbs (Fig. 3). Moisture contents in topsoil (0–20 cm) were less under plantation than pasture during the rainy season (Fig. 3).

The amounts of inorganic N in topsoil (0–20 cm) were on both sites greater under pasture than plantation during summer, but similar under both land-uses at the onset of winter (Fig. 4). The amount of inorganic N in topsoil under pasture was much larger at Moltoni than at Gibbs. Amounts of inorganic N in topsoil under plantation did not vary greatly throughout the year: average inorganic N contents were about 11 and 3 $kg\ N\cdot ha^{-1}$ at Moltoni and Gibbs, respectively.

Amounts of total organic C and total N stored over greater depth in soil (100 cm at Moltoni and 90 cm at Gibbs) are presented in Table II. At Moltoni amounts of C and N are comparable in soils under pasture and plantation, but for Gibbs the data indicate higher ($P < 0.05$) amounts of C and N under pasture than under the trees.

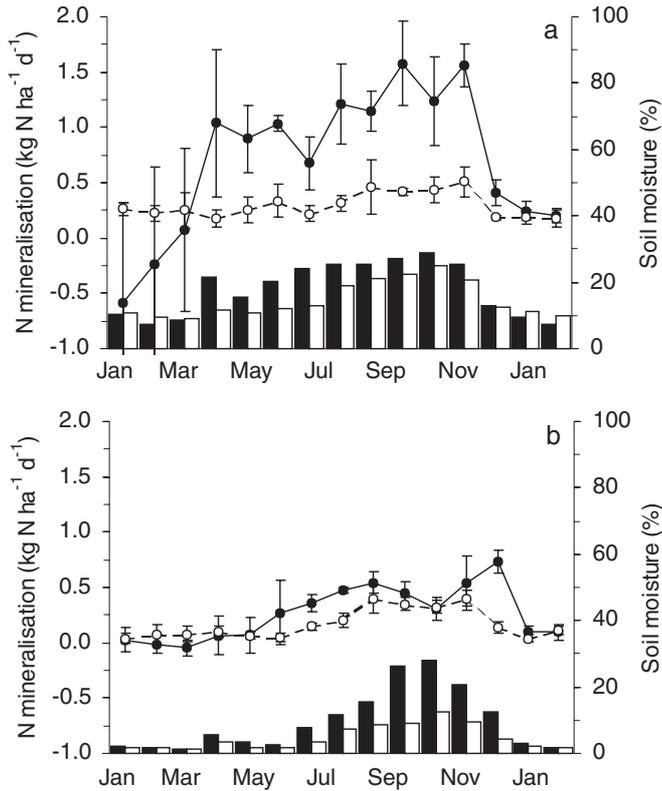


Figure 3. Measured seasonal soil moisture (bars) and net N mineralisation (lines) in soil (0–20 cm) under pasture (closed, black) and plantation (open, white) at (a) Moltoni and (b) Gibbs. Measurements started on 11/01/1997. Error bars indicate standard errors of the mean ($n = 4$).

3.2. Model simulations

3.2.1. The equilibrium state under pasture

We ran G'DAY to equilibrium for both sites using the parameters for pasture in Table III under different assumptions about the rate of biological N fixation and grazing intensity (Fig. 5). Biologically fixed N is directly added to the soil inorganic N pool in the model. The grazing intensity indicates the proportion of the total annual foliar pasture production removed by grazers. A higher grazing intensity in the model means higher N removals from the plant-soil system by animals including N volatilisation from urine and faeces. Simulated amounts of annual net N mineralisation at equilibrium are plotted against N-fixation rates at 3 grazing intensities in Figure 5. At Moltoni, modelled annual N mineralisation at equilibrium varied from less than 100 (scenario with 25 kg N·ha⁻¹·yr⁻¹ fixed, all grazing intensities) to 520 kg N·ha⁻¹·yr⁻¹ (scenario with 200 kg N·ha⁻¹·yr⁻¹ fixed and 40% grazing). At the less productive Gibbs site, modelled N mineralisation was lower and ranged between 60 and 290 kg N·ha⁻¹·yr⁻¹ (Fig. 5b).

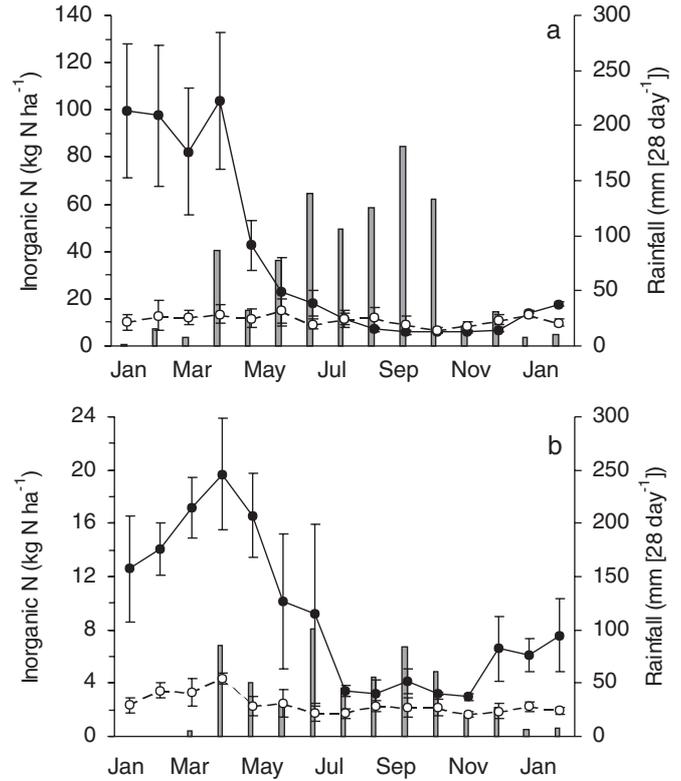


Figure 4. Measured seasonal total inorganic N content in soil (0–20 cm) under pasture (closed, black) and plantation (open, white) at (a) Moltoni and (b) Gibbs. The bars indicate rainfall over 28 day intervals. Measurements started on 11/01/1997. Error bars indicate standard errors of the mean ($n = 4$).

A typical stocking rate for pasture in the region is 8 sheep per hectare, which removes about 40% of the year's total herbage production [47]. Assuming a grazing intensities of 55% (intermediate cattle grazing at Moltoni) and 40% (light sheep grazing at Gibbs), the rates of biological N fixation that yielded an annual N mineralisation rate corresponding most closely to the measured values were about 120 and 50 kg N·ha⁻¹·yr⁻¹ for Moltoni and Gibbs, respectively (Fig. 5).

Simulated seasonal rates of N mineralisation and amounts of soil inorganic N under pasture at equilibrium for these scenarios of N fixation and grazing at the respective sites are shown in Figure 6, as the initial state (soil inorganic N) and equilibrium fluxes (net N mineralisation) before establishment of the eucalypt plantation. A direct comparison of model results with field measurements is not appropriate here because we ran the model to equilibrium with long-term daily averages of temperature, rainfall and solar radiation, whereas the field measurements represented one particular year. Nevertheless, the model reproduced reasonably well the magnitude and seasonality of N mineralisation and inorganic N content under pasture at both sites. The assumption of a

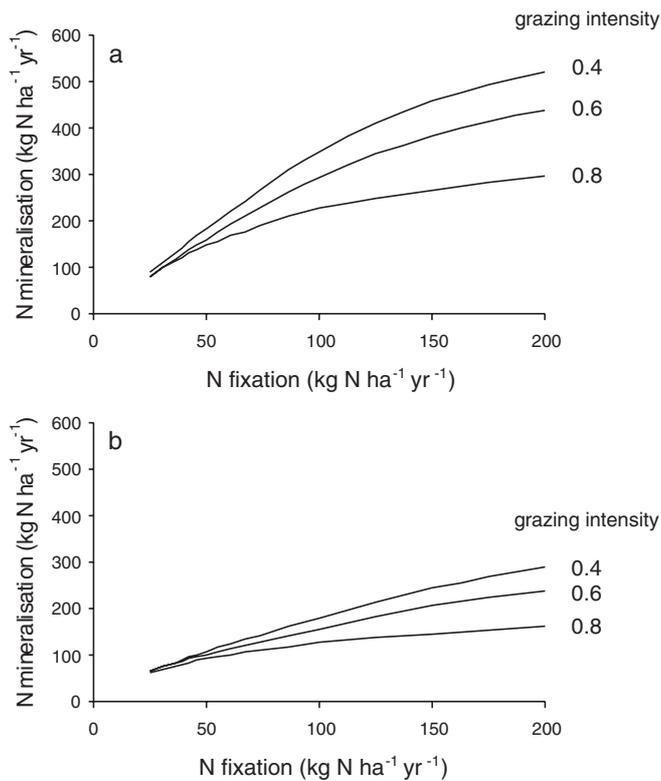


Figure 5. Dependence of simulated annual net N mineralisation under pasture at equilibrium state on biological N fixation rate and grazing intensity for (a) Moltoni and (b) Gibbs.

higher N fixation rate at Moltoni compared to Gibbs supports the observation of higher productivity potential at that site. In general, the amounts of N fixed in pastures relate primarily to the legume content and NPP of pastures [37]. Estimates of amounts of foliage N fixed in pastures in Western Australia range from 30 to 190 kg N·ha⁻¹·yr⁻¹ [37].

Simulated losses of N through leaching and gaseous emission from soil under the pastures at equilibrium (with values for λ_i given in Tab. III) were 61 and 42 kg N·ha⁻¹·yr⁻¹ for Moltoni and Gibbs, respectively (Tab. IV). No field measurements from our sites are available to verify these predictions. However, under pasture-wheat rotations on sandy soils in the wheat belt of Western-Australia, which receives considerably less rainfall (300–500 mm·yr⁻¹) than the sites of this study, 17–28 kg N·ha⁻¹ was found to leach below 1.5 m under the pasture phase [2]. Data on gaseous losses of N in grazed legume based pastures are scarce, but they indicate that N losses from soil through gaseous emission are small in absence of chemical fertilizer N [24].

The model predicted average NPP at equilibrium of 9.6 and 5.2 Mg C·ha⁻¹·yr⁻¹, respectively for the Moltoni and Gibbs pastures (Tab. IV). The difference in modelled NPP between sites is largely due to a greater supply of water and N at Moltoni than Gibbs. The corresponding rates of shoot production were 5.8 and 3.1 Mg C·ha⁻¹·yr⁻¹ at Moltoni and

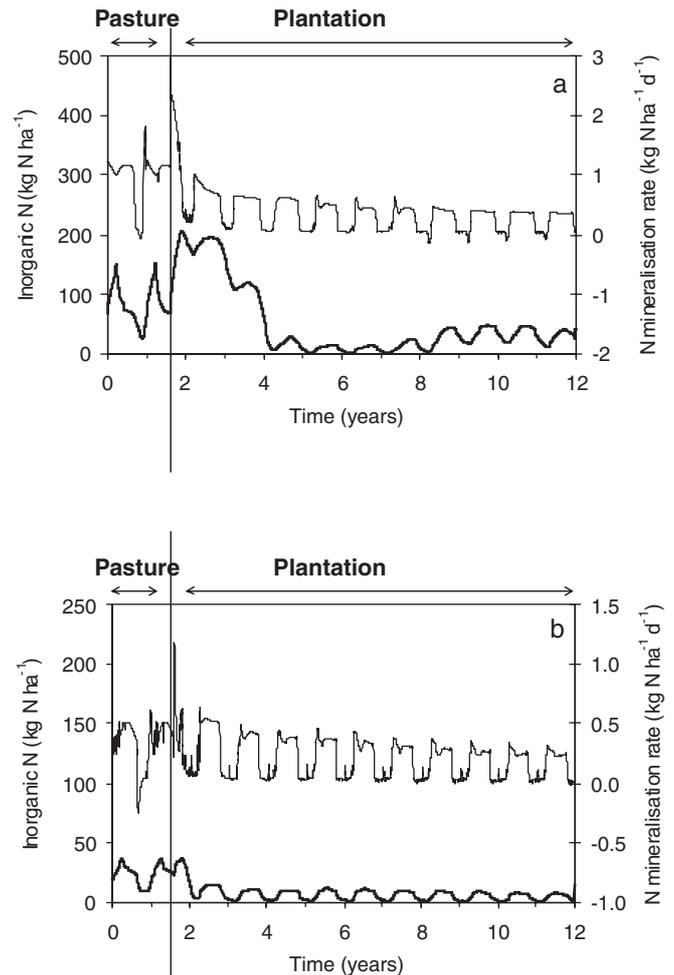


Figure 6. Simulated seasonal patterns of net N mineralisation (fine line) and inorganic N content (bold line) with transition of improved annual pasture to eucalypt plantation for (a) Moltoni and (b) Gibbs. Time 0 corresponds to 1st January. Pasture to plantation conversion occurs on 1st August of second year.

Gibbs, respectively. The normal range of herbage production of improved pastures in the region is 1.5 to 6.0 Mg C·ha⁻¹·yr⁻¹, generally related to growing-season rainfall and inputs of nutrients [6].

3.2.2. Pasture – plantation transition

Thus, initial amounts of litter and soil C and N, and distribution among pools at the time of plantation establishment were determined by running the model to equilibrium under pasture with the “old” SOM pool kept constant. Given the relatively short history (< 40 years) of the pasture at these sites, this equilibrium can be viewed as an approximate (or quasi) equilibrium, which assumes that the “old” SOM pool with a ‘slow’ turnover time is effectively constant at the time-scale of the pasture history, while the fluxes of C and N into all

Table IV. Simulated values for some ecosystem variables under pasture and plantation. Values in parentheses are percent change expressed for plantation (first rotation, 10 yrs) relative to pasture.

Variable	Moltoni		Gibbs	
	Pasture	Plantation	Pasture	Plantation
NPP ^a (Mg C·ha ⁻¹ ·yr ⁻¹)	9.6	23.4 (+144%)	5.2	10.1 (+94%)
N inputs ^a (kg N·ha ⁻¹ ·yr ⁻¹)	125	5.0 (-96%)	55	5.0 (-91%)
N losses ^a (kg N·ha ⁻¹ ·yr ⁻¹)	61 ^e	19 (-69%)	42 ^e	7.3 (-83%)
Litter C production ^a (Mg C·ha ⁻¹ ·yr ⁻¹)	7.7 ^f	7.1 (-8%)	4.5 ^f	3.7 (-18%)
Litter N production ^a (kg N·ha ⁻¹ ·yr ⁻¹)	333 ^f	91 (-73%)	116 ^f	44 (-62%)
C mineralisation ^b (Mg C·ha ⁻¹ ·yr ⁻¹)	7.7	5.7 (-26%)	4.5	3.6 (-20%)
N mineralisation ^b (kg N·ha ⁻¹ ·yr ⁻¹)	324	97 (-70%)	114	62 (-46%)
N standing biomass ^{c,d} (kg N·ha ⁻¹)	82	488 (+495%)	34	230 (+576%)
Plant C:N ^c	20.2	309 (+1430%)	52.3	236 (+351%)
Soil C ^c (Mg C·ha ⁻¹)	187.0	183.9 (-2%)	129.9	127.7 (-2%)
Soil N ^c (Mg N·ha ⁻¹)	8.2	7.6 (-7%)	4.8	4.5 (-6%)
Soil C:N ^c	22.8	24.2 (+6%)	27.1	28.4 (+5%)

Calculations are based on the average value (over year) under pasture and

^a on the average value over 10 years under eucalypt plantation;

^b on the average value in the 10th year under eucalypt plantation;

^c on the final value after 10 years under eucalypt plantation;

^d total aboveground: foliage, stem and branches N;

^e excluding N losses by animal offtake;

^f including animal faeces.

other 'fast' plant, litter and soil pools are in equilibrium and balanced by the total output.

The temporal patterns of net N mineralisation and soil inorganic N following plantation establishment are shown in Figure 6, when model parameters were changed to account for the pasture-plantation transition (Tab. III). Rates of net N mineralisation were predicted to peak shortly after plantation establishment, primarily due to release of N from the decomposing residues of the preceding pasture. At the establishment of plantation, it was assumed that N fixation suddenly ceases and that all standing pasture biomass is transferred to the litter pools. In reality, understorey vegetation is totally suppressed only at canopy closure [44], and, as a result, model predictions are probably overestimating N mineralisation and could be improved by assuming a more gradual transition. On the other hand, site preparation before tree planting may also accelerate the decomposition of litter and SOM due to mechanical disturbance of the soil structure. It is difficult to quantify the extent of these perturbations on decomposition rates.

After establishment of the plantation, N mineralisation rates decreased steadily at both sites (Fig. 6). After 10 years of plantation growth, annual amounts of net N mineralisation were about 70% and 45% less under plantation than pasture, respectively at Moltoni and Gibbs (Tab. IV). These predicted changes in N mineralisation closely reflect differences measured in the field between pasture and plantation at the respective sites (Fig. 3). At Moltoni, predicted amounts of inorganic N showed a substantial peak after plantation establishment, but decreased to low values under the plantation (Fig. 6), which again was in accordance with field observations (Fig. 3). At Gibbs, the simulated amount of inorganic N increased only slightly after plantation establishment and remained low throughout the rotation (Fig. 6). The transient increase of soil inorganic N in young plantation stands has been observed in several experimental studies, and is mainly due to the asynchrony between rates of N mineralisation and plant uptake [19, 31, 44].

A major uncertainty of the simulations is the magnitude of the N losses from the plant-soil system (see also Appendix).

In the simulations, we assumed that on a yearly basis a constant fraction (λ_i) of soil inorganic N is lost from the ecosystem. Although this is a gross simplification, it does result in credible simulations. Simulated N losses were largest at plantation establishment, while decreasing to low values after 3 years (results not shown). Averaged over the entire rotation length predicted N losses were 19 and 7 kg N·ha⁻¹·yr⁻¹ at Moltoni and Gibbs, respectively (Tab. IV). They were higher at Moltoni than at Gibbs because soil N mineralisation rates were higher at the former site whereas the demand for N by young trees was similar. Nitrogen losses through leaching and gaseous emission from soil were about 70% (Moltoni) and 80% (Gibbs) less under the eucalypt plantation than under pasture (Tab. IV). Differences in rooting depth between pasture and plantation were represented in the model by halving the rate constant of N loss (λ_i) under plantation compared to pasture (Tab. III). This indicates the lower potential for N losses under plantation compared to pasture. However, the main reason for the large difference in predicted N losses between plantation and pasture is the higher level of soil inorganic N under pasture. Under pasture, N supply is in excess of plant requirements due to inputs of biological N fixation. Ideally, when modelling N dynamics under plantations, we should alter the $\lambda_i:\lambda_u$ ratio gradually over time to reflect changes in rooting depth and soil exploration with tree age. More detailed experimental data are needed, however, to validate such parameterisation. Other factors, including soil texture, soil pH and nitrification rates, will also influence the extent of N losses. However, these site characteristics are not explicitly included in our model as factors for simulating fluxes of N loss.

Under steady-state conditions, the annual rates of C and N mineralisation are equal to the respective amounts of litter C and N input over a year. In our quasi-equilibrium simulations with the “old” SOM pool kept constant, predicted production of litter N (including animal faeces-N) under pasture was slightly larger than predicted N mineralisation due to a net flux of N into “old” SOM. Rates of net N mineralisation are directly affected by changes in litter quality and quantity that occur with conversion of pasture to plantation. Litter from eucalypt plantations has lower quality or decomposability than litter from pasture mainly because of the presence of woody material and the higher lignin content in foliar and fine root litter (Tab. III). The changes in simulated litter C and N quantity with plantation establishment are given in Table IV.

Simulated NPP doubled under eucalypts compared to pasture, despite lower inputs of N and decreased availability of soil N in the plantation system (Tab. IV). This increase in NPP was mostly due to the decreased plant N:C ratio and, hence, increased N use efficiency of the eucalypt stands compared to pasture. However, under plantation a smaller proportion of NPP is transferred to litter compared with pasture because tree biomass pools, especially stems, have larger turnover times than pasture biomass pools. The result is lower rates of litter C production under plantation compared to pasture. At the highly productive Moltoni site, the input of litter C was about 8% less under the plantation, and at the less

productive Gibbs site, was about 18% less (Tab. IV). The corresponding decreases in input of litter N were much larger: 73% and 62% for Moltoni and Gibbs, respectively. These larger decreases in input of litter N than litter C were due to the decreased N:C ratio in plant biomass and litter under plantation compared to pasture.

The predicted amount of total soil N decreased by 6 to 7% after 10 years of afforestation at both sites (Tab. IV), and was an underestimation of the decline measured in the soil profiles at Moltoni (14%), and especially at Gibbs (44%) (Tab. II). However, O’Connell et al. [34] found, on average, no change in total soil N in topsoil (0–20 cm) between pasture and plantation across a much broader range of sites in south-western Australia. Simulated soil C:N ratio increased slightly (5 to 6%) at both sites (Tab. IV), consistent with experimental data. In a study of 10 paired pasture-plantation sites in the region, Mendham et al. [27] found that the C:N ratio in the topsoil (0–10 cm) was only marginally higher under first-rotation eucalypt plantation compared to pasture.

3.2.3. Multiple rotations

Model predictions indicated that we were able to reproduce the major changes in amounts of soil inorganic N and rates of net N mineralisation with the transition of improved pasture to a 10-year-old eucalypt plantation. Insofar as the model is verified by these data, we may explore the long-term dynamics of C and N cycling over subsequent rotations of the plantation. However, we recognise that long-term extrapolation of observations of a short-term nature may entail large error propagation and, that, therefore, these model predictions do need to be further tested against measured experimental data.

We ran the model for each site over a number of 10-year rotations under two harvest residue management scenarios (see material and methods): (1) “no residues”, i.e. removal of all above-ground harvest residues at each harvest; and (2) “with residues”, i.e. retention of all above-ground harvest residues (leaves and branches).

Nitrogen exported from site with harvest in the “with residues” scenario correspond in the model to the accumulated N in stems, which were about 200 and 60 kg N·ha⁻¹ for the first rotation at Moltoni and Gibbs, respectively. We assumed hereby a N:C ratio for stem of 0.0015 (Tab. III). The amounts of N that are exported with stem and harvest residues in the “no residue” scenario are in the model simulations the predicted standing aboveground biomass N. These amounts were for the first rotation 488 and 230 kg N·ha⁻¹, respectively at Moltoni and Gibbs (Tab. IV). O’Connell and Grove [31] and O’Connell et al. [32] estimated on experimental plots that about 260 and 520 kg N·ha⁻¹ are exported with wood and harvest residues, respectively from a low and highly productive first-rotation *E. globulus* stand in south-western Australia. In the model the predicted amounts of N exported in stem and harvest residues decrease over successive rotations in accordance with the decline in stem productivity.

Leaf harvest residues are mainly fresh, green residues and have a different biochemical composition than leaf litter,

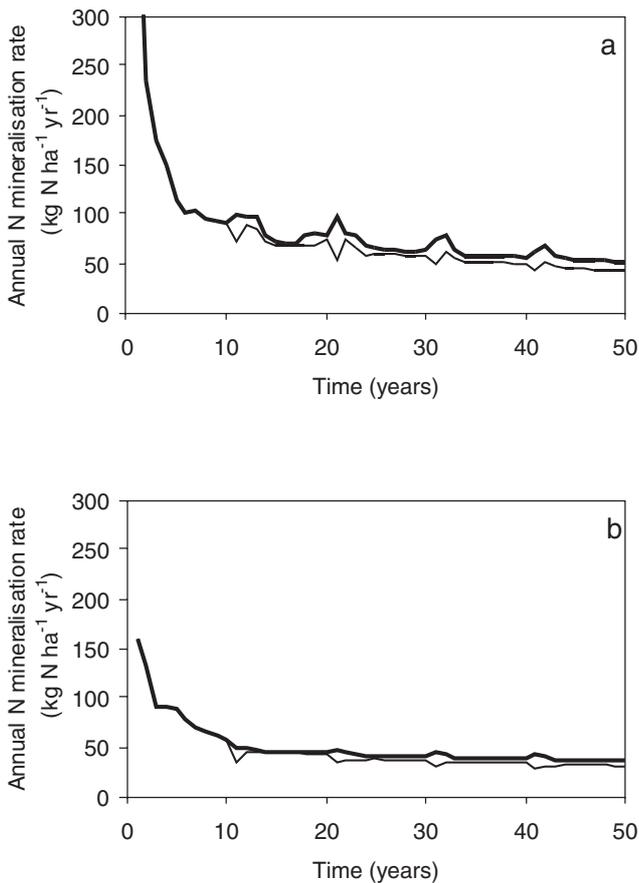


Figure 7. Simulated annual net N mineralisation over 5 rotations at (a) Moltoni and (b) Gibbs. Bold line is “with residues” scenario; fine line is “no residues” scenario.

which consists of senescent tissues. Foliar harvest residues have lower lignin content than leaf litter (Tab. III), resulting in a faster decomposition in the model, and their N content is approximately twice that of leaf litter, due to the absence of N retranslocation. Because of this difference in N content, simulations predict that foliar harvest residues have a higher potential for N supply than leaf litter and, in contrast with leaf litter, do not entail strong N immobilisation in the early phase of decomposition (results not shown).

Simulated rates of net N mineralisation decreased steadily from the second rotation onwards at both sites and for both scenarios of residue management (Fig. 7). In these long-term simulations, the overall negative balance between N inputs and outputs (atmospheric N deposition minus N losses from soil and N removals in harvest), and N immobilisation in SOM have a substantial impact on net N mineralisation rates.

The largest differences in simulated rates of N mineralisation between the two scenarios were predicted immediately after harvest. In the “no residues” scenario, there was a short period of decreased net N mineralisation, corresponding to the decomposition of coarse roots. In the “with residues” sce-

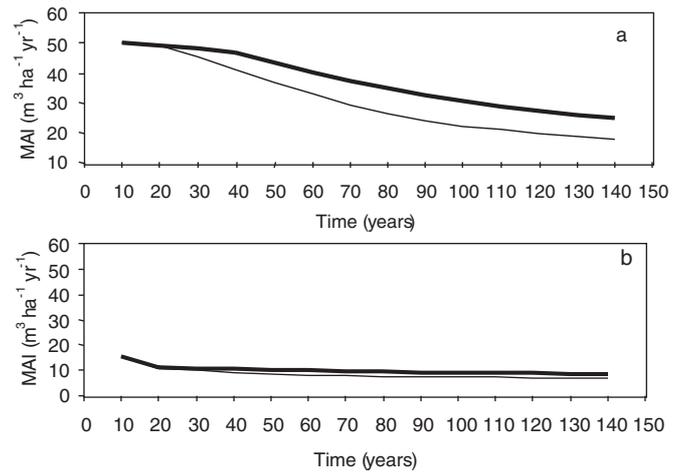


Figure 8. Simulated MAI over 15 rotations at (a) Moltoni and (b) Gibbs. Bold line is “with residues” scenario; fine line is “no residues” scenario.

nario, this decline was offset by increased net N mineralisation due to the decomposition of leaf material. As a result, the cumulative difference in net N mineralisation after 5 rotations (50 years) between the two scenarios was about 390 and 225 kg N·ha⁻¹, respectively at Moltoni and Gibbs. These values are consistent with the small differences in N mineralisation that have been measured in the region on field plots in second-rotation eucalypt plantations where harvest residues were retained or removed [33].

In the model, the amount of soil inorganic N, and, hence, rate of N mineralisation affects NPP and stand productivity. Consequently, the decline in N mineralisation over successive rotations caused a decline in predicted plantation productivity (Fig. 8). The pattern of this simulated decline over a period of 15 rotations differed between the two sites. At Moltoni, there was a large predicted decrease in N mineralisation (Fig. 7) after the first rotation, but only modest decrease in MAI (Fig. 8). This indicates that the N supply under pasture was in excess of the N demand by plantations. From the third (for “no residues”) and fifth (for “with residues”) rotation onwards, soil N supply becomes critical to productivity, and its gradual decline leads to important losses of productivity. After 15 rotations, the predicted decline in MAI was about 60 and 45%, respectively, for the “no residues” and “with residues” scenarios. At Gibbs, the reduction in productivity was largest in the second rotation, but thereafter the decline was less and the plantation system moves towards steady-state conditions. In absolute terms, the difference in productivity at Gibbs after 15 rotations between the two scenarios was small (< 3 m³·ha⁻¹·yr⁻¹).

These model simulations suggest that retention of harvest residues will improve soil N supply for the next rotation relative to removal (burning) of the residues. However, the model predicts a decline in N supply over many decades despite

residue retention. The model results further suggest that residue retention is really only beneficial at the high rainfall Moltoni site. For non water-limited sites such as Moltoni, plantation productivity will probably depend largely on the rates of soil N supply. For water-limited sites such as Gibbs, depletion of the soil water store over successive rotations may be a more important factor than N supply causing productivity decline.

Although residue retention will partly offset the decline in productivity over time, applications of fertiliser N will generally be necessary to maintain current levels of productivity. The model allows us in fact to define the N addition required to sustain a given yield. This analysis could be based on the relationship between MAI and N supply as previously illustrated by Dewar and McMurtrie [14] in a theoretical analysis of long-term changes in forest growth. Model runs could be used to determine the N addition required to achieve that rate of N supply.

4. CONCLUSIONS

We used a linked plant-soil model, G'DAY, to investigate changes in supply of soil N after conversion of pasture to eucalypt plantations, and predicted the consequences for stand productivity in the long-term.

Predicted rates of N mineralisation and amounts of inorganic soil N under this change in land-use were consistent with measurements in two paired-site field experiments. It suggests that the mechanistic underpinnings of our model were sufficiently valid to explore future C and N dynamics under plantations. However, detailed experimental data are lacking for a thorough validation of the model.

Simulations showed that conversion of pasture to plantation does reduce soil N supply, but not necessarily NPP because N use efficiency is much higher in eucalypt plantations than in pasture. In fact, NPP increases twofold in young plantations, but this does not result in increased litter C input, due to the smaller turnover rates of the plant biomass pools in eucalypts compared to pasture. Quite the opposite, input of litter N considerably decreases under plantation, due to the reduced N:C ratio of tree litter. Simulations also indicated a significantly smaller net input of N (biological N fixation plus atmospheric N deposition minus N losses) in the plantation compared to pasture, a transfer of N from soil to plant and an increase in the C:N ratio of both vegetation and soil. Each of these changes has a direct or indirect effect on soil N supply and stand productivity.

The long-term simulation runs showed that adoption of management strategies that maintain adequate levels of N input under plantations will be critical for sustaining high productivity levels in eucalypt plantations. Retention of harvest residues has only a limited scope for preserving the levels of soil N supply under eucalypt plantations. Maintenance in soil N supply and sustained plantation productivity will rely on regular application of fertiliser N. The model predictions

need to be evaluated as more data on long-term productivity become available.

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APPENDIX

Sensitivity of net primary productivity (NPP) and soil net N mineralisation (Nmin) under first rotation *E. globulus* plantation following pasture to the rate constants for N losses (λ_l), maximal plant N uptake (λ_u), and maximal microbial uptake (λ_m)

The values of the rate constants for N losses (λ_l), maximal plant N uptake (λ_u), and maximal microbial uptake (λ_m) are uncertain in the above model runs. The sensitivity of NPP and soil net N mineralisation under plantation are summarised in Table A1. The table presents average values for a 10-year period of eucalypt growth following pasture respectively for the highly productive Moltoni site and the less productive Gibbs site. A decrease in λ_l (from 0.8 to 0.2 yr⁻¹) at Moltoni leads to an increase in NPP (+13%) and Nmin (+8%). Similarly, a decrease in λ_l from 2.0 to 0.5 yr⁻¹ at Gibbs increases NPP (+6%) and Nmin (+11%). With reduced N loss from the plant-soil system, plant N uptake and NPP are enhanced, also leading to increased N cycling through plant litter. In the same way, doubling λ_u increases NPP (+11% at Moltoni, +4% at Gibbs) and Nmin (+19% at Moltoni, +14% at Gibbs), while halving

Table A1. Sensitivity of net primary productivity (NPP, Mg C·ha⁻¹·yr⁻¹) and net N mineralisation (Nmin, kg N·ha⁻¹·yr⁻¹) to the rate constants for N losses (λ_l), maximal plant N uptake (λ_u), and maximal microbial N uptake (λ_m) under plantation. NPP and Nmin are average annual values over 10 years under first rotation eucalypt plantation following pasture. All simulations were initiated by running G'DAY to quasi-equilibrium under the respective pasture systems at Moltoni and Gibbs. Rate constants for λ_l , λ_u , and λ_m under pasture were kept constant for each simulation at a given site (values of Tab. III) to have the same initial (site-specific) conditions.

Site	λ_l	λ_u	λ_m	NPP	Nmin	
Moltoni	0.8	10.2	15.0	21.72	136.0	
	0.4	10.2	15.0	23.37	142.0	
	0.2	10.2	15.0	24.65	147.2	
	0.4	5.1	15.0	21.20	124.2	
	0.4	20.4	15.0	26.01	168.5	
	0.4	10.2	7.5	25.14	159.5	
	0.4	10.2	30.0	22.18	133.3	
	Gibbs	2.0	10.2	15.0	9.69	70.4
		1.0	10.2	15.0	10.06	75.0
		0.5	10.2	15.0	10.26	78.3
1.0		5.1	15.0	9.59	66.0	
1.0		20.4	15.0	10.47	85.8	
1.0		10.2	7.5	10.32	84.0	
1.0		10.2	30.0	9.89	69.7	

λ_u leads to decreased NPP (−9% at Moltoni, −5% at Gibbs), accompanied by decreased N mineralisation (−13% at Moltoni, −12% at Gibbs). NPP is less sensitive to λ_u at Gibbs than at Moltoni, because of water limitation to NPP at the former site. Nmin is relatively more sensitive to λ_u compared to NPP, because of the additional effect of plant N uptake on the N:C ratio of litter. Doubling λ_m reduces NPP (−5% at Moltoni; −2% at Gibbs) and Nmin (−6% at Moltoni, −7% at Gibbs), while halving λ_m leads to a +7% (Moltoni) and +3% (Gibbs) increase in NPP and a 12% (Moltoni and Gibbs) increase in N mineralisation. Decreased microbial N uptake increases NPP (and Nmin), mainly because of a relative increase in plant N uptake. It indicates the effects of competition between plant and microbial N uptake for inorganic N. The direct effect of λ_m on N mineralisation through a possible N limitation on litter decomposition when the actual N demand is larger than the potential N uptake (decreased Nmin with decreased λ_m) is thus for these simulations overruled by the indirect effect of λ_m on plant N uptake and litter N production.

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