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**Nitrogen cycling in forests with inter-
specific competition: models and
knowledge gaps in relation to
temperate eucalypt and pine
plantations**

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Confidential to RP1.3: modelling and
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Executive Summary

Process-based models of forest growth, nitrogen cycling and inter-specific competition were reviewed to summarise the current status of the field and identify priorities for future development that would enhance simulations of competitive uptake for nitrogen in forest plantations. Twelve forest productivity models and seven soil process models were reviewed as examples of the wide variety of models available. All models included some processes that were considered important, but none included all these processes in adequate detail. I concluded that, where process-based simulation of competition for nitrogen is a priority, the next generation of models should consider:

- the inclusion of uptake by competing species via solute transport theory using multiple uptake surfaces, e.g. mycorrhizae, different root cohorts, roots of competing species
- detailed forest floor carbon and nitrogen (C-N) dynamics
- urea volatilisation, including forest floor interactions
- denitrification
- ammonium leaching
- dynamic nitrogen (N) concentrations in plant N components
- multiple soil layers
- N dynamics in deep soil horizons.

Introduction

Process-based models of forest growth, e.g. CABALA and 3PG, are used in Australia and internationally to simulate wood yields and other outcomes of eucalypt and pine plantation growth under various management, climate, and pest and disease scenarios (Battaglia and Sands 1998). These models currently simulate monoculture growth, but development to include a competing species is desirable to enable predictions of plantation growth when grown with weeds or companion crop species. Competition is of interest, because monoculture growth is rarely achieved completely despite it being a common management objective. In addition, sustainability concerns manifest in certification standards and elsewhere are creating pressures to reduce herbicide usage and increase the biodiversity and weediness of plantations (Little *et al.* 2006).

These models simulate key aspects of availability, capture and utilisation of site resources (light, water, and nutrients generally or N specifically) for fixing carbon and allocating it to biomass components on a daily or monthly basis. Development and validation of these models has mainly focused on the resources light and water, with less emphasis on N or other nutrients. Amongst below-ground resources, the emphasis on water was justified, because its constraint on production is not easily removed. Low nutrient availability is commonly alleviated by the use of fertilisers, but water availability is less easily managed with irrigation or plantation design (e.g. spacing and thinning).

Economic and environmental concerns will probably ensure that most plantations are not fertilised to the extent that nutrient limitations are entirely removed, especially if there is an increase in the coverage of weeds. Hence, as these models develop to include competing species, there will also be a need to validate and improve the representation of various aspects of nutrient cycling.

My aim here was to identify gaps in available models in relation to nutrient cycling and growth in forest plantations with competing vegetation. Firstly, an overview is provided of key aspects of N cycling and below-ground competition. This is followed by a review of forest growth models in the context of single- or multi-species systems in monoculture plantations, and in agroforestry, shelterbelt or mixed forest systems. A review of more detailed N cycling and competition models is then followed by a list of improvements that should be considered for forest productivity models.

Overview of nitrogen cycling

Aspects of the N cycle relevant to forest plantations are summarised schematically in Figure 1. Losses of N from a soil-plant system can be by harvesting, burning and other forms of volatilisation, erosion, and leaching. Inputs occur via biological N fixation, application of fertilisers, and atmospheric deposition or atmospheric uptake. Some useful, more detailed reviews of N cycling are provided by Carlyle (1986), Brady (1990), Hansen *et al.* (1991), Tisdale *et al.* (1990), de Willigen (1991), Webb *et al.* (2001), and Wu and McGechan (1998).

Plants take up N mainly as inorganic N either as ammonium (NH_4) and nitrate (NO_3), and some plants have a preference for one form more than the other. Trace amounts of organic N as amino acids or mineral N as nitrite (NO_2) might also be taken up, but are likely to be of minor importance in commercial forest plantations. Most soil N, however, is in an unavailable form as various kinds of organic N with different periods of turn-over. A sizeable and highly dynamic component of soil organic N is in live microbial biomass and soil fauna. In soils that have significant proportions of expandable clays, NH_4 can be reversibly trapped between the clay lattices and only slowly available for uptake. There is also vertical stratification of N forms in soil, from mostly organic forms in the forest floor and surface soil horizons to mainly mineral forms in some sub soils where NO_3 has accumulated as result of leaching from surface horizons. Horizontal heterogeneity in concentrations of all forms of N is high in forest soils compared to agricultural soils.

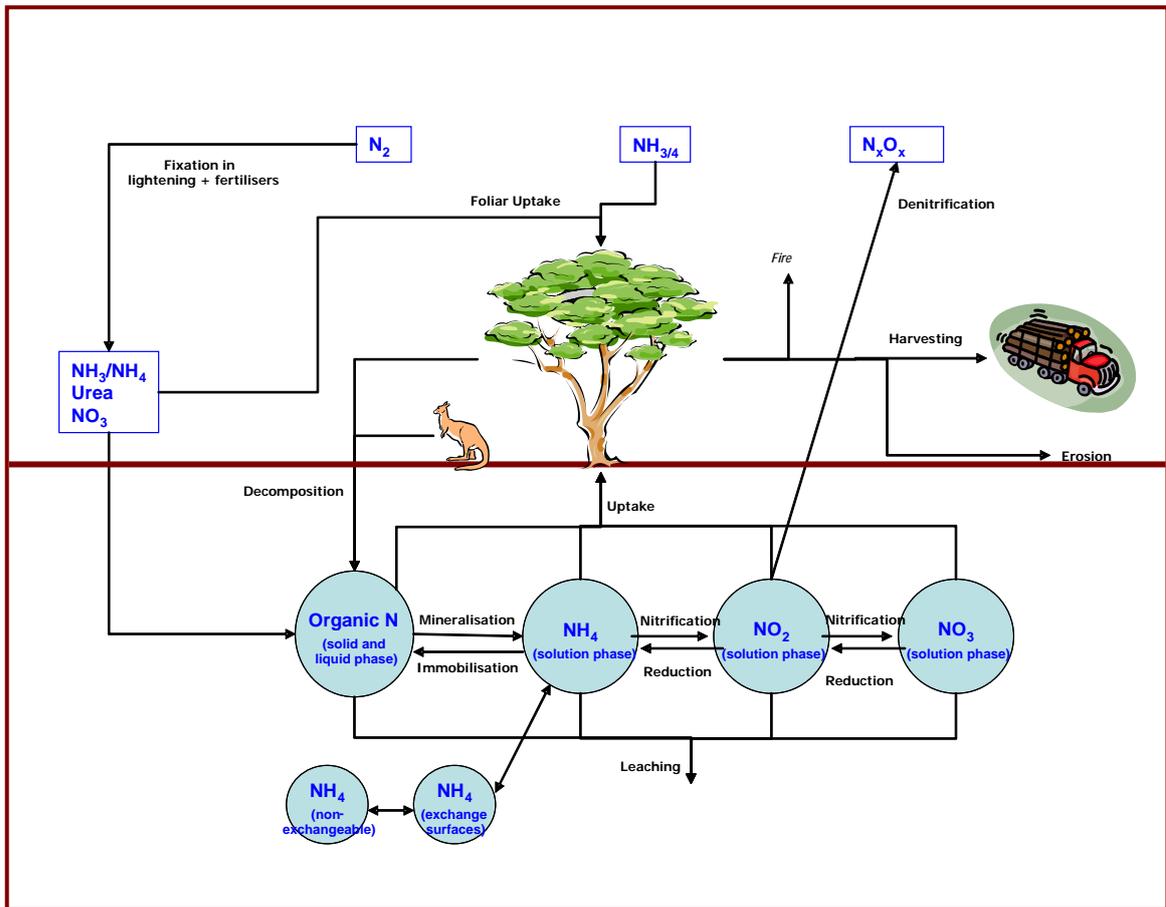


Figure 1. Components of the N cycle important in plantation forestry

Plants take up N mainly through fine roots, but uptake via mycorrhizal hyphae is also possible. Plant canopies can also absorb N deposited in particulate, liquid or gaseous forms that dissolve prior to uptake by leaf cells. Foliar sources of N can be significant in polluted environments or where foliar sprays are applied.

Plant N is almost entirely organic, but total N and component N concentrations vary widely in plant tissues both spatially and temporally. Upon uptake by roots, NH_4 is immediately incorporated into amino acids that can be stored, or transported in the

xylem stream to other parts of the plant. In contrast, NO_3 can be reduced to NH_4 either in roots or in other plant parts, prior to its incorporation into amino acids. Excess N is stored as high concentrations of organic N and as NH_4 in vacuoles, and negative feedbacks to active uptake and passive exudation processes help regulate net uptake in relation to plant demand, and the overall status of plant nutrition.

To maintain an adequate N supply to plants, mineral N in soil needs to be replaced either by mineralisation of the soil organic pool or by the addition of mineral N from external sources, i.e. fertilisers or atmospheric inputs. Mineralisation refers to the conversion of organic N to NH_4 (also referred to as ammonification), which is achieved by exo-enzymes produced by many types of soil fungi and bacteria (soil microbial biomass). The microbial biomass takes up N from the soil mineral N or amino acid pool, which for the former is a process known as immobilisation and hence the reverse of mineralisation. The balance of these two processes is known as net N mineralisation, which can be positive or negative. Soil NH_4 is available for nitrification, which is a two-stage, microbial process, i.e. the production of NO_2 followed by NO_3 . In aerobic conditions, the second stage is limited by low NO_2 concentrations, but in anaerobic conditions nitrification is incomplete and NO_2 accumulates. Like all biological processes, rates are strongly temperature and water dependent. The physical and chemical nature of soil organic N also influences the rate of mineralisation.

Denitrification, which is the main source of volatile N loss from soils, occurs in water-logged, anaerobic conditions when NO_2 is reduced to gaseous N_xO_x compounds, but this process also requires the appropriate microbes, a source of energy (carbon (C)), and suitable temperatures. These conditions not only occur in many water-logged soils, but also in some sub-soils where NO_3 has accumulated after leaching.

Soil NH_4 is a cation that competes with others (mainly calcium, magnesium, potassium, sodium, aluminium and hydrogen) for soil cation exchange surfaces, the net result of which keeps most NH_4 bound to the solid phase (typically 90 per cent) but in rather rapid, quasi-equilibrium with the liquid phase. In contrast, NO_3 has no solid-phase interaction, except in some soils that have appreciable anion exchange capacity. Both NH_4 and NO_3 are prone to leaching, but NO_3 much more so because of its minimal interaction with the solid phase.

Fertiliser N can be added in many different mineral and organic forms. A common form of organic N fertilisation in plantation forestry is in the form of urea, which is very soluble. Once dissolved, urea moves into the litter or soil. The urea molecule is hydrolysed by urease enzymes that are ubiquitous in soils, but are probably less plentiful in forest litter layers. The high pH generated by dissolving urea is quickly buffered in soils, but in litter, where pH buffering is minimal, it might linger. At high pHs ($\text{pH} > 7$) NH_4 is directly volatilised to NH_3 . Hence, where urea hydrolysis releases NH_4 into a high pH environment, N is lost to the atmosphere. This process, known as urea volatilisation occurs to some extent in most plantations, but is exacerbated by non-leaching rainfall, high temperatures, and probably by applications to forest litter layers (May and Carlyle 2005).

Approximately 70 per cent of our atmosphere is N in the form of N₂. This form of N is not directly available to plants, but instead is converted to NH₃ via lightening, biological N fixation, or artificial N fixation in the fertiliser industry. Burning fossil fuels in power stations, cars and elsewhere also contributes to atmospheric NH₃ and NO_x. There is concern about the global scale of man-induced changes to the global N cycle because anthropogenic transfers of atmospheric N to biologically available forms on land has approximately equalled the natural transfer rate (Vitousek *et al.* 1997).

Overview of the mechanisms underlying competition for nutrients

To understand competition for nutrients at a mechanistic level, it is first important to understand a number of other aspects of nutrient supply and uptake. Nutrients move to uptake surfaces, i.e. fine roots (or mycorrhizal hyphae), via mass-flow, diffusion or interception (Tinker and Nye 2000). At a root surface, uptake occurs as an active process governed by enzyme kinetics. Passive release of nutrients also occurs. The net rate of nutrient uptake is subject to feedback controls in the plant that lead to high spatial and temporal variability in the uptake kinetics of a root system. Access to available nutrients in a particular volume of soil is governed by the amount of uptake surface and its sink strength in relation to competing surfaces of other plants. The amount of surface is often characterised as root-length density, and its sink strength as a combination of root diameter and uptake kinetics.

If the uptake of a nutrient at a root surface is greater than its rate of supply, a zone of depletion will develop near the root where concentrations are lowest. Conversely, zones of accumulation can also occur if the rate of uptake is less than the rate of supply. These zones of depletion or accumulation spread out around a root at a rate dictated by the same soil and plant properties that govern diffusion and mass-flow. The more a nutrient interacts with the solid phase, the slower it's rate of diffusion and the slower the rate of spread of the zone of depletion or accumulation. For example, zones of depletion for NO₃ spread rapidly (several cm per day), which contrasts with phosphate (PO₄) in a highly phosphorous (P) -sorbing soil where a depletion zone will be only a few mm wide after many days.

A molecule of nutrient in solution, if not directly intercepted by a growing root, will move in a direction dictated by the well-defined principles of bulk flow of solution (i.e. mass-flow) and diffusion down a concentration gradient. A one-dimensional visualisation of this system led to the concept of a no-transfer-boundary, which is the position between two competing roots where the nutrient does not move in either direction. Large diameter roots have larger sink strength than small roots. Therefore, if all else is equal, a plant with larger diameter roots will have available to it nutrients from a larger volume of soil (Figure 2).

If competition for a nutrient is defined as a reduction in nutrient uptake by one root system due to the presence of another root system, it will only occur if zones of depletion overlap, i.e. competition commences only when depletion zones extend to the no-transfer boundary, i.e. overlap, and it only becomes important for plant growth if competition is for a nutrient that limits plant growth.

Nutrient cycling in forest growth models

Since this review focuses on mechanistic models, I found it useful to compare forest growth models using eight main attributes, i.e. forest system, silvicultural flexibility, light capture and photosynthesis, water, nitrogen, carbon allocation, time-step, and tree species to which they had been applied (Table 1). The forest system attribute provided three groups under which the models could be discussed, i.e. those suitable for plantations, agro-forestry, or mixed-forest systems.

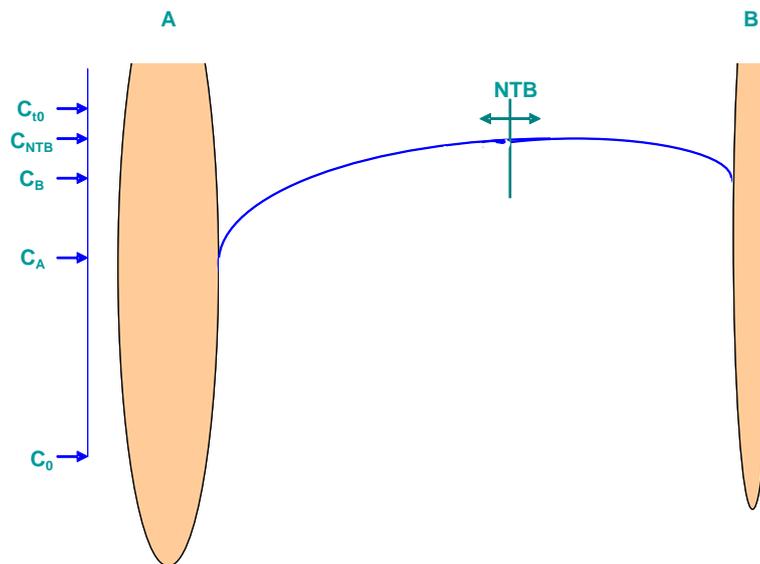


Figure 2. Schematic diagram of depletion zones for two roots of contrasting size (A and B) that have just begun to compete, i.e. depletion zones have started to overlap. C = concentration in solution, NTB = no transfer boundary, C_0 = zero concentration, C_{10} = initial concentration

Plantation models: 3PG, CABALA, G'DAY PGSM, and TREGRO

Five plantation productivity models were identified for comparison, i.e. *3PG*, *CABALA*, *G'DAY*, *PGSM*, and *TREGRO*, which had many commonalities, but also significant differences in emphasis.

The 3PG model is widely used to simulate plantation growth for management and research purposes (Almeida *et al.* 2004, Esprey *et al.* 2004, Sands and Landsberg 2002). This model mechanistically accounts for light and water, but it simulates the degree of nutrient limitation on tree growth by using only a fertility factor (FR) that ranges from zero (full nutrient limitation) to one (no nutrient limitation). For 3PG, fertilised plantations can be assumed to have no nutrient limitation (Sands and Landsberg 2002) or empirical predictors of these ratings can be developed using fertiliser experiments or a twin plot approach (Stape *et al.* 2006). Because FR is not nutrient-specific, and it is a fixed value for an entire simulation, this model has an inadequate representation of nutrient dynamics to be useful in the mechanistic

prediction of nitrogen availability. Another major limitation of this model for plantations is its low silvicultural flexibility. The attractiveness of this model to current forest managers is its reduced need for input data relative to other mechanistic models, partly because it runs on a monthly rather than daily time step, which lends itself more readily to spatial applications using graphical information systems.

The CABALA model is also used by several forest managers and researchers; while it requires more expertise and data input than 3PG, it produces more mechanistic detail that has been validated for various aspects of water and light use (Battaglia *et al.* 2004). This model has high silvicultural flexibility and uses a C allocation routine that is dynamic on a daily basis. This model also realistically simulates some aspects of N dynamics under some conditions, e.g. net N mineralisation at two out of three eucalypt plantation sites in Western Australia (Battaglia *et al.* 2004).

The soil N sub-model of CABALA is the CERES model, which requires about 50 parameters (Goodwin and Jones 1991). Many of these parameters are difficult or impossible to measure and are therefore the values provided by the authors that can be varied to enable tuning during calibration for specific sites. A few measured soil parameters affect site-specific predictions, e.g. total C and N concentrations and pH. In many respects, and in common with other detailed soil N models, this model simulates many of the processes of soil N turnover that are probably necessary for one plantation rotation of several decades. The CERES model and several others are discussed later in more detail.

The G'DAY model (Corbeels *et al.* 2005a, 2005b, 2005c) has many similarities to CABALA, but some important differences. Although G'DAY includes a C-N turnover module that was specifically developed for forest plantations, and copes well with harvest residue management options, it apparently lacks many of the other silvicultural options that are important in plantations, e.g. espacement designs, pruning, and thinning.

The PGSM model was designed to simulate tree growth in a uniform stand subject to stresses such as ozone and acid rain; it was most recently applied to *Pinus ponderosa* (Chen *et al.* 1998). This model includes hydrological and biogeochemical sub-models that have been reported separately, (i.e. Chen *et al.* 1982 and Gherini *et al.* 1985), which have many aspects in common with other models reported here. Because the emphasis of this model is on stand growth responses to stress, it includes the potential for partial canopy and root system mortality, which was unique amongst the models reviewed. The PGSM model (more particularly its geochemistry sub model, ILWAS) simulates nitrification at a rate asymptotically in relation to the concentration of NH_4 , and, uncommon amongst models, it includes uptake of NH_4 and NO_3 in direct proportion to their concentrations in soil solution (Gherini *et al.* 1985). This latter aspect is partially in common with some of the more mechanistic approaches described below.

The TREGRO model predicts individual tree growth from environmental and physiological parameters; it also takes into account soil N availability, but only by using fixed concentrations of nutrients in solid and liquid phases (Weinstein *et al.* 1991), and hence lacked the dynamic feedback required for mechanistically simulating nutrient cycling (Tiktak and van Grinsven 1995). In a later application,

nutrients were treated more dynamically by applying solute transport theory (Weinstein and Yanai 1994). Both PGSM and TREGRO have low silvicultural flexibility, which is an important limitation for these plantation models.

Agroforestry and shelterbelt models: SBELTS, APSIM, HyPAR and WaNuLCAS

In several models designed for applications in agroforests or shelterbelts, nutrients receive little or no attention and are therefore assumed to be non-limiting. Trees are also modelled very simplistically in some shelterbelt models. Instead, environmental factors other than N are of most interest, and the aim is to predict agricultural crop growth and yield over one season, rather than tree growth over many seasons. These limitations were evident, for example, when the SBELTS model was used to model soybean growth behind a shelterbelt of Eugenei trees (Qi *et al.* 2001). Similar limitations were evident when the Sirius model was used to model wheat growth behind shelterbelts of coppiced willows, and this work also highlighted the need to predict shelterbelt effects on N availability (Foereid *et al.* 2002). Three other agroforestry and shelterbelt models were identified in which tree growth over several years has been of interest, and soil and plant N dynamics were simulated to various degrees, i.e. APSIM, HyPAR, and WaNuLCAS.

The APSIM modelling framework has been used to simulate agroforestry options by linking a FOREST module (the basic components of which are similar to 3PG and CABALA) with modules for water, nutrients, and agricultural crop productivity (Huth *et al.* 2001, 2003). The APSIM FOREST module was validated for a plantation of *Eucalyptus grandis* with various combinations of fertilisation and irrigation, but it has low silvicultural flexibility (Huth *et al.* 2001). Instead, this module was developed mainly to predict impacts of shelterbelts on adjacent agricultural productivity and broader system responses in hydrology and salinity (Huth *et al.* 2001). The soil N module of APSIM, like CABALA, is based on the CERES model. Some aspects of the APSIM soil N module have been verified in agricultural (Probert *et al.* 1998, Dalal *et al.* 2004) and forestry applications (Snow *et al.* 1999). In an agricultural context, the APSIM model has also been used to simulate weed competition effects on N uptake and growth of maize (Keating *et al.* 1999). These simulations predicted that a low level of weed competition would cause a 20 per cent decrease in maize grain yield if 40 kg N per hectare (ha^{-1}) was applied to an infertile soil in Zimbabwe, but no validation was reported.

The HyPAR model (Mobbs *et al.* 1998) is an agroforestry model that combines the Hybrid ecosystem model (discussed below; Friend *et al.* 1997) with an agricultural crop growth model (PARCH; Bradley and Crout 1994). Soil N dynamics in this model used the Century soil sub model (Parton *et al.* 1993) as a reasonable balance between the level of parameterisation required and the detail of mechanisms simulated (Friend *et al.* 1997). However, HyPAR validation focused on water and biomass.

Table 1. Some distinguishing characteristics of forest production models considered in this review

Model	Forest system	Silvicultural flexibility	Light capture and photosynthesis ¹	Water	Nitrogen	C Allocation	Minimum time step	Tree species applications	References
3PG	Even-age, single species plantations	Low	RUE	Simple, 1-layer	Simple nutritional factor	Semi-fixed patterns; monthly stresses	Monthly	Numerous	Landsberg and Waring (1997) Sands and Landsberg (2002)
CABALA	Even-age, single species plantations	High	BL (modified)	Detailed water dynamics with tipping bucket, Three layers	Detailed, CERES-based. Three layers. Simple uptake.	Dynamic with daily stresses	Daily	<i>Eucalyptus globulus</i> <i>Eucalyptus nitens</i> <i>Pinus radiata</i>	Battaglia <i>et al.</i> (2004)
G'DAY	Even-age, single species plantations	Moderate	Sun-shade	Detailed	Detailed	Fixed patterns	Daily	<i>Eucalyptus globulus</i>	Corbeels <i>et al.</i> (2005a, 2005b, 2005c)
PGSM	Even-age, single species plantations	Low	RUE	Detailed	Simple	Dynamic with annual stresses	Daily	<i>Pinus ponderosa</i> <i>Pinus taeda</i>	Chen <i>et al.</i> (1994) Gherini <i>et al.</i> (1985) Chen <i>et al.</i> (1998)
TREGRO-ZELIG	Even-age, single species plantations, or mixed forests	Low	RUE	Detailed water dynamics	Detailed, one layer, based on solute transport theory. No report of N. Detailed uptake.	Fixed patterns	Hourly	<i>Picea rubens</i> <i>Pinus ponderosa</i> <i>Abies concolor</i>	Weinstein <i>et al.</i> (1991) Weinstein and Yanai (1994) Weinstein <i>et al.</i> (2005)
APSIM	Shelter-belts for agroforestry; Even-age, single species plantations	Low	RUE	Detailed	Detailed, CERES-based	Fixed patterns	Daily	<i>Eucalyptus argophloia</i> <i>Eucalyptus grandis</i>	Huth <i>et al.</i> (2001) Huth <i>et al.</i> (2003)

HyPAR	Agroforestry	Low	BL	Detailed, 15-layer	Not included	Fixed patterns	Daily	Eucalypts, Leuceana, Oil palm	Mobbs <i>et al.</i> (1998) Cannel <i>et al.</i> (1998)
WaNuLCAS	Agroforestry systems	Low	RUE	Detailed	Detailed, Century-based, four layers	Fixed patterns	Daily	<i>Eucalyptus grandis</i> <i>Hevea brasiliensis</i> <i>Sesbania</i> <i>Peltophorum</i> <i>Gliricidia</i> <i>Grevilla robusta</i> <i>Cassia spectabilis</i>	van Noordwijk and Lusiana (1999) Radersma <i>et al.</i> (2005) Pinto <i>et al.</i> (2005)
Hybrid	Mixed, natural ecosystem	Low	BL	Simple, one layer	Detailed, one layer	Fixed patterns	Grass daily Trees annually	Tropical broadleaves	Freind <i>et al.</i> (1997)
ForNBM	Mixed forest	Low	MP	Detailed, one layer	Detailed, one layer	Fixed patterns	Monthly	Mixed hardwood forest	Zhu <i>et al.</i> (2003a, 2003b)
TEM	Mixed forests at regional scale	Low	MP	Simple, one layer	Simple, one layer	Fixed patterns	Monthly	Tropical and temperate forests	Raich <i>et al.</i> (1991)
TREE-BGC	Mixed forests at tree or ecosystem scales	Low	BL	Simple, one layer	Simple (proportional to C)	Fixed patterns	Daily (hydrology, photosynthesis, respiration) and yearly (growth, N cycle)	<i>Pseudotsuga menziesii</i>	Korol <i>et al.</i> (1991) Korol <i>et al.</i> (1995)

¹Photosynthesis approach as defined by Medlyn et al (2003) maximum production (MP), radiation use efficiency (RUE), big leaf (BL)

The WaNuLCAS model is another agroforestry model (van Noordwijk and Lusiana 1999). This model simulates the spatial patterns of dynamic processes associated with light, water and N, and it has been applied in a variety of situations including hedgerow-intercropping, tree fallow-crop rotation mosaics, and parkland systems (van Noordwijk and Lusiana 1999, Pinto *et al.* 2005, Radersma *et al.* 2005). This model is similar to CABALA in overall structure and level of detail, but the tree module includes only a low level of silvicultural flexibility and C allocation is via fixed patterns. Simulation of N mineralisation is based on the Century model (discussed below), but soil N dynamics have not been a focus during validations of WaNuLCAS. Of most relevance to plantation forestry is the use of this model for simulating a eucalypt-sugarcane system. This application indicated that poor simulation of microclimate in tree-crop associations was the most severe limitation of the model (Pinto *et al.* 2005). Soil N dynamics were not validated in this context. Soil-plant P dynamics were recently added to this model with some success (Radersma *et al.* 2005).

Mixed forest models: Hybrid, TREGRO-ZELIG, Raich, TREE-BGC, SINIC, ForNBM

Forest growth and yield models used by the industry and forest researchers for wood yield predictions have generally evolved from those that are highly empirical (with no depiction of above- or below-ground processes) to highly mechanistic (where these processes are included), or they adopt a hybrid approach (Peng 2000). Mechanistically, several models have been used to simulate growth and other aspects of mixed forests that are naturally regenerated with native species, but usually not as plantations. Because these forests are managed on cycles of many decades, appropriate models are commonly designed to span longer time scales than those designed for plantations, which are usually grown for cycles of only one to three decades per rotation.

The Hybrid model (Friend *et al.* 1997) was produced with the intention of representing the terrestrial biosphere in a total earth system model. A modification of the Century sub model was used to simulate soil N dynamics, and vegetation is made up of several generalised plant types. Simulation of canopy processes by this model compared favourably with that of 11 other forest production models (Medlyn *et al.* 2003). This and other mixed forest models discussed here have a low level of silvicultural flexibility and soil is represented by only one layer.

The single species (plantation) TREGRO model described above has been linked to a forest community gap succession model ZELIG (Urban *et al.* 1991) to simulate succession dynamics of a multi-species forests (Weinstein *et al.* 2005). In this application, ozone was the stress used to drive succession, and nutrients were considered non-limiting.

The ForNBM model (Zhu *et al.* 2003 a, Zhu *et al.* 2003b) is another mixed forest ecosystem model, but in contrast to others discussed here, ForNBM includes less detail on canopy processes driving growth, but more detail on nutrient cycling, below-ground processes and predicting nutrient concentrations in streams. However, this model works at a fairly coarse time-step (monthly) and includes only one soil layer. Simulation of N cycling includes the main processes, i.e. mineralisation, nitrification, uptake and leaching, that are modulated by environmental variables and organic matter quality (C:N ratio) in rather empirical representations. In contrast to most other

models reviewed here, considerable emphasis is placed on processes associated with acidification and nutrient geochemical balances, including the dynamics of base cations and protons (acidity).

Raich *et al.* (1991) described the TEM model used to simulate C and N dynamics in multi-species forests at a continental scale, but it required vegetation-type-specific parameterisations, and tuned coefficients that controlled transfers between various C and N pools. Although this model lacks the detail of many processes, it has been very widely applied at regional and global scales with climate-change (e.g. McGuire *et al.* 2000 and others, cited by Medlyn *et al.* 2003). As noted by Constable and Friend (2000), other models also have been used to simulate forest ecosystem responses to climate-change, e.g. the CARBON model (Bassow *et al.* 1990), the ECOPHYS model (Host and Isebrands 1994), and the W91 model (Webb 1991), but these models assume that nutrients are non-limiting. Although many models focus on C pools and fluxes, they include parallel N processes that allow N pools to be tracked, e.g. RothC (Paul and Polglase 2004).

TREE-BGC (Korol *et al.* 1995) was developed from a forest ecosystem model (FOREST-BGC; Running and Coughlan 1988, Running and Gower 1991) that treated the forest canopy and soil as simple uniform layers for simulating cycles of carbon, water and nitrogen. TREE_BGC included a disaggregation of stand-level estimates of photosynthesis into individual trees. Soil N dynamics is rather simply represented, because its pools are defined proportionally to C. In this model, there is no mechanistic, below-ground competition for water or N.

Most models here considered water and light use mechanistically to some degree, but N cycling and C allocation was variably represented amongst the models, and competition for N was either disregarded totally or included non-mechanistically. All models used a time-step useful for plantation scenarios, i.e. at least monthly; many worked at daily time-steps, and some at even finer time scales. Of all the models reviewed, only CABALA had a high degree of silvicultural flexibility, detailed processes for light-carbon, water, and nitrogen, daily-dynamic C allocation, and it ran on a daily time-step with several soil layers.

Nitrogen cycling and detailed soil process models

Key aspects of N cycling have been known for decades (Figure 1), and most of these processes are included with some degree of detail in the models mentioned above. Additional processes that have been elucidated more recently were not represented in most of these models, e.g. abiotic immobilisation, organic N uptake, and speciation of gaseous N losses, but significant knowledge gaps remain around these processes, and we can reasonably assume that they are of only minor importance for predicting tree growth in productive forest plantations.

Examples of models that include detailed N processes are summarised in Table 2, i.e. for the models Century, CERES, NuCM, Thornley, SINIC, LEACHM, and GLEAMS. Several others that include other aspects of biogeochemical cycling were reviewed by Homann *et al.* (2000) and Jandl (1998). Apart from these, many other

agricultural productivity, N fertiliser management, and NO₃ leaching models also capture key aspects of N cycling. These models are too numerous to mention comprehensively, but a useful review was provided by de Willigen (1991), and a few more recent examples were provided by Beier and Eckersten (1998), Fehér *et al.* (1991), Hansen *et al.* (1991), Krysanova and Haberlandt (2002), Probert and Keating (2000), Webb *et al.* (2001), Wu and McGechan (1998).

The models listed in Table 2 provide a number of commonalities and contrasts. They all simulated nitrification, fertiliser inputs, and gaseous losses, and did not simulate nitrite, organic N uptake, or abiotic immobilisation. For all other attributes, there were substantial differences amongst these models. For example, only the NuCM model explicitly included a forest floor litter layer. Four models used only one organic matter pool, compared to Century and CERES that used five and four, respectively. The models variably included water and temperature modifiers of mineralisation or nitrification, but almost all included soil chemistry and organic matter quality modifiers. The models also variably included lateral or vertical redistribution of N. Only the LEACHM model utilised the principles of solute transport to redistribute N within the soil profile.

Six of the seven models listed worked on a daily time-step; the one exception was Century, which has a monthly time-step. Of these models with a daily time-step, only four had a purpose that included inter-annual N dynamics. Of these, only CERES focused on N availability for crop growth; the other three (SINIC, LEACHM and GLEAMS) were focused on nitrate export via runoff and leaching.

Instead of predicting N mineralisation from other soil measures and climate variables, a laboratory measure of mineralisable N provides an index of soil organic matter quality that can be modified by water and temperature coefficients to predict daily rates of net N mineralisation (O'Connell and Rance 1999, Paul *et al.* 2002). These estimates are therefore site-specific, but avoid some of the complexity of more detailed mechanistic predictions. While this approach may be useful, it has not yet been tested in a more holistic forest productivity model. Predictions of net N mineralisation even by this method include a high degree of error. For example, the 95 per cent confidence limit of prediction is c. 20-40 kg N per hectare per year (ha⁻¹ year⁻¹) (Paul *et al.* 2002), which is approximately equal to the annual rate of N uptake in many plantation forests.

A limitation of many C-N cycling models may be their incomplete simulation of forest floor litter accumulations during a rotation that immobilise nutrients and modify the patterns of soil water and temperature. As this layer can be a significant source of available N and a modifier of N mineralisation rates in the underlying soil, its simplistic representation in many models is likely to distort the simulated behaviour of forest N cycling. Paul and Polglase (2004b) found that the decomposition of pine and eucalypt litter needed to be simulated with temperature and water modifiers, but the inclusion of litter chemistry was not necessarily an advantage. Corbeels *et al.* (2005a, 2005b, 2005c) also demonstrated the need to include water and temperature drivers in simulations of litter decomposition, but, in contrast, they found that litter chemistry was needed to adequately represent the C and N dynamics of the litter and soil organic matter pools when simulating multiple rotations of eucalypt plantation growth. This C-N sub model was based on C and N transformations as represented in

the daily time-step model NCSOIL (Molina *et al.* 1997), and it replaced the monthly time-step sub model Century that was previously used.

As seen in Table 2, models that focus on N outputs to streams include soil N availability modules. For example, Hong *et al.* (2005) included N dynamics in a hydrology model to simulate the inter-annual variation in stream NO₃. Simulations using this model, SINIC, reproduced most of the patterns in stream NO₃ observed over several decades. Further simulations suggested that the interactive effects of soil water and temperature on net N mineralisation were more of a determinant of stream NO₃ than atmospheric N deposition. A spatially explicit version of the model has also been used to demonstrate that factors affecting N mineralisation, uptake and leaching, which vary considerably within a catchment, need to be accounted for to accurately simulate NO₃ export (Hong *et al.* 2006a). While reasonably satisfied with the performance of SINIC, the authors suspected that the simplistic representation of soil organic matter as a stable pool may have been related to a tendency to over-estimate NO₃ export after several decades (Hong *et al.* 2005).

Some models that focus on soil chemistry and leaching processes, e.g. the LEACHN, DAISY and DSINIT2 models (Hutson and Wagonet 1991, Abrahamsen and Hansen 2000, Fehér *et al.* 1991), simulate vertical water movement using mechanistic hydraulic principles (i.e. Richard's equation), and provision can also be made for macro-pore flow (Jabro *et al.* 1995). Such models provide advantages at small time (daily) and spatial (soil core) scales, but the overall advantage for longer term and broader spatial scales is not clear, because much simpler models have also performed adequately under these conditions (e.g. Hong *et al.* 2006b, Webb *et al.* 2001, Kysanova and Haberlandt 2002). Others have also chosen simplicity over complexity. For example, Friend *et al.* (1997) considered three soil N sub models for inclusion in the Hybrid model. They thought the Thornley and Verberne (1989) model placed too much emphasis on microbial kinetics, and that the Raich *et al.* (1991) model required too many plant-species-specific parameters. Instead, they chose to use the Century model (Parton *et al.* 1993). If complexity is desired, organic N uptake could be one consideration. For example, the SOILN model (Beier and Eckersten 1998) includes many of the N pools and fluxes described in the models above, and in addition it includes an option for organic N uptake from dead plant material in the form of amino acids.

Table 2. Summary of soil processes in selected N models applied to forest ecosystems

Model	Century	CERES	NuCM	Thornley	SINIC	LEACHM	GLEAMS
Purpose	Century and decadal soil C-N dynamics; N availability for ecosystem; regional ecosystem scale	Inter-annual soil C-N dynamics; N availability for crop growth; paddock scale	Annual-decadal forest nutrient cycling responses to atmospheric deposition; stand scale	Century and decadal plantation C-N dynamics; stand scale	Inter-annual nitrate export; catchment scale	Inter-annual nitrate export; plot scale	Inter-annual nitrate export; plot scale
Litter layer	N ¹	N	Y	N	N	U	U
Multiple soil layers	N	Y	Y	N	Y	Y	Y
Lateral compartments	N	N	N	N	Y	N	N
Daily time-step	N (monthly)	Y	Y	Y	Y	Y	Y
Number of organic matter (OM) pools	5	4	1	1	1	1	2
Gross or net mineralisation	Gross	Net	Net	Gross	Net	Gross	Gross
Mineralisation-nitrification driver – water	Y	Y	N	N	Y	Y	Y
Mineralisation - nitrification driver – temperature	Y	Y	N	Y	Y	Y	Y
Mineralisation - nitrification driver – chemistry	U	Y	N	N	N	Y	U
Mineralisation - nitrification driver – OM quality	Y (C:N ratio, soil texture)	Y (C compounds; protection factor; C:N ratio)	Y (C:N ratio)	Y (C:N ratio)	N	Y	Y
Nitrification	Y	Y	Y	Y	Y	Y	Y

Nitrite	N	N	N	N	N	N	U
Lateral redistribution	N	N	N	N	Y	N	N
Vertical redistribution	N	Y	Y	N	Y	Y	Y
Microbial uptake	Y	Y	N	Y	N	Y	Y
Root uptake	N (all mineral N available)	N (all mineral N available)	N (all mineral N available)	Y	N (all mineral N available)	Y	N (all mineral N available)
Mycorrhizal uptake	N	N	U	Y	N	N	N
Urea dynamics	Y	Y	U	N	N	Y	U
Fertiliser inputs	Y	Y	Y	Y	Y	Y	Y
Biological N fixation	Y	N	Y	N	N	N	Y
Below-ground litter	Y	Y	Y	Y	N	N	U
Above-ground litter	Y	Y	Y	Y	N	N	U
Gaseous losses	Y	Y	Y	Y	Y	Y	Y
Abiotic immobilisation	N	N	U	N	U	N	N
Organic N uptake	N	N	N	N	N	N	N
Solute transport theory	N	N	N	N	N	Y	N
References	Parton <i>et al.</i> (1993) Paustian <i>et al.</i> (1992) Carter <i>et al.</i> (1997) Kelly <i>et al.</i> (1997)	Goodwin and Jones (1991)	Johnson <i>et al.</i> (2000) Johnson <i>et al.</i> (1999)	Thornley and Cannell (1992) Thornley and Verbene (1989)	Hong <i>et al.</i> (2005, 2006a, 2006b)	Hutson and Wagenet (1991) Allen <i>et al.</i> (2004) Lee and Jose (2005)	Webb <i>et al.</i> (2001) Knisel <i>et al.</i> (1993) Michael <i>et al.</i> (1996)

¹ Y = yes, N = no, U = uncertain.

Integration across spatial and temporal scales is an important issue that has led to a variety of approaches. One approach offering promise for predicting nitrate export from catchments requires the output of small-scale, detailed simulations to be 'learnt' by fuzzy logic prior to its application to larger scales (Haberlandt *et al.* 2002).

Many of the listed models include most of the main points listed above, but none include the entirety. In the past, models included compromises to economise on runtime and inputs, but currently, with larger computing power and more information available on inputs, these limitations should be of less concern. Concerns remain, however, about matching modelling detail with situation-specific parameterisation, since many parameters are very difficult to measure on a site-specific basis, and many modellers justifiably want to reduce the potential for over-parameterisation by including only enough detail of relevant process to adequately meet specific modelling objectives. Whilst designing models, we need to remember that increased complexity does not always provide a better result (de Willigen 1991, Paul and Polglase 2004b), and that an adequate output does not necessarily validate all underlying components of a model. While striving to represent mechanisms, at some level in all models there will always be a degree of empiricism and the potential to obtain the right outcome for the wrong reason (Johnson *et al.* 2000).

Fertilisation with N as urea is common in plantation forestry, but current models handle urea in fairly simplistic ways. For example, any addition is assumed to be immediately dissolved and added as NH_4 to the surface soil layer without accounting for potential losses via volatilisation, which can account for more than half of the N applied under extremely adverse conditions. Adverse conditions include just enough precipitation or dew to dissolve the fertiliser granules and move them into the very surface of the soil or litter layer where the urease enzyme acts to hydrolyse urea to form NH_4 . Accompanying the release of NH_4 is the production of hydroxide ions, which raise the pH in the immediate vicinity of the granule. In alkaline environments ammonium deprotonates to form ammonia (NH_3). It will then continue to volatilise. Rates of these enzymatic and chemical processes increase with temperature, but the risk of volatilisation is reduced if enough precipitation occurs to disperse the urea and NH_4 into a greater soil volume that can better buffer soil pH changes. Hence, urea volatilisation when applied to soils is most rapid in the tropics under low rainfall conditions. Nevertheless, under these conditions in plantation forestry it is sometimes still more cost-effective to use urea than other more expensive forms of N fertiliser (based on personal observation in Brazil).

In plantation forestry, another potential complication with urea fertilisation occurs when it is applied to plantations that have already established a litter layer. Forest floor litter layers contain urease enzymes, but they have low pH buffer capacity. Under these conditions, urea volatilisation can be important even in temperate conditions (May and Carlyle 2005). Importantly, most of this volatilisation occurs during the first few days. Thus, if significant rain does not occur in this period, substantial amounts of N may be lost. In a recent study it was shown that over 45 per cent of N from urea was lost, even under conditions of relatively high rainfall (150 mm over 30 days), leading to substantially smaller (30 per cent) tree growth responses to urea compared with other forms of N fertiliser (May and Carlyle unpublished).

The models reviewed here together suggest that mechanistic modelling of N cycling suitable for forest productivity and water quality predictions could include the following aspects.

- Uptake by roots and mycorrhizae via solute transport and uptake kinetic processes
- Multiple uptake surfaces, e.g. mycorrhizae, different root cohorts, roots of competing species.
- Dynamic N concentrations in plant N components
- Several soil horizons, e.g. five, including litter and deep subsoil layers
- Daily timestep
- At least two pools of organic matter quality (active and stable)
- Water, temperature, chemistry (pH) and organic matter quality (e.g. C:N ratio, physical and chemical fractions) effects on processes
- Gross or net N mineralisation (ammonification)
- Nitrification (with intermediate nitrite production)
- Plant uptake of NH_4 and NO_3
- Vertical redistribution, including leaching of mineral N and macro-pore flow
- Urea volatilisation
- Fertiliser applications
- Below- and above-ground litter production and turnover

The first three points will be particularly important for maintaining temporal realism in the rates of NH_4 and NO_3 uptake within a soil horizon (Smethurst *et al.* 2004). In reviewing the status of N cycling models for sugarcane production, Thorburn *et al.* (2005) came to a number of similar conclusions.

Under some circumstances, a few other processes might also be important:

- Denitrification and other gaseous N production processes
- Microbial uptake of mineral N
- Lateral redistribution of mineral N
- Deep soil processes, e.g. N uptake and denitrification
- Abiotic immobilisation of mineral N (e.g. clay fixation of NH_4 , OM complexation of NO_3)
- Uptake of organic N

Below-ground nutrient competition models

Competition models in forest plantations have traditionally involved the adaptation of highly empirical growth models designed to predict wood yield (Miina and Pukkala 2002, Mason and Dzierzon 2006, Richardson *et al.* 2006). This can be achieved by an 'age-shift' or other modification of the competition-free relationship between age and wood yield that is based on some measure of competition intensity, e.g. size, biomass or coverage of competing vegetation (Mason 2006, South *et al.* 2006). One option is to derive an index of competition based on distance-to-neighbour or other measures of the amount or proximity of competing plants in the growing space of individual trees (Richardson *et al.* 2006). Other approaches modify tree growth curves by employing more explicit representations of resource availability as affected by competition. For example, the VMAN model discounts user-defined, age-dependent maximum growth

by applying modifiers for the levels of competition for water and light (Watt *et al.* 2004). Although the modifiers are applied as simple empirical factors, they are based on water budgeting and light capture processes and applied on a monthly basis. Therefore, overall model outputs by VMAN are sensitive to these processes. Such hybrid models that combine empiricism and sensitivity to environmental constraints avoid the criticism of process-based models that they are too complex and over-parameterised (Mason and Dzierzon 2006).

Below-ground competition for nutrients has been rarely considered mechanistically in forest productivity models, with only a few examples becoming available during the past decade. A simple example is provided in the large-scale dynamic vegetation model TEM-LPJ, where competition for N is considered to be implicit because soil N pools are tracked separately for each plant functional type (Pan *et al.* 2002). However, these authors noted that it would be desirable to more explicitly include competition for a common soil N resource.

An explicit representation of competition would need to consider the amounts and N uptake characteristics of each competing root type (Comerford *et al.* 1994). The only means of doing so requires the simulation of uptake surfaces (i.e. roots or mycorrhizal hyphae) that can take up N by active, enzymatic processes that are modulated by plant N status. Further, supply (movement) of N in available forms to uptake surfaces needs to be consistent with the principles of solute transport, i.e. mass flow and diffusion (Tinker and Nye 2000). These principles are not difficult to apply, as indicated by the following examples.

The mechanistic principles for modelling nutrient uptake by competing root systems were first described by Nye and Tinker (1977; recently up-dated as Tinker and Nye 2000), which led to the COMP8 model that could also be used for single-species simulations (Smethurst *et al.* 1993). In the interim, a different single-species model called UPTAKE was also developed (Barber and Cushmann 1981, Barber 1995). UPTAKE employed a numerical solution to solve the equations for estimating the nutrient concentration at an average root surface, and it is still used as an accurate standard for comparison with other models. Although COMP8 employed simpler and quicker analytical approximations of these equations, an approach that has proven to be adequate, it still had to use a numerical solution to determine the no-transfer-boundary between two roots that could then be used to define the soil volume available to each type of root. Some variations to these approaches have also been suggested by other authors (e.g. Reginato and Tarzia 2002, Yanai 1994).

The UPTAKE and COMP8 models can be seen as single soil compartment sub models suitable for inclusion in ecosystem models that grow plants and cycle nutrients and water, because root growth, water content and mineral N concentrations need to be defined as inputs for each soil compartment to be modelled. There are three examples where these models have been included in forest production models, and two of these include the option of competing species.

Solute transport principles as modelled by Yanai (1994) were included in a version of TREGRO (Weinstein *et al.* 1991), but their application to nutritional issues seems to have been limited to a simulation of magnesium-ozone interactions in *Pinus*

ponderosa and *Picea rubens* (Weinstein and Yanai 1994), and inter-specific competition was not a simulation option.

The COMP8 model, which simulated competition, forms the basis of the SSAND (soil supply and nutrient demand) model (Comerford *et al.* 2006) that has shoot and root growth and soil water defined as inputs. Hence, SSAND is not a productivity model. SSAND however, includes the option of identifying fertiliser regimes that would bridge a gap between nutrient demand and nutrient supply.

The COMP8 nutrient supply and uptake equations, but only as a single-species application, were included in the PCATS model and linked to the CABALA forest productivity model to simulate simultaneous N and P uptake by a eucalypt plantation (Smethurst *et al.* 2004). Under standardised conditions, PCATS output was checked successfully for accuracy against that of the UPTAKE model. Plantation growth and N and P content was adequately simulated across the range of fertiliser treatments for a few years, but later under-predictions of biomass developed because simulation-fixed values of nutrient concentrations in most plant tissues did not match known decreases with age. Whilst these simulations allowed us to identify several aspects of the CABALA-PCATS linked model system that needed improvement, they also demonstrated that the mechanistic description of nutrient supply and uptake in a forest productivity model was attainable with current knowledge and computing systems.

One concern about mechanistic simulations of below-ground processes that included competition has been the complexity and computing power required for these simulations. This concern was allayed to some degree when it was shown that a three year CABALA-PCATS simulation took only 30 s on a 2.4 gigahertz, Pentium-4, Windows-based computer (Smethurst *et al.* 2004), but this simulation was for only one species and did not include competition for light and water. Therefore, the logical next step for mechanistic modelling of plantation growth that accounts for inter-specific competition will be to simulate light, water and N use by two competing species. This advance will require more complexity and computing power than has been used previously, but recent advances in computing power will probably allow these processes to be included with acceptable run-times.

Conclusions

Stand-level simulations of forest productivity and N cycling that include competition would benefit from the following attributes, all of which are not included in any current model:

- Uptake by competing species via solute transport theory using multiple uptake surfaces, e.g. mycorrhizae, different root cohorts, roots of competing species
- Detailed forest floor C-N dynamics
- Urea volatilisation, including forest floor interactions
- Denitrification
- Ammonium leaching
- Dynamic N concentrations in plant N components
- Multiple soil layers and deep soil processes, i.e. N uptake and denitrification

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References

- Abrahamsen P, Hansen S (2000) Daisy: an open soil-crop-atmosphere system model. *Environmental Modelling and Software* **15**, 313-330
- Allen SC, Jose S, Nair PKR, Brecke BJ, Nkedi-Kizza P, Ramsey CL (2004) Safety-net role of tree roots: evidence from a pecan (*Carya illinoensis* K, Koch)-cotton (*Gossypium hirsutum* L.) alley cropping system in the southern United States. *Forest Ecology and Management* **192**, 395-407.
- Almeida AC, Landsberg JJ, Sands PJ, Ambrogi MS, Fonseca SB, Barddal SM, Bertolucci FL (2004) Needs and opportunities for using a process-based productivity model as a practical tool in *Eucalyptus* plantations. *Forest Ecology and Management* **193**, 167-177.
- Barber SA (1995) 'Soil Nutrient Bioavailability.' (Wiley & Sons: New York, USA)
- Barber SA, Cushman JH (1981) Nitrogen uptake model for agronomic crops. In 'Modelling Waste-Water Renovation'. (Ed IK Iskandar) pp. 382-409. (Wiley: New York)
- Bassow SL, Ford ED, Keister AR (1990) A critique of carbon-based tree growth models. In 'Process Modelling of Forest growth Responses to Environmental Stress'. (Eds Dixon RK, Meldahl RS, Ruark GA, Warren WG) pp. 50-57. (Timber Press: Portland, Oregon, USA)
- Battaglia M, Sands P (1998) Process-based forest productivity models and their application in forest management. *Forest Ecology and Management* **102**, 13-32.
- Battaglia M, Sands P, White D, Mummery D (2004) CABALA: a linked carbon, water and nitrogen model for forest growth for silvicultural decision support. *Forest Ecology and Management* **193**, 251-282.
- Beier C, Eckersten H (1998) Modelling the effects of nitrogen addition on soil nitrogen status and nitrogen uptake in a Norway spruce stand in Denmark. *Environmental pollution* **102**, S1:409-414.
- Bradley RG, Crout NMJ (1994) 'PARCH-User Guide.' (Tropical Crops Research Unit: University of Nottingham, Sutton Bonnington, Leicestershire, UK)
- Brady NC (1990) 'The Nature and Properties of Soils 10th Edition.' (MacMillan: New York)
- Cannell MGR, Mobbs DC, Lawson GJ (1998) Complementarities of light and water use in tropical agroforests II. Modelled theoretical tree production and potential crop yield in arid to humid climates. *Forest Ecology and Management* **102**, 275-282.
- Carlyle JC (1986) Nitrogen cycling in forested ecosystems. *Forestry Abstracts* **47**, 307-326.
- Carter MR, Parton WJ, Rowland IC, Schultz JE, Steed GR (1993) Simulation of soil organic matter and nitrogen changes in cereal and pasture systems of southern Australia. *Australian Journal of Soil Research* **31**, 481-491.
- Chen CW, Dean JD, Gherini SA, Goldstein RA (1982) Acid rain model – hydrologic module. *Journal of Environmental Engineering ASCE* **108**, EE3:455-472.

- Chen CW, Tsai WT, Gomez LE (1994) Modelling responses of Ponderosa pine to interacting stresses of ozone and drought. *Forest Science* **40**, 267-288.
- Chen CW, Tsai WT, Lucier AA (1998) A model of air-tree-soil system for ozone impact analysis. *Ecological Modelling* **111**, 207-222.
- Comerford NB, Cropper Jr. WP, Li H, Smethurst PJ, Van Rees KCJ, Jokela EJ, Adégbidi H, Barros NF (2006) Soil supply and nutrient demand (SSAND): A general nutrient uptake model and an example of its application to forest management. *Canadian Journal of Soil Research* **86**, 665-673.
- Comerford NB, Smethurst PJ, Escamilla J (1994) Nutrient uptake by absorbing surfaces of root systems of trees. *New Zealand Journal of Forestry Science* **24**, 195-212.
- Constable JVH, Friend AL (2000) Suitability of processed-based tree growth models for addressing tree response to climate change. *Environmental Pollution* **110**, 47-59.
- Corbeels M, McMurtrie RE, Pepper DA, O'Connell AM (2005a) A process-based model of nitrogen cycling in forest plantations Part I. Structure, calibration and analysis of the decomposition model. *Ecological Modelling* **187**, 426-448.
- Corbeels M, McMurtrie RE, Pepper DA, O'Connell AM (2005b) A process-based model of nitrogen cycling in forest plantations Part II. Simulating growth and nitrogen mineralisation of *Eucalyptus globulus* plantations in south-eastern Australia. *Ecological Modelling* **187**, 449-474.
- Corbeels M, McMurtrie RE, Pepper DA, Mendham DS, Grove TS, O'Connell AM (2005c) Long-term changes in productivity of eucalypt plantations under different harvest residue and nitrogen management practices: a modelling analysis. *Forest Ecology and Management* **217**, 1-18.
- Dalal RC, Weston EJ, Strong WM, Probert ME, Lehane KJ, Cooper JE, King AJ, Holmes CJ (2004) Sustaining productivity of a Vertosol at Warra, Queensland, with fertilisers, no-tillage or legumes. 8. Effect of duration of lucerne ley on soil nitrogen and water, wheat yield and protein. *Australian Journal of Experimental Agriculture* **44**, 1013-1024.
- de Willigen P (1991) Nitrogen turnover in the soil-crop system; comparison of fourteen simulation models. *Fertilizer Research* **27**, 141-149.
- Esprey LJ, Sands PJ, Smith CW (2004) Understanding 3-PG using a sensitivity analysis. *Forest Ecology and Management* **193**, 235-250.
- Fehér J, van Genuchten MT, Kienitz G, Németh T, Biczók G, Kovács GJ (1991) DISNIT2, a root zone water and nitrogen management model. In 'Hydrological Interactions Between Atmosphere, Soil and Vegetation'. Proceedings of the Vienna Symposium, IAHS Publ. no. **204**, pp. 197-205. August 1991.
- Foereid B, Bro R, Mogensen VO, Porter JR (2002) Effects of windbreak strips of willow coppice – modelling and field experiment on barley in Denmark. *Agriculture, Ecosystems and Environment* **93**, 25-32.
- Friend AD, Stevens AK, Knox RG, Cannell MGR (1997) A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). *Ecological Modelling* **95**, 249-287.
- Gherini SA, Mok L, Hudson RJM, Davis GF, Chen CW, Goldstein RA (1985) The ILWAS model: formulation and application. *Water, Air, Soil Pollution* **26**, 425-459.

- Goodwin DC, Jones CA (1991) Nitrogen dynamics in soil-plant systems. In 'Modeling Plant and Soil Systems.' (Eds JH Hanks, JT Ritchie) ASA-CSSA-SSSA, Agronomy Series 31. pp. 287-321.
- Haberlandt U, Krysanova V, Bárdossy A (2002) Assessment of nitrogen leaching from arable land in large river basins Part II. Regionalisation using fuzzy rule based modelling. *Ecological Modelling* **150**, 277-294.
- Hansen S, Jensen HE, Nielsen NE, Svendsen H (1991) Simulation of nitrogen dynamics and biomass production in winter wheat using the Danish simulation model DAISY. *Fertilizer Research* **27**, 245-259.
- Homann PS, McKane RB, Sollins P (2000) Belowground processes in forest-ecosystem biogeochemical simulation models. *Forest Ecology and Management* **138**, 3-18.
- Hong B, Swaney DP, Woodbury PB, Weinstein DA (2005) Long-term nitrate export pattern, from Hubbard Brook Watershed 6, driven by climatic variation. *Water, Air, and Soil Pollution* **160**, 293-326.
- Hong B, Swaney DP, Weinstein DA (2006a) Simulating spatial nitrogen dynamics in a forested reference watershed, Hubbard Brook Watershed 6, New Hampshire, USA. *Landscape Ecology* **21**, 195-211.
- Hong B, Weinstein DA, Swaney DP (2006b) Assessment of ozone effects on nitrate export from Hubbard Brook Watershed 6. *Environmental Pollution* **141**, 8-21.
- Host GE, Isebrands JG (1994) An interregional validation of ECOPHYS, a growth process model of juvenile poplar clones. *Tree Physiology* **14**, 933-945.
- Huth NI, Carberry PS, Poulton PL, Brennan LE, Keating BA (2003) A framework for simulating agroforestry options for the low rainfall areas of Australia using APSIM. *European Journal of Agronomy* **18**, 171-185.
- Huth NI, Snow VO, Keating BA (2001) Integrating a forest modelling capability into an agricultural production systems modelling environment - current applications and future possibilities. In 'Modelling and Simulation'. Proceedings of the International Congress. pp. 1895-1900. (Australian National University: Canberra, Australia)
- Hutson JL, Wagonet RJ (1991) Simulating nitrogen dynamics in soils using a deterministic model. *Soil Use and Management* **7**, 74-78.
- Jabro JD, Toth JD, Dou Z, Fox RH, Fritton DD (1995) Evaluation of nitrogen version of LEACHM for predicting nitrate leaching. *Soil Science* **160**, 209-217.
- Jandl R (1998) Modelling processes in forest soils – problems, simplification and caveats. *Ecological Engineering* **10**, 33-51.
- Johnson DW (1999) Simulated nitrogen cycling response to elevated CO₂ in *Pinus taeda* and mixed deciduous forests. *Tree Physiology* **19**, 321-327.
- Johnson DW, Sogn T, Kvindesland S (2000) The nutrient cycling model: lessons learned. *Forest Ecology and Management* **138**, 91-106.
- Keating BA, Carberry PS, Robertson MJ (1999) Simulating N fertiliser response I low-input farming systems 2. Effects of weed competition. In 'Modelling Cropping Systems'. Proceedings of the International Symposium. APSIM Publication **564**.
- Kelly RH, Parton WJ, Crocker GJ, Grace PR, Klír J, Körschens M, Poulton PR, Richter DD (1997) Simulating trends in soil organic carbon in long-term experiments using the Century model. *Geoderma* **81**, 75-90.
- Knisel WG (1993) GLEAMS: Groundwater Loading Effects of Agricultural Management Systems, version 2.10. Publication Number 5. (Coastal plain

- Experiment Station, Biological and Agricultural Engineering Department: University of Georgia, USA)
- Korol RL, Running SW, Milner KS (1995) Incorporating inter tree competition into an ecosystem model. *Canadian Journal of Forest Research* **25**, 413-424.
- Korol RL, Running SW, Milner KS, Hunt ER (1991) Testing a mechanistic carbon balance model against observed tree growth. *Canadian Journal of Forest Research* **21**, 1098-1105.
- Krysanova V, Haberlandt U (2002) Assessment of nitrogen leaching from arable land in large river basins Part I. Simulation experiments using a process-based model. *Ecological Modelling* **150**, 255-275.
- Landsberg JJ, Waring RH (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management* **95**, 209-228.
- Lee KH, Jose S (2005) Nitrate leaching in cottonwood and loblolly pine biomass plantations along a nitrogen fertilization gradient. *Agriculture, Ecosystems and Environment* **105**, 615-623.
- Little KM, Willoughby I, Wagner RG, Adams P, Frochot H, Gava J, Gous S, Lautenschlager RA, Örlander G, Sankaran KV, Wei RP (2006) Towards reduced herbicide use in forest vegetation management. *Southern African Forestry Journal* **207**, 63-79.
- Mason EG (2006) Interactions between influences of genotype and grass competition on growth and wood stiffness of juvenile Radiata pine in a summer-dry environment. *Canadian Journal of Forest Research* **36**, 2,454-2,463.
- Mason EG, Dzierzon H (2006) Applications of modelling to vegetation management. *Canadian Journal of Forest Research* **36**, 2,505-2,514.
- May BM, Carlyle CJ (2005) Nitrogen volatilisation from urea fertiliser in mid-rotation *Pinus radiata* plantations in south-eastern Australia. *Australian Forestry* **68**, 20-26.
- McGuire AD, Clein JS, Melillo JM, Kicklighter DW, Meier RA, Vorosmarty CJ, Serreze MC (2000) Modelling carbon responses of tundra ecosystems to historical and projected climate: sensitivity of pan-Arctic carbon storage to temporal and spatial variation in climate. *Global Change Biology* **6**, 141-159.
- Medlyn B, Barrett D, Landsberg J, Sands P, Clement R (2003) Conversion of canopy intercepted radiation to photosynthate: review of modelling approaches for regional scales. *Functional Plant Biology* **30**, 153-169.
- Michael JL, Smith MC, Knisel WG, Neary DG, Fowler WP, Turton DJ (1996) Using a hydrological model to determine environmentally safer windows for herbicide application. *New Zealand Journal of Forestry Science* **26**, 288-297.
- Miina J, Pukkala T (2002) Application of ecological field theory in distance-dependent growth modelling. *Forest Ecology and Management* **161**, 101-107.
- Mobbs DC, Cannell MGR, Crout NMJ, Lawson GJ, Friend AD, Arah J (1998) Complementarity of light and water use in tropical agroforests I. Theoretical model outline, performance and sensitivity. *Forest Ecology and Management* **102**, 259-274.
- Monila JAE, Crocker GJ, Grace PR, Klír J, Körschens M, Poulton PR, Richter DD (1997) Simulating trends in soil organic carbon in long-term experiments using the NCSOIL and NCSWAP models. *Geoderma* **81**, 91-107.
- Nye PH, Tinker PB (1977) 'Solute Movement in the Soil-Root System.' (Blackwell Scientific: Oxford, UK)

- O'Connell AM, Rance SJ (1999) Predicting nitrogen supply in plantation eucalypt forests. *Soil Biology and Biochemistry* **31**, 1,943-1,951.
- Pan Y, McGuire AD, Melillo JM, Kocklighter DW, Sitch S, Colin PI (2002) A biogeochemistry-based dynamic vegetation model and its application along a moisture gradient in the continental United States. *Journal of Vegetation Science* **13**, 369-382.
- Parton WJ, Scurlock JMO, Ojima DS, Gilmanov TG, Scholes RJ, Schimel DS, Kirchner T, Menaut J-C, Seastedt T, Garcia Moya E, Kamnalrut A, Kinyamario JI (1993) Observations and modelling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles* **7**, 785-809.
- Paul KI, Polglase PJ (2004a) Calibration of the RothC model to turnover of soil carbon under eucalypt and pines. *Australian Journal of Soil Research* **40**, 1,011-1,026.
- Paul KI, Polglase PJ (2004b) Prediction of decomposition of litter under eucalypts and pines using the FullCAM model. *Forest Ecology and Management* **191**, 73-92.
- Paul KI, Polglase PJ, O'Connell AM, Carlyle JC, Smethurst PJ, Khanna PK (2002) Soil nitrogen availability predictor (SNAP): A simple model for predicting mineralisation of nitrogen in forest soils. *Australian Journal of Soil Research* **40**, 1,011-1,026.
- Paustian K, Parton WJ, Persson J (1992) Modelling soil organic matter in organic-amended and nitrogen-fertilized long-term plots. *Soil Science Society of America Journal* **56**, 476-488.
- Peng C (2000) Growth and yield models for uneven-aged stands: past, present and future. *Forest Ecology and Management* **132**, 259-279.
- Pinto LFG, Bernardes MS, van Noordwijk M, Pereira AR, Lusiana B, Mulia R (2005) Simulation of agroforestry systems with sugarcane in Piracicaba, Brazil. *Agricultural Systems* **86**, 275-292.
- Probert ME, Dimes JP, Keating BA, Dalal RC, Strong WM (1998) APSIM's water and nitrogen modules and simulation of the dynamics of water and nitrogen in fallow systems. *Agricultural Systems* **56**, 1-28.
- Probert ME, Keating BA (2000) What soil constraints should be included in crop and forest models? *Agriculture, Ecosystems and Environment* **82**, 273-281.
- Qi X, Mize CW, Batchelor WD, Takle ES, Litvina IV (2001) SBELTS: A model of soybean production under tree shelter. *Agroforestry Systems* **52**, 53-61.
- Radersma S, Lusiana van Noordwijk M (2005) Simulation of soil drying induced phosphorus deficiency and phosphorus mobilization as determinants of maize growth near tree lines on a Ferralsol. *Field Crops Research* **91**, 171-184.
- Raich JW, Rastetter EB, Melillo JM, Kicklighter DW, Steudler PA, Peterson BJ, Grace AL, Moore III B, Vörösmarty CJ (1991) Potential net primary productivity in south America: application of a global model. *Ecological Applications* **1**, 399-429.
- Reginato JC, Tarzia DA (2002) An alternative formula to compute the nutrient uptake for roots. *Communication in Soil Science and Plant Analyses* **33**, 821-830.
- Richardson B, Watt MS, Mason EG, Kriticos DJ (2006) Advances in modelling and decision support systems for vegetation management in young forest plantations. *Forestry* **79**, 29-42.
- Running SW, Coughlan JC (1988) A general model of forest ecosystem processes for regional applications I. Hydrological balance, canopy gas exchange and primary production processes. *Ecological Modelling* **42**, 125-154.

- Running SW, Gower ST (1991) FOREST-BGC, A general model of forest ecosystem processes for regional applications. II. Dynamic Carbon allocation and nitrogen budgets. *Tree Physiology* **9**, 147-160.
- Sands PJ, Landsberg JJ (2002) Parameterisation of 3-PG for plantation grown *Eucalyptus globulus*. *Forest Ecology and Management* **163**, 273-292.
- Smethurst PJ, Comerford NB (1993) Simulating nutrient uptake by single or competing and contrasting root systems. *Soil Science Society of America Journal* **57**, 1,361-1,367.
- Smethurst P, Mendham D, Battaglia M, Misra R (2004) Simultaneous prediction of nitrogen and phosphorus dynamics in a *Eucalyptus nitens* plantation using linked CABALA and PCATS models. In 'Eucalyptus in a Changing World' Proceedings of the IUFRO Conference. pp.565-568. (Aveiro, Portugal) 11-15 Oct. 2004.
- South DB, Miller JH, Kimberley MO, Vanderschaaf CL (2006) Determining productivity gains from herbaceous vegetation management with 'age-shift' calculations. *Forestry* **79**, 43-56.
- Snow VO, Smith CJ, Polglase PJ, Probert ME (1999) Nitrogen dynamics in a eucalypt plantation irrigated with sewage effluent or bore water. *Australian Journal of Soil Research* **37**, 527-544.
- Stape JL, Binkley D, Jacob WS, Takahashi ENA (2006) Twin-plot approach to determine nutrient limitation and potential productivity in *Eucalyptus* plantations at landscape scales in Brazil. *Forest Ecology and Management* **223**:358-362.
- Thorburn PJ, Meier EA, Probert ME (2005) Modelling nitrogen dynamics in sugarcane systems: recent advances and applications. *Field Crops Research* **92**, 337-351.
- Thornley JHM, Cannell MGR (1992) Nitrogen relations in a forest plantation-soil organic matter ecosystem model. *Annals of Botany* **70**, 137-151.
- Thornley JHM, Verberne ELJ (1989) A model of nitrogen flows in grassland. *Plant, Cell and Environment* **12**, 863-886.
- Tiktak A, van Grinsven HJM (1995) Review of sixteen forest-soil-atmosphere models. *Ecological Modelling* **83**, 35-53.
- Tinker PB, Nye PH (2000) 'Solute Movement in the Rhizosphere.' (Oxford University Press: Oxford, England)
- Tisdale SL, Nelson WL, Beaton JD (1990) 'Soil Fertility and Fertilizers 4th Edition.' (MacMillan: New York)
- Urban DL, Bonan GB, Smith TM, Shugart HH (1991) Spatial applications of gap models. *Forest Ecology and Management* **42**, 95-110.
- van Noordwijk M, Lusiana B (1999) WaNuLCAS, a model of water, nutrient and light capture in agroforestry systems. *Agroforestry Systems* **43**, 217-242.
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* **7**, 737-750.
- Watt MS, Kimberley MO, Richardson B, Whitehead D, Mason EG (2004) Testing a juvenile tree growth model sensitive to competition from weeds, using *Pinus radiata* at two contrasting sites in New Zealand. *Canadian Journal of Forest Research* **34**, 1,985-1,992.
- Webb WL (1991) Atmospheric CO₂, climate change, and tree growth: a process model I. Model structure. *Ecological Modelling* **56**, 81-107.

- Webb TH, Lilburne LR, Francis GS (2001) Validation of the GLEAMS simulation model for estimating net nitrogen mineralisation and nitrate leaching under cropping in Canterbury, New Zealand. *Australian Journal of Soil Research* **39**, 1,015-1,025.
- Weinstein DA, Beloin RM, Yanai RD (1991) Modeling changes in red spruce carbon balance and allocation in response to interacting ozone and nutrient stresses. *Tree Physiology* **9**, 127-146.
- Weinstein DA, Laurence JA, Retzlaff WA, Kern JS, Lee EH, Hogsett WE, Weber J (2005) Predicting the effects of tropospheric ozone on regional productivity of ponderosa pine and white fir. *Forest Ecology and Management* **205**, 73-89.
- Weinstein DA, Yanai RD (1994) Integrating the effects of simultaneous multiple stresses on plants using the simulation model TREGRO. *Journal of Environmental Quality* **23**, 418-428.
- Wu L, McGechan MB (1998) A review of carbon and nitrogen processes in four soil nitrogen dynamics models. *Journal of Agricultural Engineering Research* **69**, 279-305.
- Yanai RD (1994) A steady-state model of nutrient uptake accounting for newly grown roots. *Soil Science Society of America Journal* **58**, 1,562-1,571.
- Zhu Z, Arp PA, Meng F, Bourque CP-A, Foster NW (2003a) A forest nutrient cycling and biomass model (ForNBM) based on year-round, monthly weather conditions, part I: assumption, structure and processing. *Ecological Modelling* **169**, 347-360.
- Zhu Z, Arp PA, Meng F, Bourque CP-A, Foster NW (2003b) A forest nutrient cycling and biomass model (ForNBM) based on year-round, monthly weather conditions, part II: calibration, verification, and application. *Ecological Modelling* **170**, 13-27.