CenW: A Generic Forest Growth Model

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Abstract

CenW is a comprehensive forest growth model based on linked flows of carbon, energy, nutrients and water in trees and the soil. Overall model function depends on physiological plant factors, the size of plant pools, such as foliage mass, environmental factors, such as temperature and rainfall, and the total amount and turn-over rates of soil organic matter, which drives the mineralisation of soil organic nitrogen.

The model was validated against experimental data obtained for *Pinus radiata* from the Biology of Forest Growth (BFG) site near Canberra, Australia. The BFG experiment was conducted over five years, and included controls and treatments with irrigation and/ or fertiliser addition. Growth rates across treatments ranged about 2½ -fold. The model realistically simulated water use, foliage production and turn-over rates, foliar nitrogen dynamics, wood production and stand architecture over a wide range in response to variations in the availability of water and nitrogen from experimental treatments and natural variations in rainfall. The model can be used to simulate the effects of silvicultural treatments, such as stand thinning or fertiliser addition, or to assess the growth effect of changes in environmental conditions.

Introduction

In Australia, growth rates of *Pinus radiata* can vary at least 5-fold across sites (e.g. Turvey *et al.* 1990, Grierson *et al.* 1992). Much of this variation is attributable to differences in water and/ or nutrient availability, and there can be important interactions between these limitations. Under severely water limited conditions, smaller nutrient additions are needed to satisfy tree

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requirements than under conditions with greater water availability. In commercial plantations, attempts are made to schedule fertiliser additions and other silvicultural manipulations to optimise financial returns from these management efforts.

Forest growth models are important tools to guide forest management, to maintain forest inventories over large areas and to assess the impact of climate variability and change. They are also important scientific tools to understand the major factors that control forest structure and function in response to both internal and external factors. In the past, forest managers had to rely on empirical models that were based on observations of forest growth in existing forests in response to age or size, stocking and site characteristics. However, these models cannot respond to climatic factors and can therefore simulate neither short-term variation in growth rates in response to changing climatic conditions, such as annual rainfall, nor the longer-term effects of climate change, including increased CO_2 concentration, on forest growth. They are also not always well suited to simulate management manipulations, such as thinning or fertiliser application.

More recently, there has been growing interest in managing the biosphere for maximising carbon storage in order to mitigate against climate change. Biospheric carbon pools, such as tree components and soil organic matter interact strongly and have greatly differing turn-over times and other characteristics.

Stem wood, for example, tends to have low nutrient concentrations and may be able to accumulate over long periods, whereas foliage tends to have high nutrient concentrations, fast turn-over and an important functional role in light interception and photosynthetic carbon gain. It is not easy to capture the complex dynamics of these different pools of carbon and nutrients and their interactions.

Hence, there has been a long-standing interest in using mechanistically-based models for simulating forest growth. A range of such models has been developed (see the reviews by Ågren *et al.* 1991, Titak and van Grinsven 1995, Battaglia and Sands 1998). Ryan *et al.* (1996) comprehensively compared the leading forest growth models against the BFG (Canberra, Australia) and SWECON (Jadraas, Sweden) observational data sets. That comparison was revealing as it showed the strengths and weaknesses of the various models and the differences between them. On the whole, there was considerable disagreement between the models, and none of the models could adequately simulate the full range of observed data. Some accurately simulated some aspects of the data, but did poorly on others, or did not even include them. In particular, none of the models was able to adequately simulate the nutrient uptake characteristics at the two sites. The models that came closest to correctly simulating nutrient dynamics were poor at simulating stand growth (Ryan *et al.* 1996).

This comparison highlighted the difficulties inherent in modelling the growth of trees in complex ecosystems with a range of interacting cycles and generally incomplete information about all of them. Yet, there is still a pressing need to have models that are responsive to environmental factors and are able to integrate them into a combined growth response. The model CenW was, therefore, developed to provide a model that includes all the relevant environmental factors that affect tree growth, especially interception of radiation, CO_2 uptake, water use, and nitrogen cycling.

CenW aims at being comprehensive without becoming complex. It includes most of the factors known to be important for tree function, yet keeps the relationships between these factors as simple and transparent as possible. It also aims for

a balance between the various processes being included, with no process becoming highly intricate and modelled in great detail while other, equally important, processes would be treated in a superficial manner.

Brief Description of CenW

The model CenW (Carbon, Energy, Nutrients and Water), has been fully described and tested elsewhere (Kirschbaum 1999a), and only a brief overview will be given here. It is a generic forest growth model that simulates the fluxes of carbon and water, the interception of solar radiation and the dynamics of nutrient cycling through plant and soil organic matter pools (Fig. 1).

The model runs on a daily time step. Photosynthetic carbon gain depends on light absorption, temperature, soil water status, foliar nitrogen concentration and any foliage damage due to frost or scorching temperatures during preceding days. Respiration rate is calculated as a constant fraction of photosynthetic carbon gain.

Fixed photosynthate is used for growth, with allocation to different plant organs determined by plant nutrient status, tree height and species-specific allocation factors. It is assumed that the ratio of above- to below-ground allocation increases with foliar nitrogen concentration. Foliar nitrogen concentrations are essentially determined through the relative rates of carbon and nitrogen uptake modified by different allocation terms. It is also assumed that 25 per cent of foliar nitrogen is retranslocated and retained in the plant before litter fall.

Water use is calculated using the Penman-Monteith equation, with canopy resistance given by the inverse of stomatal conductance, which, in turn, is linked to calculated photosynthetic carbon gain. Water is lost by transpiration and soil evaporation, and water is gained by rainfall or irrigation which together determine the soil water status for the following day.

The nutrient cycle is closed through litter production by the shedding of plant parts, such as roots,
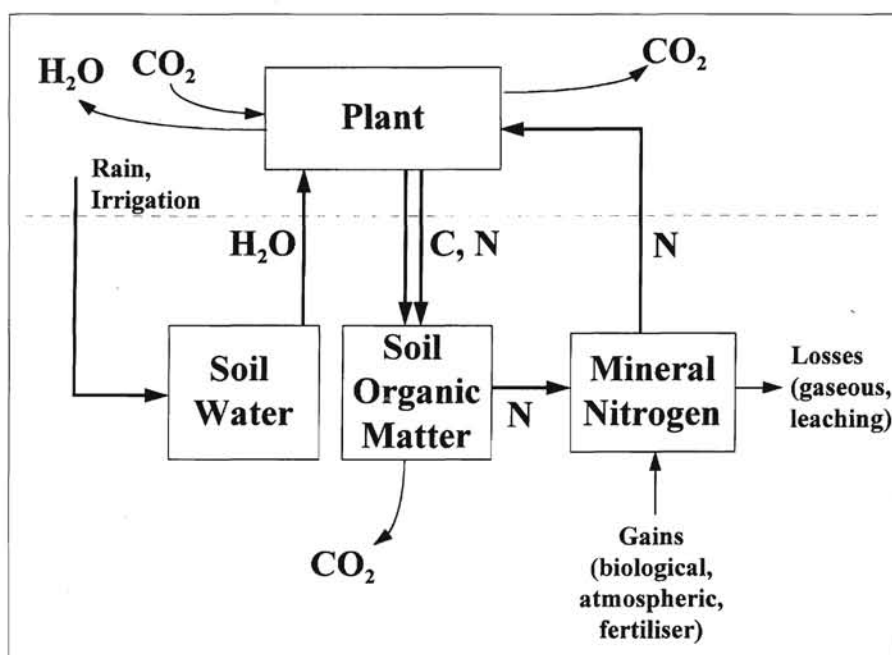

Figure 1: The basic modelling outline of CenW, showing the key pools and fluxes of carbon, nitrogen and water.

bark, branches and foliage. Litter is assumed to be produced as a constant fraction of live biomass pools. In addition, foliage is shed during drought or when canopies become too dense. Litter is then added to the organic matter pools from where carbon is eventually lost and nitrogen becomes available again as inorganic mineral nitrogen.

Nitrogen can come from atmospheric deposition, fertiliser addition or mineralisation during the decomposition of soil organic matter. Decomposition rate is determined by temperature, soil water status and soil organic matter quality in a modified formulation based on the CENTURY (Parton *et al.* 1987) model. Input litter tends to have wide a C:N ratio so that some carbon needs to be lost through decomposition before critical C:N ratios are reached in organic matter and excess nitrogen can be mineralised. The temperature dependence of organic matter decomposition is based on the equation developed by Kirschbaum (2000).

CO_2 sensitivity is calculated based on the biochemically-based model of Farquhar and co-workers (Farquhar *et al.* 1980), with the Ball-Berry formulation of stomatal

conductance (Ball *et al.* 1987) in the brief form given by Kirschbaum (1994). Leaf photosynthesis is expanded to the canopy using the algorithms of Sands (1995). Complete details of all calculations are given by Kirschbaum (1999a).

Model Testing

The model was tested against data from the Biology of Forest Growth (BFG) experiment (Benson *et al.* 1992, Raison and Myers 1992). The experiment was devised to comprehensively quantify the relevant processes affecting the growth of *P. radiata* so that differences in productivity between sites, climates and tree internal factors could be better understood. The experiment provided a wealth of information about the interactive effects between nitrogen nutrition and water availability on various plant processes and plant growth. Without irrigation, fertiliser addition resulted in only minor increases in growth, whereas growth could be considerably increased by irrigation alone (Benson *et al.* 1992, Snowdon and Benson 1992). In irrigated treatments, growth could be further increased if fertiliser was added as well.

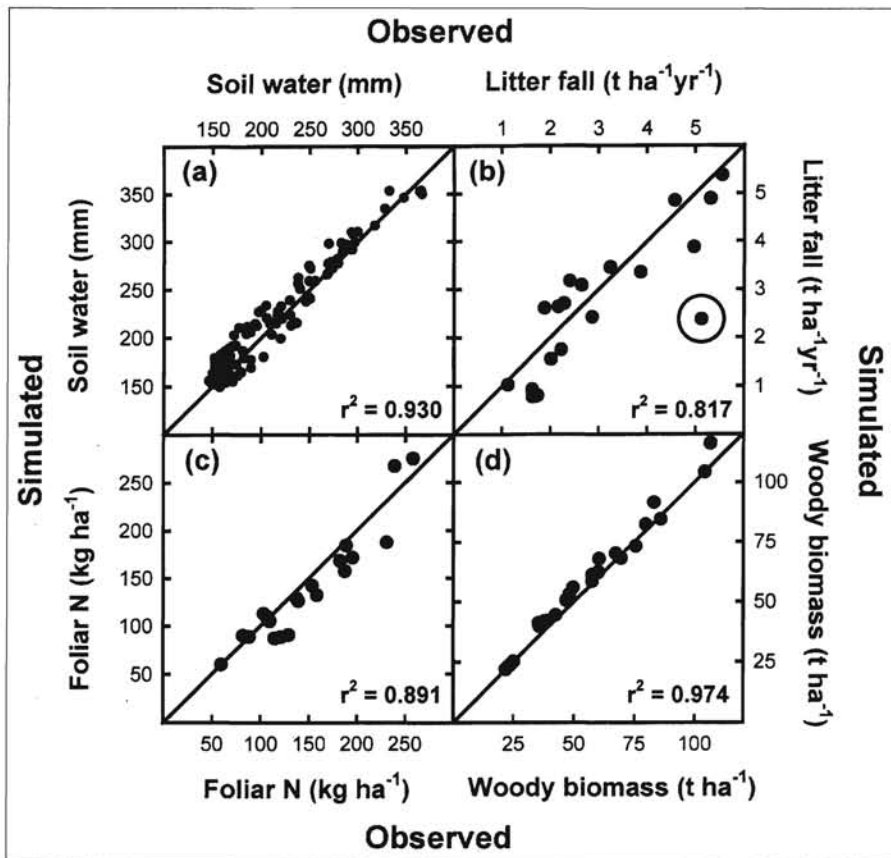Modelled soil water contents agreed closely with modelled soil

Figure 2: Observed versus modelled data. Observed data are shown on the horizontal axes, and modelled data on vertical axes. Shown are stored soil water in the Control (in a), litter fall rates (in b), foliar nitrogen amounts (in c) and total woody biomass (in d). Data in (b) to (d) are shown for all treatments and years. Solid lines in each panel are 1:1 relationships, and r^2 values in each panel give the variation explained by the 1:1 line. In Fig. 2B, the r^2-value excludes the circled point obtained at the commencement of the experimental period (see text). All data have been redrawn from Kirschbaum (1999a).

to be maintained for some years after the initial fertiliser application.

The modelling of foliar nitrogen dynamics constituted a sensitive test of the model as foliar nitrogen dynamics integrate several important plant processes. Foliar nitrogen dynamics depend on foliar biomass growth and senescence, but also on rates of nitrogen mineralisation and uptake, and conversely on the dependence of photosynthesis on foliar nitrogen concentrations.

As a final, and ultimate test, modelled woody biomass over four years and five treatments closely agreed with observations over all years and experimental treatments (Fig. 2d). These growth responses integrated the whole of all processes that contributed towards overall growth. Good correspondence was achieved in all the different treatments that were primarily affected by either water or nutrient limitations, or by inherent physiological limitations.

Silvicultural Application

The good agreement between observed and modelled responses over a wide range conditions provides the confidence to apply the model to simulate silvicultural manipulations, such as thinning or fertiliser application (Kirschbaum 1999a). The response to fertiliser application, in particular, can only be modelled once the degree of different limitations has been established. More nutrients are required by plants, and hence a greater response to fertiliser application is likely when other factors, especially water availability, are less limiting (Kirschbaum 1999a). Within a given set of limitations, the model is then able to simulate the likely response of plant growth and nutrient reserves to fertiliser addition.

Figure 3 shows growth responses and foliar nitrogen following the application of 400 kg N ha⁻¹, applied at various stand ages. These simulations were run with rainfall augmented by irrigation, which maximises the expected effect of fertiliser application. The application of fertiliser increased productivity about two-and-a-half-fold under the conditions modelled here, with similar absolute increases for fertiliser addition at different stand ages.

water contents, with no systematic bias towards consistent over- or underestimation of observed values (Fig. 2a). This included the early part of the experimental period when rainfall exceeded tree water use and soil water was at the maximum that the soil could hold. Over the next three years, rainfall was insufficient to meet transpirational demand and the soil was partly dry, with modelled tree water use gradually decreasing in a way that matched observed reductions.

Modelled litter fall agreed fairly well over the four years and five treatments (Fig. 2b). The observations spanned a five-fold range of values across all treatments and years. The magnitude of observations was well simulated for all years and treatments except in the irrigated and fertilised treatment in the first year of treatment when litter fall was exceptionally high.

This particular observation could not be reproduced with the model, and there were no readily apparent reasons for the exceptionally high observed litter fall rate observed in that year. For all other years and treatments, agreement was good, although there remained a degree of scatter which would have been partly due to measurement errors. Importantly, the overall magnitude of foliage dynamics was correctly simulated.

Modelled amounts of foliar nitrogen also closely agreed with observed values, covering both the lowest nitrogen contents in the Control and irrigated treatments and the high contents in the treatments receiving both fertiliser and irrigation (Fig. 2c). Much of the dynamics in the treatments fertilised with solid fertiliser were related to the ability of trees for luxury uptake of nitrogen which allowed high nitrogen contents
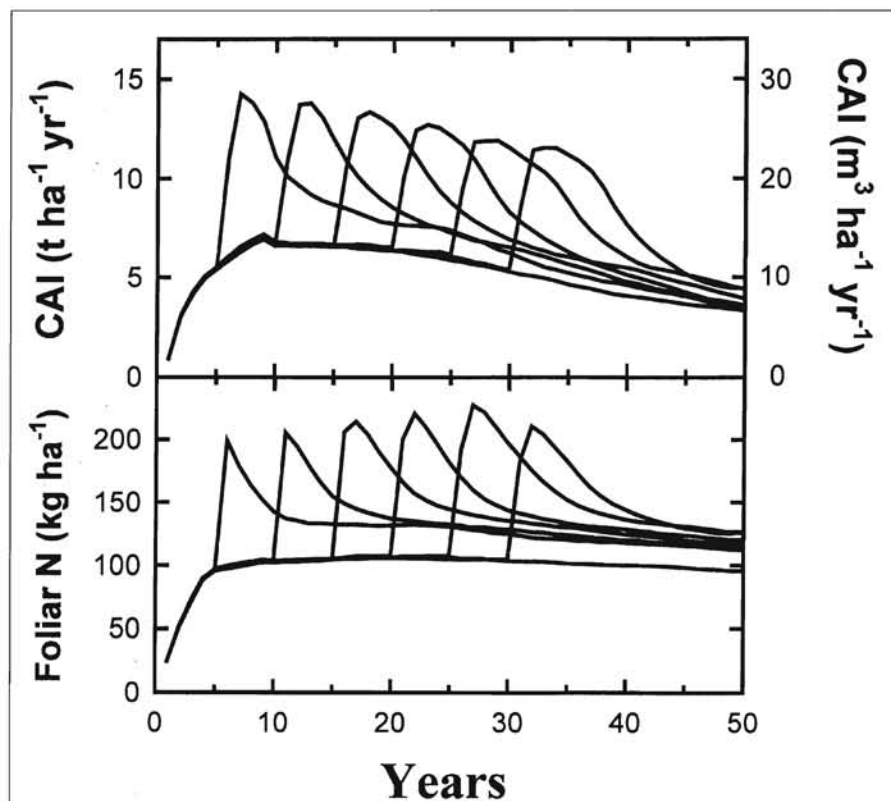
Figure 3: Modelled response to fertiliser application at different ages. The lowest curve shows the simulation with no fertiliser being added, and the other curves each describe a separate simulation, with fertiliser added at 5-yearly intervals. Data have been redrawn from Kirschbaum (1999a).

These increases were made possible by an approximate 100 kg increase in total foliar nitrogen content. Total foliar nitrogen contents remained elevated up to the end of the 50-year growth period through increases in the amount of nitrogen recycled from various pools in the system. Even when fertiliser was applied as early as at age five, it still increased foliar nitrogen by 10 kg ha^{-1} 45 years later through continued elevation of nitrogen mineralisation rates. Nitrogen is eventually lost from the system, but losses in nutrient-deficient forests systems without significant leaching tend to be small.

Conclusions

CenW was successfully able to simulate all aspects of tree growth at the BFG experimental site. This included water balance and carbon and nitrogen dynamics reflected in amounts of nitrogen in live foliage and foliage litter fall and wood production rates. Related features, such as mean stem diameters, were also simulated successfully (data not shown).

These simulations were possible with the model run completely by external driving variables, initial soil and stand conditions, standard climatic observations and silvicultural manipulations. No adjustments of plant internal parameters were required.

The model is comprehensive, including essentially all relevant pools and processes that determine forest growth under a range of natural conditions and in response to silvicultural manipulations. This comprehensiveness was achieved while keeping individual relationships as simple and transparent as possible.

The model can be used for a range of applications such as testing the impacts of climate change on forest growth (Booth *et al.* 1999, Kirschbaum 1999b), assessing the effect of silvicultural manipulations (Fig. 3) or long-term sustainability. It can also be used as a sophisticated carbon-accounting tool and for explanatory runs that help to understand the reasons for any observed plant responses (Kirschbaum 1999a).

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