

The Control Of Ecosystem Carbon Dynamics By The Linkages Between Above and Belowground Processes

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Introduction

To grow, plants need carbon, which they can fix in photosynthesis, and inorganic nutrients, which they generally obtain from the soil, such as nitrogen and phosphate. The response of plant growth to environmental variables, such as CO₂ or temperature, can be modified by the availability of these soil nutrients. Furthermore, soil nutrient availability itself can also be affected by environmental factors, such as temperature or soil moisture.

There are three elements that are closely associated with carbon in soil organic matter: nitrogen, phosphorus and sulphur. For every increase of carbon in plant biomass or soil organic matter, an amount of these elements needs to be sequestered along with carbon.

Since plant function is impaired if the nutrient to carbon ratio falls below an optimal level, the availability of these nutrients in an ecosystem can constrain the amount of carbon that can be stored.

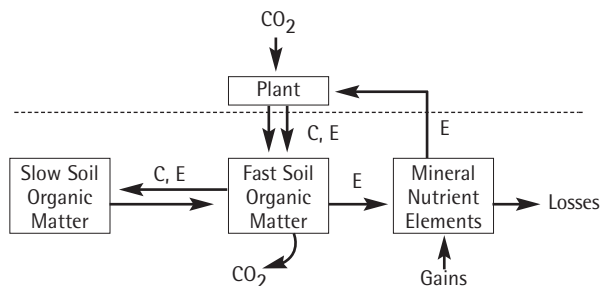


Figure 1: Diagrammatic representation of the inter-relationships between carbon and nutrient cycles. Nutrient cycles are denoted as 'E' and could represent nitrogen, phosphorus or sulphur.

Other elements, such as calcium, magnesium, iron, etc. are also important for plant performance. However, these elements are not contained in SOM. Hence, the degree of sufficiency or deficiency in an ecosystem with respect to these nutrients is independent of any loss or build-up of soil organic carbon.

However, it is not possible for organic carbon to accumulate without concomitant immobilisation of nitrogen, phosphorus and sulphur. Hence, the availability of these nutrients determines, in part, at what rate organic carbon can accumulate in any system.

Similarly, when organic carbon is lost through decomposition, additional amounts of nutrients are mineralised, and this can stimulate plant productivity in systems where nutrient availability had previously been limiting.

Nutrient availability can in both cases provide a negative feedback effect that mitigates against rapid changes in soil organic carbon. This negative feedback can, of course, only operate under conditions where productivity in the system is, indeed, limited by nutrition.

Critical Ratios

Rastetter *et al.* (1992) showed that ecosystem carbon storage can be increased only

- 1) if the total amount of nutrients in an ecosystem increases; or
- 2) if the ratio of carbon:nutrients increases within the same pools; or
- 3) if nutrients are re-allocated from pools with low carbon to nutrient ratios to pools with higher ratios.

These three possible effects on carbon storage are addressed to some further extent in the following.

1. NUTRIENT GAINS AND LOSSES

All nutrients can be lost in erosion or gained in alluvial or aeolian deposits. These rates tend to be very low unless unsustainable land-use practices cause enhanced erosion. However, even the very small exchange rates can be important

in determining ecosystem nutrient balances in the very long term. Nitrogen tends to be more mobile than phosphorus or sulphur, and it can be lost through gaseous losses after conversion to N_2O or N_2 or gained in biological nitrogen fixation. The slow rate of nutrient accumulation is probably the main reason for the observed slow build-up in soil organic matter after soils have been newly colonised by vegetation (Schlesinger 1990).

Under forest or agricultural management, large quantities of nutrients can also be added in fertilisers. Fertiliser use of phosphorus-based fertilisers in Australia has remained fairly steady over the past 20 years at about 300-400 ktP yr^{-1} . Nitrogen fertilisers were used at similar application rates until about 1990, but their use has more than doubled over the past 10 years, and in 2000, over 1 MtN yr^{-1} was applied in fertilisers.

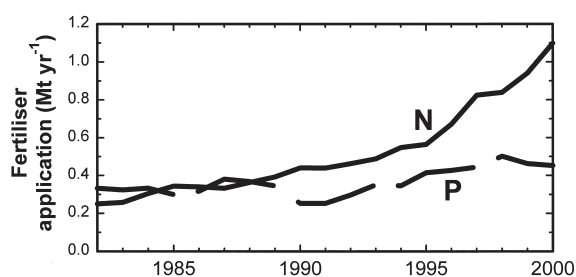


Figure 2: Annual application of nitrogen and phosphorus fertilisers in Australia (after ABARE 2001).

The increased use of nitrogen fertilisers has partly been due to a shift in agriculture from crop/pasture rotations towards greater use of the cropping phase, prompted by a fall in the wool price. The reduced use of leguminous pastures has meant a reduced input of biologically fixed nitrogen and greater reliance on industrially manufactured nitrogen. Total nitrogen input into Australia's agroecosystems has, therefore, probably changed by less than implied by the steep increase in nitrogen fertiliser use.

Nitrogen is relatively mobile, with fairly high rates of loss and gain, but an estimated large positive overall balance (Table 2). Phosphorus is relatively less mobile, and the amounts in ecosystems generally remain fairly constant. However, in the context of the movement of phosphorus in and out of the pool that can interchange with carbon in soil organic matter, the exchange with inorganically bound forms must be considered as a gain or loss from the organically exchangeable pool and that can lead to behaviour similar to that of more mobile nutrients (Kirschbaum *et al.* 1998). Sulphur is intermediate in its mobility in and out of ecosystems.

All nutrients can be lost at significant rates in the export of produce, and for phosphorus, that is considered to be the most significant loss from Australian ecosystems (Table 2). The best estimates of gains and losses of nutrients suggest a significant increase in all three elements in Australia. This implies a considerable potential for soil carbon stores to have also increased in Australia.

INPUTS	Nitrogen	Sulphur	Phosphorus
Atmos. deposition	1.15	0.77	0.08
Fertiliser	0.38 ¹	0.33	0.38
Fixed by plants ²	1.9		
TOTAL	3.4	1.1	0.46
LOSSES			
Produce export	0.42	0.05	0.06
Urban discharge	0.03	0.08	0.01
Erosion	0.02-0.1	0.01	0.01-0.03
Leaching	0.24	0.09	0
Volatilisation	0.37	0.01-0.15	0
Fire	1.2	0.12	0.004
TOTAL	2.3	0.35-0.5	0.08-0.11
BALANCE	1.1	0.6-0.75	0.35-0.38

¹ Nitrogen gain through fertiliser addition was greater in more recent years than estimated by McLaughlin *et al.* (1992, see Figure 2), but the older number is still given here for consistency with the other data in the Table, which are all estimated for the same period.

² The estimate for plant fixation can be further subdivided into pastures: 1.5 MtN yr^{-1} ; crops 0.2 MtN yr^{-1} ; forests: 0.2 MtN yr^{-1} .

Table 2: Estimated gains and losses of nutrients for the Australian continent (after McLaughlin *et al.*, 1992, and State of the Environment Advisory Council, 1996).

2. VARIABILITY IN THE CARBON : NUTRIENT RATIO

Nutrient concentrations in biomass components tend to reflect the availability of respective nutrients. Jeffreys (1999), for example, showed that both foliar and stemwood nitrogen concentrations varied up to about 2-fold with extremes in site fertility, with a strong correlation between foliar nitrogen concentration and the nitrogen concentration in 1-yr old sapwood.

This suggests that there is a degree of variability, but within fairly narrow bounds. If nutrients become more abundant because of fertilisation or enhanced mineralisation rate, C:N ratios may narrow, whereas if growth is stimulated through other processes, such as favourable weather or increasing CO_2 concentration, nutrients may become relatively less available, and C:N ratios may widen (Comins and McMurtrie 1993;

Kirschbaum *et al.* 1994, 1998; McMurtrie and Comins 1996; Kirschbaum 1999b).

It is particularly important whether C:nutrient ratios in soil organic matter can change to reflect site fertility, or whether these ratios are inherent and immutable properties of the chemical nature of humic substances in the soil.

Different C:N ratios are clearly evident in fresh litter which does reflect the nutrient status of live material despite nutrient retranslocation before senescence. There is also evidence that at least part of more resistant soil organic matter fractions are formed from recalcitrant fractions of fresh litter (Baldock *et al.* 1992). This material would presumably reflect the original C:N ratio, but the extent of shifts in C:N ratio are likely to be only slight.

3. NUTRIENT RE-ALLOCATION BETWEEN POOLS

Soil N:C ratios tend to be in the range of 1:10 to 1:20 (Post *et al.* 1985), foliar N:C ratios are typically 1:25 - 1:50, and wood N:C ratios tend to be about 1:500 to 1:1000 (Jeffreys 1999). Hence, any shift of nitrogen from the soil to wood could lead to a large increase in site carbon storage even without the input of any additional nitrogen into the system.

When trees are first established on tree-less soil, essentially all their nutrient requirements must come from the mineralisation of soil organic matter. Soil organic matter amounts are likely to decrease over the early growth period as carbon inputs in litter are only slight over the first few years of a new stand's growth. Nonetheless, for a constant site nutrient budget, site carbon storage is likely to increase substantially as nutrients are shifted from pools with narrow C:N ratios, such as SOM, to pools with wider ratios, especially wood.

In response to warming, soil organic matter is likely to be lost (Kirschbaum 1993). However, if it allows woody biomass on the site to increase, the loss of soil carbon can even lead to an increase in overall carbon storage on the site (McKane *et al.* 1997).

How Important Are The Linkages Between Above and Belowground Processes?

To assess to what extent the inclusion or omission of explicit treatment of above- to belowground processes can influence NPP and site carbon storage, the model CenW (Kirschbaum 1999a) was used and run either in its fully coupled mode, or with the internal linkages removed by keeping foliar nitrogen concentration constant. The model was then run with a 60-year sequence of observed daily weather for Canberra. The model was initialised with soil-organic matter amounts that corresponded to fairly low site fertility. Allocation factors were selected to run the model essentially as a shrub model, with no stand build-up over time so that ageing effects (Battaglia 2001) could be ignored.

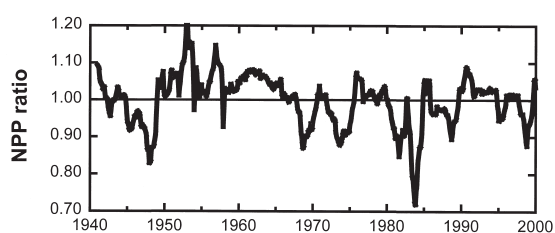


Figure 3: Ratio of two simulations of net primary production: one with and one without inclusion of the linkages between above and low-ground processes. Shown is the ratio of calculated NPP in the two simulations (with and without feed-backs). The simulations were based on the observed Canberra climate. NPP was re-calculated monthly as the NPP over the preceding 12 months.

The simulations showed that systems feed-backs can significantly alter calculated net primary production (NPP). Over the long-term, the average of the two NPP simulations was very close to 1, but there was often a 10% divergence in the ratio of the two simulations over periods of several years (Fig. 3). In seasons with good growing conditions (high rainfall), nutrient constraints prevented stands from making maximum use of the favourable climatic conditions. Conversely, in seasons with unfavourable weather, the relatively greater nutrient availability ensured a degree of compensation.

Climatic variability could also cause considerable changes in soil carbon storage (Fig. 4). Soil organic carbon storage over the sixty-year simulation showed changes in carbon storage by up

to 5tC ha^{-1} (the lower curve in the bottom panel of Fig. 4), with these changes sometimes occurring over periods of just a few years. They were mainly due to changes in litter storage and only to a lesser extent by changes in other organic matter pools.

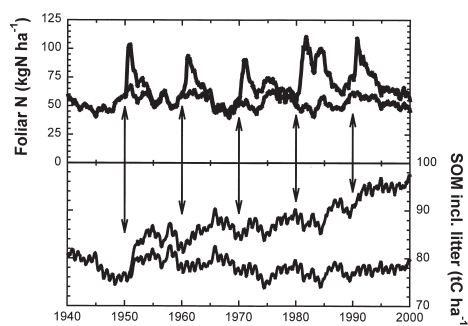


Figure 4: Simulations of the effect of fertiliser addition on foliar nitrogen contents and soil organic carbon storage (including litter). The lower curves in each panel show simulations without fertiliser addition, and the upper curves show simulations with fertiliser additions. Arrows indicate the times when 100 kgN ha^{-1} were added to the stand.

Organic carbon storage could, however, be affected greatly by the addition of fertiliser. Growth in Canberra is generally water limited so that all available water is used by stands of trees. Without deep drainage, there is only negligible leaching of nitrogen. Because the system is also nutrient limited, there is generally no significant nitrification so that gaseous losses are also small. Added nutrients are therefore generally retained in the system under the conditions modelled here.

Under those conditions, fertiliser addition could lead to significant enhancement of site carbon storage, with the addition of a total addition of 500 kgN ha^{-1} leading to enhanced soil carbon storage by more than 15 tC ha^{-1} (Fig. 4). Applied fertiliser initially enhanced foliar nitrogen contents, but that was lost again over a number of years as foliage was shed, but the intermittently enhanced productivity led to greater carbon fixation, thus greater litter fall and that led to a build-up of soil organic matter (Fig. 4).

This pattern was repeated over subsequent fertiliser additions, but from about the fourth additions onwards, the system was brought to a higher overall fertility status which was then reflected in permanently raised foliar nutrient contents.

These particular simulations gave a relatively high sensitivity to the inclusion of feed-back processes because the site was initialised as a nutrient-limited site. These feed-backs would

have played no role in systems with non-limiting nutrition. At the same time, responses could have been even more pronounced in systems less limited by water availability.

Implementation of Linkages Between Above- and Belowground Processes In Various Models

For this workshop, a number of models were reviewed. Brief descriptions of all these models have been provided by Kirschbaum *et al.* (2001). All of these simulate the flow of carbon, but not all treat nutrients as well (Table 2). Some simulate only plant-growth processes and others only soils processes. Only APSIM, CENTURY, CenW, G'Day and GRAZPLAN explicitly model the linkages between above- and belowground processes, and only the agriculturally-based models CENTURY and GRAZPLAN are regularly used with nutrients other than nitrogen as well.

	N	P	S	Above-ground		Soil
				Modelled	Set	Modelled
APSIM	Y	Y ¹	-	Y	-	Y
CENTURY	Y	Y	Y	Y	-	Y
CenW	Y	-	-	Y	-	Y
FuIICAM	Y	-	-	Y	-	Y
G'Day	Y	Y ³	Y ³	Y	-	Y
Gendec	Y ⁴	-	-	-	Y	Y
GRASP	-	-	-	Y	-	-
GRAZPLAN	Y	Y	Y	Y	-	Y
Linkages	Y	-	-	Y	-	Y
Promod	-	-	-	Y	-	-
Roth-C	-	-	-	-	Y	Y
Socrates	-	-	-	Y ⁵	Y ⁵	Y
3-PG	-	-	-	Y	-	-

¹Under development. Phosphorus has so far been implemented only for maize (M. Probert, CSIRO Tropical Agriculture, pers. comm., 2001).

²The dependence on nitrogen is the same as for Gendec.

³G'Day has been run with phosphorus and sulphur for a single application by Kirschbaum *et al.* (1998). Apart from that, the model has only been run with nitrogen.

⁴Gendec, requires nitrogen availability as an input into determining decomposition-rate constants. This needs to be supplied as a user input (K.I. Paul, CSIRO Forestry and Forest Products, pers. comm., 2001).

⁵Socrates can be run with either option as selected by users.

Table 2: Nutrients included in various models.

The models that include nutrient cycling in the whole systems generally include all relevant processes of nutrient gains and losses (Table 3), and omissions are either regarded as unimportant in those stands or could be readily included for specific model applications.

GAINS	Atmospheric deposition	Biological fixation	Fertiliser addition	Others
APSIM	Y	Y	Y	Organic sources, manure
CENTURY	Y	Y	Y	
CenW	Y	Y	Y	
G'Day	Y	Y	Y	
GRAZPLAN		Y	Y	Animal biomass, supplementary feed

LOSSES	Volatilisation	Leaching removal	Produce	Fire	Erosion
APSIM	Y	Y	Y	Y	Y
CENTURY	Y	Y	Y	Y	Y
CenW	Y	Y	Y		
G'Day	Y	Y	Y	Y	
GRAZPLAN	Y	Y	Y		

Table 3: Nitrogen gains and losses included in those models that include nitrogen cycling.

APSIM

APSIM is essentially a modelling shell, and its precise operation varies depending on the particular modules that are used in specific implementations. However, the shell has the facility to handle carbon and nitrogen in both plant and soil components, and changes in either domain will flow through to the appropriate response in the other domain.

Soil nitrogen dynamics are modelled in considerable detail, with separate simulation of ammonia and nitrate pools. Volatilisation and nitrogen losses only occur during the transformation from ammonia to nitrate. Similarly, leaching losses are restricted to those from the nitrate pool.

CENTURY

The soil modelling component of CENTURY can simulate dynamics of N, P and S in addition to carbon dynamics (Parton *et al.* 1988). Growth processes are modelled, but only in a simple implementation. While nitrogen feed-backs on growth are included, further interactions with other growth processes, or water dynamics, are not included.

CenW

In CenW, growth is dependent, in parts, on foliar nitrogen concentration, which is determined by the availability of nitrogen through mineralisation in the soil. The rate of mineralisation itself is determined by the amount of litter carbon, which has an immobilising effect. Hence, growth and litter production can be reduced by a shortage of mineralised nitrogen, and a shortage of nitrogen can be induced by increased carbon influx from litter production. This provides a strong negative feed-back effect between carbon and nutrient fluxes, and a constraint on rapid changes in soil organic matter. A loss of soil organic matter leads to enhanced mineralisation of nutrients, thereby stimulating productivity of carbon, and re-establishing some of the lost carbon reservoir.

FullCAM

FullCAM combines the three models: 3PG for above-ground productivity, Gendec for litter decomposition and RothC for soil organic matter dynamics. This is linked to the CAMFor accounting tool. The model does not explicitly model pools of elements other than carbon although nitrogen availability is an input in controlling decomposition in Gendec, and a general fertility index is used as a modifier in calculating light-use efficiency and allocation in 3PG.

G'Day

The feed-back processes in G'Day are similar to the ones described for CenW above.

Gendec

Gendec is a litter decomposition model that is used as part of the combined FullCAM model. It only deals with carbon dynamics, although nitrogen is included as a rate-modifying factor. Pools of nitrogen are not explicitly modelled, and the model has no production module.

GRAZPLAN

GRAZPLAN models grass growth in dependence on weather variables and nutrient availability. Nutrients are taken up to satisfy growth requirements. Nutrients are shed in senescence or through herbivory and carbon and nutrients are moved to soil pools. Soil nitrogen and phosphorus dynamics are modelled in considerable detail, including separate treatment of fixed and available phosphorus. Thus, nutrient fluxes are modelled explicitly which allows for feed-backs on subsequent plant productivity.

GRASP

GRASP is a 'pasture growth' model which combines a soil water model and a model of above-ground dry-matter production. Nitrogen uptake is calculated as a function of cumulative transpiration since the start of the growing season. However, nitrogen pools are not explicitly modelled in either the plant or soil, even though nitrogen dynamics and constraints are believed to be important in many Australian systems. Hence, interactions between above- and belowground processes are not represented in GRASP.

Linkages

Linkages simulates the growth of individual trees (gap model) based on climatic variables and site fertility. Nitrogen dynamics are also modelled through litter fall, decomposition and soil organic matter formation. Feed-back effects between organic-matter decomposition and subsequent nitrogen availability are included in a simple form.

Promod

Promod simulates forest growth in response to climatic conditions and site fertility. However, it does not explicitly model nutrient dynamics and can therefore not simulate any system feed-backs.

Roth-C

Roth-C only simulates soil-carbon dynamics. Nitrogen is only introduced to the extent that it can affect plant productivity through supplied nitrogen fertiliser. Plant productivity must be prescribed as a user-supplied input, or via linkage with another model as has been done in FulCAM. Some linkages can be emulated through modification of plant-growth inputs by the user, but linkages between above- and belowground processes are not explicitly included in the model

Socrates

Socrates only simulates soil-carbon dynamics. Nitrogen is included to the extent that it can affect plant productivity through supplied nitrogen fertiliser and affect the decomposition of fresh litter. Plant productivity can be either prescribed or modelled through simple plant-growth routines, but they are not linked to soil organic matter dynamics.

3-PG

The 3-PG model calculates growth as a function of absorbed radiation multiplied by a number of calculated stress factors. In the latest version, this includes a nutrition-related parameter.

Nutrition is also included through affecting the allocation to above and-below ground growth. The model has no explicit pools of soil or plant nitrogen or other nutrients. Hence, feed-backs between plant productivity and soil organic matter dynamics are not included.

Large-Scale Applications

Linkages are clearly important, but can they be implemented at a large enough scale to run simulations for all of Australia? The models reviewed here are all stand models, and models that include nutrient cycling could be used just as readily as models without those cycles. Additional data requirements essentially concern the estimation of fertility across the continent, which probably should be used as a model constraint in any case.

Implementation of the relevant feed-back processes is basically model-internally generated and requires no further external data inputs. The degree of feed-back control is partly dependent on the parameterisation chosen for factors such as critical nutrient concentrations, but the nature of these feed-back processes is based on long-established theory.

Hence, inclusion of these feed-back processes is feasible at any scale, including the continental scale. It would be particularly important for simulating changes in the carbon balance of the continent following some perturbation, such as increasing CO₂ concentration or changing climate. It is not likely that meaningful results for the response to such external perturbations can be obtained without some attempt to include system-internal feed-back processes (Medlyn *et al.* 2000).

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