A large, light gray stylized leaf graphic is centered on the page. It features a central stem with three leaves of varying sizes and orientations. The background consists of several overlapping, curved, light gray lines that create a sense of movement and depth.

# Net Ecosystem Exchange

WORKSHOP PROCEEDINGS  
CRC FOR GREENHOUSE ACCOUNTING  
APRIL 2001



**Greenhouse**  
Accounting

CRC

© Commonwealth of Australia 2001  
ISBN 0957959702

This work is copyright. The Copyright Act 1968 permits fair dealing for study, research, news reporting, criticism or review. Selected passages, tables or diagrams may be reproduced for such purposes provided acknowledgment of the source is included. Major extracts from the document may not be reproduced without the written permission of The Chief Executive, CRC for Greenhouse Accounting, GPO Box 475, Canberra ACT 2601, Australia.

This is a collection of papers provided by contributors to the Net Ecosystem Exchange Workshop held by the CRC during April 2001.

Views expressed in the volume are those of the authors and not necessarily those of the Commonwealth Government nor the Cooperative Research Centre. Neither the authors nor the Commonwealth nor the CRC accept responsibility for any advice or information that relates to this material.

Edited by: Dr Miko U.F. Kirschbaum and Rowena Mueller (CRC for Greenhouse Accounting)

Published by:  
The Communications Office  
CRC for Greenhouse Accounting  
GPO Box 475  
CANBERRA ACT 2601

email: [office@greenhouse.crc.org.au](mailto:office@greenhouse.crc.org.au)  
www: [www.greenhouse.crc.org.au](http://www.greenhouse.crc.org.au)

Preferred way to cite this publication:  
Kirschbaum, M.U.F. and Mueller, R. (2001) Net Ecosystem Exchange. Cooperative Research Centre for Greenhouse Accounting.

The CRC for Greenhouse Accounting is a national independent scientific research centre established in 1999 as an unincorporated joint venture under the AusIndustry CRC Program.

Acknowledgments:  
Thanks are due to all workshop participants for their contributions.

Artwork: ANU Graphics  
Photograph: Mr Jeff Wilson, ANU  
Printer: Canprint Communications

# Foreword

---

More than a third of Australia's current greenhouse gas emissions are caused by human activities such as forestry, agriculture and changes in land use. In order to reduce our net emissions from the land, it is necessary to adopt new management practices to lower them; increase carbon sinks through afforestation and reforestation; and minimise future emissions through limits on further deforestation. It is also necessary to understand and account for carbon exchange rates.

Accounting for carbon exchange between the biosphere and the atmosphere is a formidable scientific task thanks to the sheer size and complexity of the biosphere. Human and natural factors also interact in intricate ways within the biosphere to determine the ultimate size and direction of the carbon fluxes (exchanges) involved. Biospheric models are widely used by scientists to help summarise and organise current understanding of the component processes and for simulating both current exchange rates and likely future exchange under climate change and modified land management regimes.

This is the CRC's second publication. The collection of work represents the scientific contributions of numerous Australian experts assembled for the *Net Ecosystem Exchange Workshop* held by the CRC in Canberra from 18-20 April, 2001. It presents reviews and analyses of the major eco-physiological factors that affect carbon exchange and features these factors using a range of biospheric models.

It is hoped that the publication of this set of papers will ensure circulation of the best scientific understanding at present with respect to the modelling of net ecosystem carbon exchange for Australia.

Prof Ian Noble FTSE  
Chief Executive  
Cooperative Research Centre for Greenhouse Accounting

April 2001

# Contents

---

NEE Workshop Agenda	1
Definitions Of Some Ecological Terms Commonly Used In Carbon Accounting	2
Brief Description Of Several Models For Simulating Net Ecosystem Exchange In Australia	8
Modelling Radiation Absorption by Plant Canopies	30
Radiation Conversion	33
Plant Respiration	38
The Role of Allocation in Modelling NEE	43
Stand Age Effects on Productivity in Forests: Representation in Models and Influence on Net Ecosystem Exchange	50
Phenology and Reproduction	58
How Does Ecosystem Water Balance Influence Net Primary Productivity? - A Discussion	62
Other Soil Constraints on Net Primary Production	71
Nutrient Uptake and Use in Plant Growth	75
The Control Of Ecosystem Carbon Dynamics By The Linkages Between Above and Belowground Processes	82
Carbon Dynamics and Nutrient Mineralisation	89
Temperature and Moisture Effects on Decomposition	95
Soil Texture Effects on Decomposition and Soil Carbon Storage	103
Acidic Soil pH, Aluminium and Iron Affect Organic Carbon Turnover in Soil	111
Charcoal and Other Resistant Materials	116
Effect of Mechanical Disturbance (Cultivation) on Soil Carbon Dynamics	120
Plant Litter and Decomposition: General Concepts and Model Approaches	124
Rapporteur Reports	130
NEE Workshop Participants	135

# NEE Workshop Agenda

---

## DAY 1 - WEDNESDAY 18 APRIL 2001

- Radiation interception - *Ying Ping Wang*
- "The Australian Journal of Plant Physiology" - *Jennifer McCutchan*
- Radiation conversion - *Belinda Medlyn*
- Respiration - *Roger Gifford*
- Discussion - *Wang, Medlyn and Gifford*
- Allocation - *Craig Barton*
- Mortality and stand age effects on productivity - *Michael Battaglia*
- Other factors (phenology, reproduction etc.) - *Chris Beadle, as presented by Michael Battaglia*
- Discussion - *Barton and Battaglia*  
- Wrap up Session

## DAY 2 - THURSDAY 19 APRIL 2001

- Introduction
- The impact of ecosystem water balance on NPP - *Derek Eamus*
- Other soil constraints (impedence, acidity, salinity, water logging) - *Robert Edis*
- Nutrient uptake and use in plant growth - *John Evans and Everard Edwards*
- Discussion - *Eamus, Edis, Evans and Edwards*
- CO<sub>2</sub> concentration - *Graham Farquhar*
- Temperature effects on growth - *Marilyn Ball and David Barker*
- Discussion - *Farquhar, Ball and Barker*
- Linking above and belowground processes - *Miko Kirschbaum*
- Interactions between carbon dynamics and nutrient mineralisation - *Peter Grace*
- Discussion - *Kirschbaum and Grace*
- Wrap up Session

## DAY 3 - FRIDAY 20 APRIL 2001

- Introduction
- Temperature and moisture effects on decomposition rate - *Keryn Paul*
- Soil texture effects on decomposition and soil C storage - *Evelyn Krull and Jeff Baldock*
- pH, aluminium and other factors that can inhibit decomposition rates - *Ram Dalal*
- Charcoal and other resistant organic matter - *Jan Skjemstad*
- Discussion - *Paul, Baldock, Krull, Dalal and Skjemstad*
- Soil disturbance (cultivation) effects on decomposition and soil C storage - *Phil Polglase*
- Litter quality and quantity - *Marc Corbeels*
- Discussion - *Polglase and Corbeels*
- Linking the processes together - *Steve Roxburgh and Rapporteurs*
- General discussion  
- Final Wrap up Session

# Definitions Of Some Ecological Terms Commonly Used In Carbon Accounting

M.U.F Kirschbaum, D. Eamus, R.M. Gifford, S.H. Roxburgh and P.J. Sands

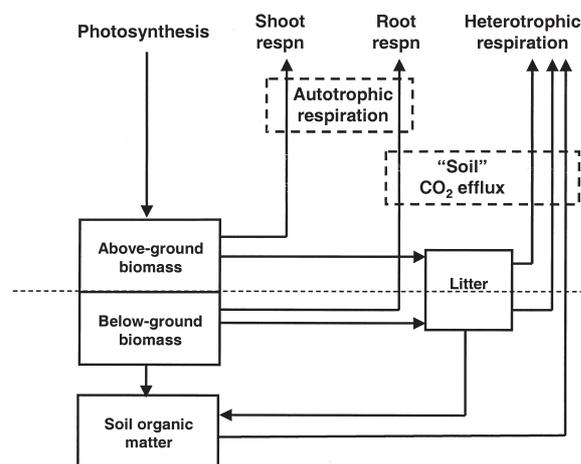
## Introduction

The papers in these Workshop Proceedings all deal with Net Ecosystem Carbon Exchange. In the interest of clarity, this and other related terms are briefly described in the following.

### AUTOTROPHIC RESPIRATION

Plants fix carbon by photosynthesis. The word "photosynthesis" is here used to denote the carbon fixed by gross photosynthesis *minus* the carbon lost by photorespiration. Some of that photosynthetically fixed carbon is lost by internal plant metabolism. This loss is termed autotrophic respiration and typically amounts to about half the carbon fixed by plants.

Figure 1: Diagrammatic representation of the main terms describing carbon fluxes in ecosystems.

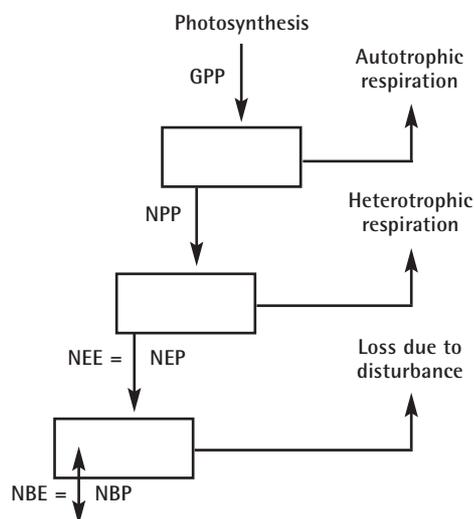


### HETEROTROPHIC RESPIRATION

Heterotrophic respiration refers to the carbon lost by organisms in ecosystems other than the plants, the primary producers, themselves. It constitutes the respiration by animals that live above-ground, which tends to be a minor component and is not represented in Figure 1, but most importantly, by all those organisms (flora and fauna) that live in the soil and the litter layer and decompose organic matter that has reached the soil

by litter fall, root turn-over, root exudation, dead organisms and faecal matter. It also includes the carbon release in the decomposition of standing dead trees and coarse woody debris.

Figure 2: Diagrammatic representation of the main terms describing system carbon balances. Arrows indicate that GPP and NPP are always positive (carbon gains by the system), NEE is usually, but not always, positive, and NBE can be positive or negative.



### SOIL CO<sub>2</sub> EFFLUX

Soil CO<sub>2</sub> efflux is comprised of autotrophic respiration from plant roots and heterotrophic respiration from soil organisms. It may also include respiration from the litter layer on top of the mineral soil as defined in individual studies.

Total soil CO<sub>2</sub> efflux is often also referred to as soil respiration, whereas other researchers refer to soil respiration as only the CO<sub>2</sub> efflux originating from heterotrophic respiration in the soil and use it as distinct from the autotrophic respiration originating from plant roots.

### GROSS PRIMARY PRODUCTION

Gross primary production (GPP) refers to the total amount of carbon fixed in the process of photosynthesis by plants in an ecosystem. A forest or grassland, for example, may fix 20 tC ha<sup>-1</sup> yr<sup>-1</sup> during the process of photosynthesis.

Total global GPP is estimated to be about 120 GtC yr<sup>-1</sup> (Gifford 1982; Bolin *et al.* 2000), and total Australian GPP can be estimated to be 2-6 GtC yr<sup>-1</sup> if one assumes that GPP is 2 times NPP and uses the estimates of NPP compiled below.

## NET PRIMARY PRODUCTION

Net primary production (NPP) refers to the net production of organic carbon by plants in an ecosystem usually measured over a period of a year or more. It is GPP minus the amount of carbon respired by plants themselves in autotrophic respiration,  $R_a$ :

$$\text{NPP} = \text{GPP} - R_a \quad (1)$$

It constitutes the total annual growth increment (both above and below ground) plus the amounts grown and shed in senescence, reproduction or death of short-lived individuals in a stand plus the amounts consumed by herbivores. Only the amount of carbon produced and lost in the year for which NPP is being calculated is counted, not what was produced in an earlier year and lost in the current year. This distinction is sometimes difficult to make in practice.

In the example of a forest or grassland, it may amount to 10 tC ha<sup>-1</sup> yr<sup>-1</sup> with an equivalent amount of carbon lost in autotrophic respiration. NPP in any system must be positive over periods of years. Otherwise, the system would soon lose all of its carbon and cease to exist.

Total global NPP is estimated to be about 60 GtC yr<sup>-1</sup> (Steffen *et al.* 1998). Estimates of NPP for Australia have recently been compiled by M.L. Roderick (unpublished). They range from about 1 GtC yr<sup>-1</sup> (D.J. Barrett, unpublished), 1.6 GtC yr<sup>-1</sup> (Kirschbaum 1999), 2.0 GtC yr<sup>-1</sup> (Field *et al.* 1998; DeFries *et al.* 1999); 2.7 GtC yr<sup>-1</sup> (Pittock and Nix 1986 - recalculated by M.L. Roderick based on the original method), 2.8 GtC yr<sup>-1</sup> (Gifford *et al.* 1992) to 3.2 GtC yr<sup>-1</sup> (Roderick *et al.* 2001).

## NET ECOSYSTEM EXCHANGE OR NET ECOSYSTEM PRODUCTION

Net Ecosystem Exchange (NEE) and Net Ecosystem Production (NEP) refer to net primary production minus carbon losses in heterotrophic respiration,  $R_h$ :

$$\text{NEE} = \text{NEP} = \text{NPP} - R_h \quad (2)$$

These terms are used somewhat interchangeably, with NEE used more often to refer to these fluxes when they are addressed from a measurement of gas exchange rates using atmospheric measurements over time scales of hours, whereas NEP is more

often used to refer to the same processes if measurements are based on ecosystem-carbon stock changes, typically measured over a minimal period of one year. However, these differences in usage are not firmly embedded in formal definitions.

In the example of a typical forest, of the total NPP of 10 tC ha<sup>-1</sup> yr<sup>-1</sup>, 5 tC ha<sup>-1</sup> yr<sup>-1</sup> might be lost in annual turn-over of foliage, fine roots, reproductive structures and other constituents with short longevity, and a similar amount might accumulate in growing stems. When the standing stock of carbon in the litter pool is not changing over time, the input of dead litter must be balanced by an equivalent carbon loss from decomposing litter. The forest's NEE would then be 5 tC ha<sup>-1</sup> yr<sup>-1</sup>.

For the example of the grassland, NEE must be closer to zero as the bulk of annually produced biomass tends to turn-over and there are not generally any accumulating biomass pools. NEE can be positive, however, if soil carbon is building up, or negative if the system is degrading and soil carbon is lost.

Total global NEE is estimated to be about 10 GtC yr<sup>-1</sup> (Steffen *et al.* 1998), but there is also a wide range of uncertainty and interannual variability around this estimate. Individual ecosystems may be in balance, or positive or negative. Most systems, however, have a positive NEE, with the gradual stock increment via NEE being balanced in the longer term by relatively sudden stock losses caused by disturbance. Disturbances may be regular, such as by annual crop harvest, or occasional and irregular as by episodic fire that may recur at the same place only every 100 years, or deforestation that may remove biomass without allowing regrowth.

## NET BIOME EXCHANGE OR NET BIOME PRODUCTION

Net Biome Exchange (NBE) or Net Biome Production (NBP) refers to the change in carbon stocks after episodic carbon losses due to natural or anthropogenic disturbances have been taken into account:

$$\text{NBE} = \text{NEE} - L_d \quad \text{or} \quad (3a)$$

$$\text{NBP} = \text{NEP} - L_d \quad (3b)$$

where  $L_d$  is the loss by major episodic disturbances. Some systems are not typically affected by irregular disturbances. In those systems, NBE = NEE.

Net biome exchange is the appropriate measure of system carbon balances over longer time periods. In the forest example, the forest is likely to grow for some decades or centuries and accumulate carbon in each year (NBE = NEE > 0;  $L_d = 0$ ).

Eventually, the carbon may be lost in a massive disturbance, such as a fire or harvesting. In the year, when that occurs, the loss due to disturbance will be much greater than the annual increment in carbon so that  $NBE \ll 0$  in that year. Summed over a longer time period, NBE will be close to zero, with the many small positive annual increments balanced by the large loss in the year of disturbance (i.e.  $NBE = \sum NEE - L_d$ ). In the grassland system,  $NEE \cong NBE$  is more likely, although systems subject to fires recurring every few years could have a pattern similar to that of forest systems, but with smaller and more frequent peaks and troughs.

Globally, NBE (including the effects of deforestation) is estimated to have been 0.2 GtC yr<sup>-1</sup> from 1980-1989 and 1.4 GtC yr<sup>-1</sup> from 1989-1998 (IPCC 2001). This suggests that the overall global accrual of ecosystem carbon is not wholly annulled by the carbon loss due to major disturbances, including deforestation. Historically (before major human influence), the quantity must have been close to 0 and can only deviate significantly from 0 while systems are out of equilibrium.

Although NBE applies to long timescales, it need not necessarily have to apply to large spatial scales despite the implication by inclusion of the term 'biome'. NBE can be monitored at the plot level over long periods, which might include disturbance events. In other words, NBE can be applied as much to the plot level as at larger spatial scales.

There is no explicit definition that distinguishes episodic loss by major disturbance ( $L_d$ ) from loss by heterotrophic respiration ( $R_h$ ). Broadly speaking, organic-matter oxidising processes that occur all year every year in an ecosystem contribute to  $R_h$ , while processes that oxidise organic matter in only some years would be classed as carbon losses due to disturbances.

## UNITS OF MEASUREMENT

All the exchange rates described here can be expressed in units of carbon amount per unit of area per unit of time, such as tC ha<sup>-1</sup> yr<sup>-1</sup>. Biochemically oriented studies often use molC m<sup>-2</sup> yr<sup>-1</sup>. However, these fluxes are often derived from other measurements taken for different purposes and for which different measurement units may be more appropriate. These units can, in principle, be easily inter-converted, but it can also be confusing if the unit of measurement is not clearly stated in individual studies, or if the numeric values change along with any conversion in units.

**Table 1: Some different units for quantifying amounts of carbon and their interconversions.**

1 Mg (megagram)	= 1,000 kg	= 1 t (tonne)
1 Gg (gigagram)	= 10 <sup>6</sup> kg	= 1 kt
1 Tg (teragram)	= 10 <sup>9</sup> kg	= 1 Mt
1 Pg (petagram)	= 10 <sup>12</sup> kg	= 1 Gt
1 kg m <sup>-2</sup>	= 10 t ha <sup>-1</sup>	
1 molC	= 12gC	
1 tC ha <sup>-1</sup>	= 8.33 molC m <sup>-2</sup>	
1 molC m <sup>-2</sup>	= 120 kgC ha <sup>-1</sup>	
1 molCO <sub>2</sub> m <sup>-2</sup>	= 440 kgCO <sub>2</sub> ha <sup>-1</sup>	

For example, most data on forest growth are given in units of wood volume increments: m<sup>3</sup> ha<sup>-1</sup> yr<sup>-1</sup>. To convert from wood volume to wood mass, the density of wood needs to be known, but that can vary widely between species between values of 0.5 to over 1 tDW m<sup>-3</sup>. Other biomass measurements may similarly be taken in units of dry weight. Dry weight typically contains about 45-50% carbon, and as the atmosphere ultimately gets emissions as CO<sub>2</sub>, forest growth could also be expressed in units of CO<sub>2</sub>. The conversion from carbon to CO<sub>2</sub> is simply based on their respective molecular weights: 12:44. So the growth of a typical forest could be expressed as:

$$15 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1} = 10 \text{ tDW ha}^{-1} \text{ yr}^{-1} = 5 \text{ tC ha}^{-1} \text{ yr}^{-1} = 18.3 \text{ tCO}_2 \text{ ha}^{-1} \text{ yr}^{-1}.$$

Fluxes in this paper have been expressed here as multiples of tonnes. One tonne equals 1,000 kg. Alternatively, these fluxes can also be expressed as multiples of grams or mols. Table 1 gives a list of conversions between gram-based, kg-based, tonne-based and mol-based quantities.

## References

- Bolin, B., Sukumar, R., Ciais, P., Cramer, W., Jarvis, P., Kheshgi, H., Nobre, C., Semenov, S. and Steffen, W. (2000). Global perspective. In: *Special Report on Land Use, Land-Use Change and Forestry*, eds. R.T. Watson, I.R. Noble, B. Bolin, N.H. Ravindranath, D.J. Verardo and D.J. Dokken, Cambridge University Press, Cambridge, UK, pp 23-51.
- DeFries, R.S., Field, C.B., Fung, I., Collatz, G.J. and Bounoua, L. (1999). Combining satellite data and biogeochemical models to estimate global effects of human-induced land cover change on carbon emissions and primary productivity. *Global Biogeochemical Cycles* 13: 803-815.

- Field, C.B., Behrenfeld, M.J., Randerson, J.T. and Falkowski, P. (1998). Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281: 237-239.
- Gifford, R.M. (1982). Global photosynthesis in relation to our food and energy needs. pp 459-495 in *"Photosynthesis: Development, Carbon Metabolism and Plant Productivity" Vol 2*. Ed. Govindjee. New York, Academic Press.
- Gifford, R.M., Cheney, N.P., Noble, J.C., Russell, J.S., Wellington, A.B., and Zammit, C. (1992). Australian land use, primary production of vegetation and carbon pools in relation to atmospheric carbon dioxide concentration. In Gifford, R.M. and Barson, M.M. (Eds.) *Australia's Renewable Resources: Sustainability and Global Change*. Bureau of Rural Resources Proceedings No. 14, AGPS, Canberra, pp. 151-187.
- IPCC (2001). Technical Summary of the Working Group I Report. Intergovernmental Panel on Climate Change (<http://www.ipcc.ch/pub/wg1TARtechsum.pdf>), 83 pp.
- Kirschbaum, M.U.F. (1999). The effect of climate change on forest growth in Australia. In: *Impacts of global change on Australian temperate forests*. (Howden, S.M. and Gorman, J.T., eds.), Working Paper Series, 99/08, pp. 62-68.
- Pittock, A.B. and Nix, H.A. (1986). The effect of changing climate on Australian biomass production: a preliminary study. *Climatic Change* 8: 243-255.
- Roderick, M.L., Farquhar, G.D., Berry, S.L. and Noble, I.R. (2001). On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia* (In press).
- Steffen, W., Noble, I., Canadell, J., Apps, M., Schulze, E.-D., Jarvis, P.G., Baldocchi, D., Ciais, P., Cramer, W., Ehleringer, J., Farquhar, G., Field, C.B., Ghazi, A., Gifford, R., Heimann, M., Houghton, R., Kabat, P., Körner, C., Lambin, E., Linder, S., Mooney, H.A., Murdiyarso, D., Post, W.M., Prentice, C., Raupach, M.R., Schimel, D.S., Shvidenko, A. and Valentini, R. (1998). The terrestrial carbon cycle: implications for the Kyoto Protocol. *Science* **280**: 1393-1394.



Papers and  
Presentations



# Brief Description Of Several Models For Simulating Net Ecosystem Exchange In Australia

M.U.F. Kirschbaum, J.O. Carter, P.R. Grace, B.A. Keating, R.J. Keenan, J.J. Landsberg, G.M. McKeon, A.D. Moore, K.I. Paul, D.A. Pepper, M.E. Probert, G.P. Richards, P.J. Sands and J.O. Skjemstad

## Introduction

This brief background paper has been compiled for the workshop on modelling net ecosystem exchange that was held in Canberra from 18-20 April 2001. It gives brief descriptions of the models that are currently available in Australia and that are of interest in modelling net ecosystem exchange for the Australian continent: APSIM, CENTURY, CenW, FullCAM, G'DAY, Gendec, GrazPlan, GRASP, Linkages, Promod, Roth-C, Socrates and 3-PG.

These models deal with the range of different ecosystems that together constitute the Australian biosphere. Some ecosystems or components of ecosystems are modelled by more than one model, but the different models approach their modelling tasks in different ways by providing more or less detail, and by including or omitting certain processes or plant or soil pools.

The workshop provided details of the treatment of various processes in each of these models which are described in other papers in this volume. This paper gives a brief description for each of these models to make it easier to better understand the overall modelling approach in the respective models and gain a better appreciation of the treatment of specific processes as they are dealt with in greater detail in the other papers of this volume.

### APSIM

APSIM (**A**gricultural **P**roduction **S**ystem **S**imulator) is a software system that allows models of crops, pastures, trees, soil water, nutrients, and erosion to be flexibly configured to simulate diverse production systems (McCown *et al* 1996; see also web site ([www.apsim-help.tag.csiro.au](http://www.apsim-help.tag.csiro.au))).

The modelling framework has been developed over the last 10 years by the APSRU group (Agricultural Production Systems Research Unit), a collaborative effort between CSIRO Tropical Agriculture (now Sustainable Ecosystems) and Old State agencies (DPI, DNR). APSRU is currently being renegotiated and it is likely that its core membership will be expanded to include CSIRO Land and Water and the Uni of Qld.

A key feature of APSIM, which distinguishes it from many vegetation specific models, is the central position of the soil rather than the vegetation. Changes in the status of the soil state variables are simulated continuously in response to weather and management. Crops, pastures or trees come and go, finding the soil in a particular state and leaving it in an altered state.

Another feature of APSIM is its "plug-in-pull-out" approach to design (Fig. 1). High order processes (for example growth of a crop, soil water balance, dynamics of soil organic matter) are represented as separate modules. This arrangement offers great flexibility for comparing alternative representations of different parts of the system without modification to the rest of the model. APSIM is well suited to modelling systems involving sequences of crops (rotations, phase farming) or mixtures of crops (intercropping, agroforestry).

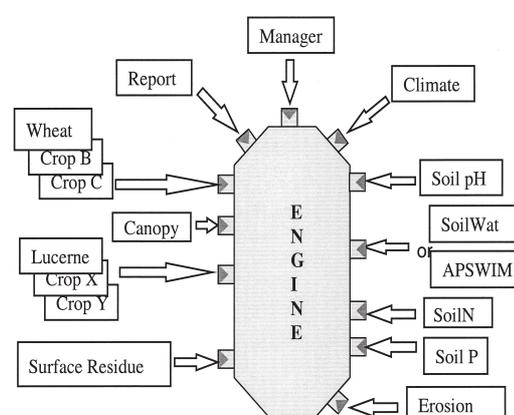


Figure 1: Diagrammatic representation of the modular structure of APSIM, illustrating the options of having alternative representations of certain processes (eg

*SoilWat or APSWIM for the water balance) and multiple crops.*

APSIM models are typically 1-dimensional, with the soil described as a multi-layered system. The recently released APSIM v 2.0 provides support for multi-point simulations for the first time. Most modules operate on a daily time-step. The minimum climatic data required to run APSIM are daily maximum and minimum temperature, radiation and rainfall.

The vegetation modules in APSIM use a simple framework to describe the daily capture and utilization of environmental resources such as solar radiation, soil water and nutrients. In response to environmental stimuli, plants develop through distinct phenological phases, a leaf canopy is produced, incident radiation is intercepted, absorbed energy is converted into assimilates which are partitioned between plant components, including yield.

The functions used in APSIM vegetation modules are outlined in greater detail on the APSIM web page, and in the document "Principles of simulating crop growth and development in APSIM" (Mike Robertson and others in APSRU, unpublished). APSIM vegetation modules generally include water and nitrogen as limiting factors; a phosphorus limitation is under development but at present is only operational for maize.

At the time of writing, modules exist for barley, canola, chickpea, cowpea, fababean, mungbean, navybean, hemp, wheat, lucerne, maize, millet, peanut, pigeonpea, sorghum, sunflower, sugarcane and cotton. A FOREST module provides a generalised vegetation treatment that has been used for *Eucalyptus*, *Pinus* and other natural plant communities.

The soil water dynamics are described by one of two modules, either SoilWat (a "cascading bucket" approach) or APSWIM (based on simultaneous solution of the Richards' equation for water flow and the advection-dispersion equation for solute transport). A comprehensive study comparing the two approaches found both to be capable of giving good descriptions of soil water content and solute movement (Verburg, 1996).

The turnover of organic matter is represented by the SoilN and Residue modules (Probert *et al* 1998). APSIM distinguishes between surface residues and residues in the soil. Within SoilN, organic materials are conceptualized as fresh organic matter (FOM), and two soil organic matter pools (BIOM and HUM) that differ in their rates of decomposition. The soil organic matter pools are considered to have non-varying C:N ratios.

Decomposition rates are determined by soil water and temperature, and in the case of FOM its C:N ratio.

APSIM has pioneered very flexible specification of management regimes in farming systems modelling. The MANAGER module is controlled by a user defined script language which enables a diverse range of management operations to be specified in ways that are conditional on the state of the simulated system. Both the timing and nature of operations such as sowing, tillage, residue management, fertilisation, irrigation, crop management, harvesting etc are all controlled from this script specified by users. All these operations can be made responsive to the state of the weather, vegetation or soil system.

APSIM is distributed under a licence system. Currently approximately 200 licences exist and the model is in active use in farming systems research in all Australian States except Tasmania, and in project activities with International Agricultural Research Centre's and the National Agricultural Research System in a number of countries in Africa, in India, China and Indonesia. APSIM testing is on-going in this diverse range of situations. Details of specific module testing can be found within the science documentation on the APSIM web page ([www.apsim-help.tag.csiro.au](http://www.apsim-help.tag.csiro.au)).

By far the most extensive testing has focused on the simulation of net primary productivity and economic yield and of simulation of the dynamics of soil water and soil carbon/nitrogen under different agricultural systems. The model's strengths are in cropping systems, with emerging capabilities in pasture and forest systems. At this point in time there is no livestock production capability in APSIM, although linkages are being explored with the GRAZPLAN / FARMWISE effort from CSIRO Plant Industry.

## CENTURY

The CENTURY version 5 agroecosystem model is the latest version of a soil organic model initially developed by Parton *et al.* (1987). This model simulates carbon, nitrogen, phosphorus, and sulphur dynamics on a monthly time step for an annual cycle over time scales of centuries and millennia and embodies the best understanding to date of the biogeochemistry of C, N, P, and S. Plant production can be simulated by using grassland/crop, forest or savanna system sub-models, with the flexibility of specifying potential primary production parameters representing site-specific plant communities. Land use change can be represented by changing the plant community type during model runs, i.e. beginning with forest, clearing to pasture then running a cropping system.

CENTURY was especially developed to deal with a wide range of cropping system rotations and tillage practices for system analysis of the effects of management, CO<sub>2</sub> fertilisation and climate change on productivity and sustainability of agroecosystems. Integrated in the model are the effects of climate, soil variables and agricultural management to simulate C, N, and water dynamics in the soil-plant system (Fig. 2). Simulation of complex agricultural management systems including crop rotations, tillage practices, fertilization, irrigation, grazing, and harvest methods are possible. The primary purposes of the model are to provide a tool for ecosystem analysis, to test the consistency of data and to evaluate the effect of changes in management and climate on ecosystems.

CENTURY simulates C,N,P,S dynamics in surface soils (0-20cm). The depth of analysis can be extended to 0-30cm by re-parameterisation. This allows analyses more aligned with the minimum default depth of 30cm proposed by the IPCC for national C inventory. Grassland/crop and forest systems have different plant production sub-models that are linked to a

common soil organic matter sub-model. The savanna model uses the grassland/crop and forest subsystems and allows for the two subsystems to interact through shading effects and N competition. The soil organic matter sub-model simulates the flow of C, N, P, and S through plant litter and the different inorganic and organic pools in the soil. A range of variables are used to describe the system being simulated.

The major input variables for the model include:

- monthly average maximum and minimum air temperature,
- monthly precipitation,
- lignin content of plant material,
- plant maximum and minimum N, P, and S content,
- soil texture,
- atmospheric and symbiotic and non symbiotic N inputs,
- initial soil C, N, P, and S amounts, and
- disturbance events (cultivation, grazing, fire, harvest, irrigation, erosion).

Input variables are available for most natural and agricultural ecosystems and can generally be estimated from existing

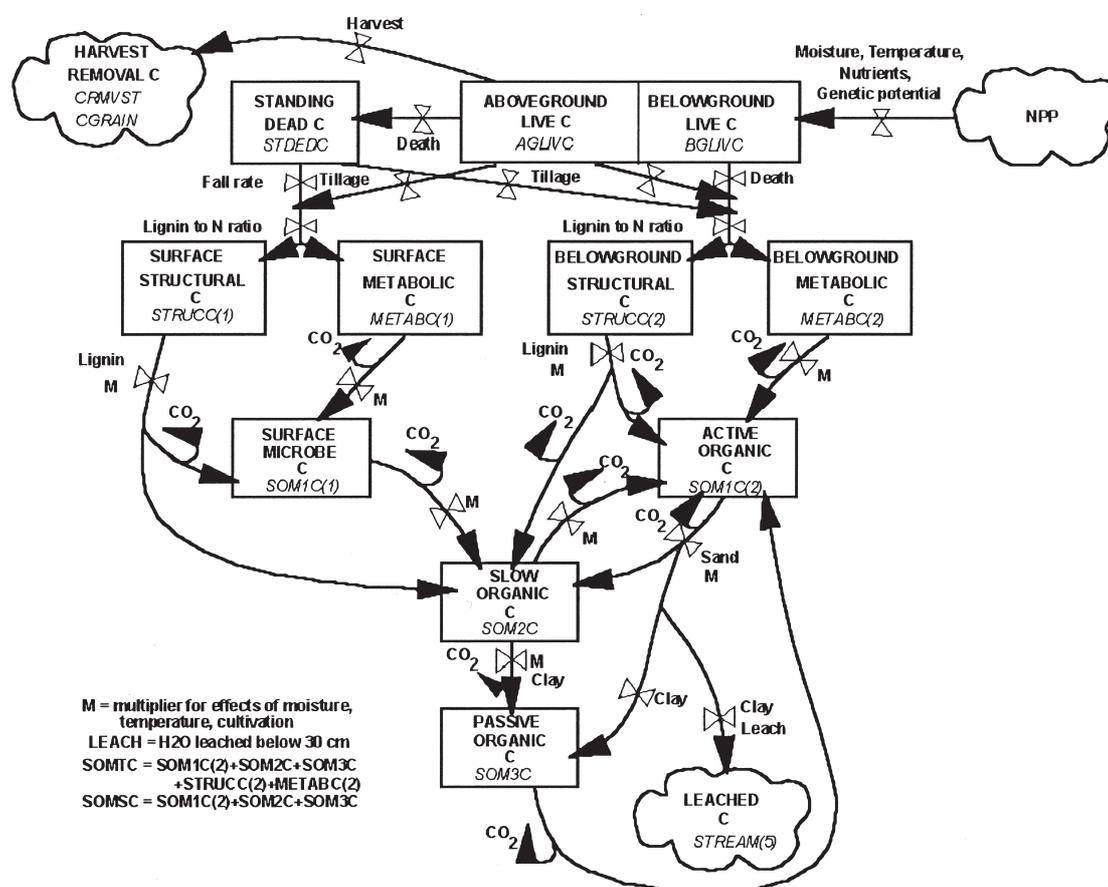


Figure 2: Basic outline of the carbon pools and flows in CENTURY.

literature or parameterised from field data. Most of the parameters controlling the flow of C in the system are in special file containing "fixed" parameters however these can be altered to simulate soils to a greater depth or control the C pool structure. The user can configure the model considering only C and N dynamics or a multiple array of elements namely, C, N, P and or C, N, P, and S. Initial soil carbon and nitrogen can be entered in parameter files or "spun up" using a long model run (> 1000 years) and or estimated within the model from simple regressions based on climate and soil texture. Climate inputs can be actual data, mean data or average climate with stochastic rainfall, this combination allows exploration of climate verses management impacts.

Simulation of carbon isotope concentrations for  $C_{14}$  and  $C_{13}$  within the soil matrix is possible within the model. This enables the user to better calibrate the model when isotope data from field studies are available. The model is most often used to simulate the C cycle at the plot or stand scale it has also been used at continental (VEMAP *et al.*, 1995) and global scales (Parton *et al.*, 1995) to simulate the carbon cycle under climate change. While the model has been developed to simulate real ecosystems at local to global scales, it can also simulate microcosm experiments where soils are incubated in the laboratory at known water content and temperature.

The strengths of the CENTURY model are: (1) its ability to model a diverse array of ecosystems. (2) Capability of simulating a wide range of disturbance events, especially those relevant to land use, land use change and forestry. (3) Its extensive use and testing around the world on a diverse array of systems.

On the other hand the model is largely empirical and the user is presented with what sometimes appears to be a bewildering array of parameters. In reality one can usually modify a small selection of these to give realistic simulations. Many of the parameters arise from the need to model a wide range of systems and disturbance events.

The plant production model sub components are probably less accurate than any number of specialist forest, crop and pasture growth models, although CENTURY seems to perform quite well in many situations. A number of other models e.g. CenW, G'DAY etc have taken elements the basic soil C/N dynamics from CENTURY and integrated them into their model structure.

The most recently released version of (CENTURY 5) (produce by a team of scientists at the Natural Resources Ecology Lab (NREL) Colorado State University) includes a layered soil physical structure, and new erosion and deposition sub-models.

The model code has been rewritten in C++, reorganised, and modified to use platform-independent configuration and output files. Added to this version is a windows based graphical-user interface providing ease of configuration and running CENTURY simulations. Documentation and the model can be downloaded from the NREL web site, <http://www.nrel.colostate.edu/projects/models.html>. New versions of CENTURY that use daily rather than monthly water balance are under development. These developments allow the modelling of non- $CO_2$  greenhouse gasses and add to the already impressive capability of this model.

Evolution of the model will continue as the understanding of biogeochemical processes improves. The identification of problem areas where processes are not adequately quantified and demand for new applications in greenhouse inventory and climate change will drive further developments.

### CenW

CenW (Carbon, Energy, Nutrients and Water) 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. CenW contains all relevant carbon and nutrient pools and the various feed-backs that may be affected by changes in any of these pools or fluxes (Kirschbaum 1999a, 2000). The incorporation of a nutrient cycle was the particular research challenge that prompted the development of CenW. The model is currently available as version 1.0.7. Its basic outline is shown in Fig. 3.

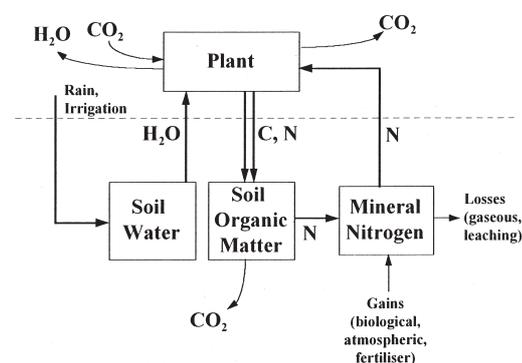


Figure 3: The basic modelling outline of CenW, showing the key pools and fluxes of carbon, nitrogen and water between these pools and the external environment (redrawn from Kirschbaum 1999a).

The model runs on a daily time step. Carbon gain is calculated in dependence on light absorption, temperature, soil water

status, foliar nitrogen concentration and any foliage damage due to frost or scorching temperatures during preceding days. Some photosynthetically fixed carbon is assumed to be lost in respiration, with daily respiration rate calculated as a constant fraction of photosynthetic carbon gain or as a function of temperature and nutritional status.

Allocation to different plant organs is determined by plant nutrient status, tree height and species-specific allocation factors. 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, soil evaporation and, under wet conditions, deep drainage.

Nitrogen can come from a constant rate of atmospheric deposition, fertiliser addition or mineralisation during the decomposition of soil organic matter. The model can be run with or without symbiotic nitrogen fixation. Decomposition rate is determined by temperature, soil water status and soil organic matter quality in a modified formulation based on the CENTURY model.

The nutrient cycle is closed through litter production by the shedding of plant parts, such as roots, bark, branches and, most importantly, 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 as inorganic mineral nitrogen.

A fraction of mineral nitrogen is lost by volatilisation in the mineralisation of organic nitrogen. There can also be nitrogen losses by leaching or off-site removal of wood.

The model requires as minimum input daily minimum and maximum temperature and rainfall. Solar radiation is desirable, but can alternatively be calculated from empirical relationships of temperature and rainfall. There is also the requirement for a large number of soils and plant-physiological parameters. Where site- and species-specific information on these parameters is not available, parameters can be estimated from related species, and site-specific information can be based on typical soils values.

The model has been tested against data from the nutrient and irrigation experiments at the BFG site near Canberra (Kirschbaum 1999a) and has been used for simulations of net primary production and the effect of climate change for the whole Australian continent (Kirschbaum 1999b). Its primary

application has been the investigation of the complex feedback effects that determine ultimate system responses in climate change simulations (Kirschbaum 1999c).

## FullCAM

The National Carbon Accounting System (NCAS) has been established by the Australian Government to provide a complete carbon accounting and projections capacity for land based (agricultural and forestry) activities.

An overall system framework (Richards, 2001) was developed to guide the development of data gathering and analytic projects and programs which could then be integrated using spatial modelling approaches. Various models were selected, calibrated and verified through these projects and programs. A range of related projects were undertaken to identify, collate and synthesise the additional data needed to operate the models continent-wide at a fine spatial and temporal resolution over a 30 year period.

To achieve this multiple pool, activity driven carbon modelling capacity the NCAS undertook the development of the *FullCAM* carbon model. *FullCAM* is an integrated compendium model and accounting tool that provides the linkage between the various sub-models. *FullCAM* has components that deal with the biological and management processes which affect carbon pools and the transfers between pools in forest, agricultural, transitional (afforestation, reforestation) and mixed (e.g., agroforestry) systems. The exchanges of carbon, loss and uptake, between the terrestrial biological system and the atmosphere are also accounted for.

The integrated suite of models that comprise *FullCAM* are: the physiological growth model for forests, *3PG* (Landsberg and Waring, 1997; Landsberg *et al.*, 2000; Coops *et al.* 1998, 2000a); the carbon accounting model for forests developed by NCAS, *CAMFor* (Richards and Evans, 2000a); the carbon accounting model for cropping and grazing systems, *CAMAg* (Richards and Evans, 2000b), the microbial decomposition model, *GENDEC* (Moorhead and Reynolds, 1991; Moorhead *et al.*, 1999), and the Rothamsted Soil Carbon Model, *Roth C* (Jenkinson, *et al.*, 1987, Jenkinson *et al.*, 1991). *FullCAM* can run any of these models in a single coordinated simulation, including any model by itself.

These models have been independently developed for the various purposes of predicting and accounting for:

- soil carbon change in agriculture and forest activities (in the case of *Roth C*);

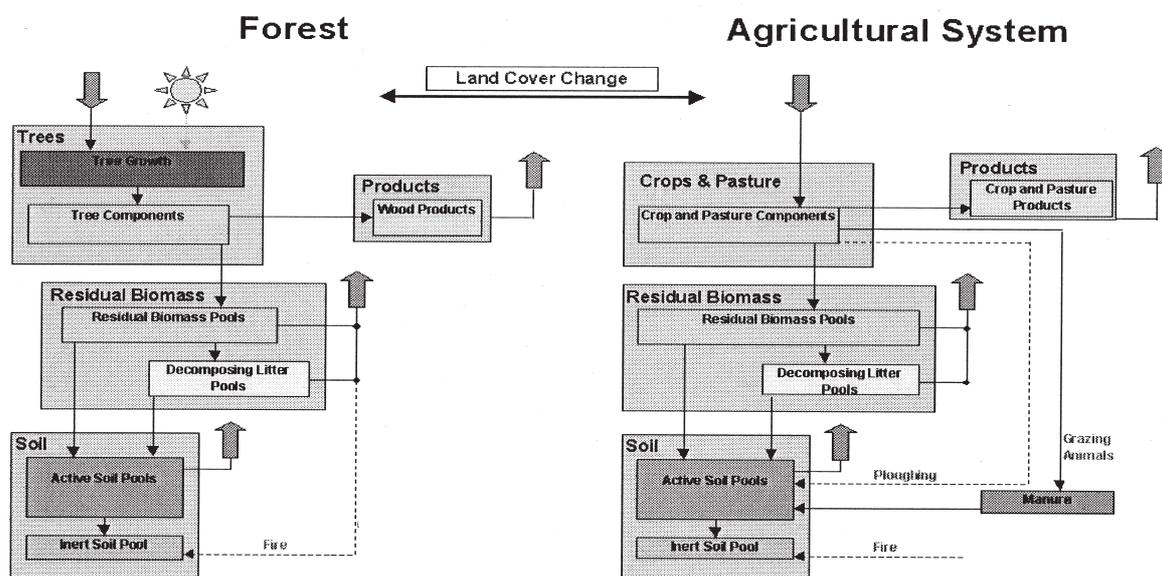


Figure 4: Diagrammatic representation of the use of the CamFor and CamAg models during land-use change.

- determination of rates of decomposition of litter (in the case of *GENDEC*); and
- prediction of growth in trees (in the case of *3PG*).

*CAMFor* and *CAMAg* are carbon accounting tools developed by the NCAS through which it is possible to apply management impacts such as fire, decomposition, harvest, cropping, and grazing, to externally generated growth and decomposition rate inputs (Fig. 4).

In preparing these models for integration into *FullCAM*, each model (except for *CAMAg*) was translated to a common Microsoft Excel workbook format. The Excel workbooks used only sheet-based formula. No 'Macros' or other code were applied. This provided a consistent and transparent model platform from which to review and integrate the various models. Having a consistent structure and format for the models allowed for the independent calibration of various models while providing for ease of later integration. The transparency of the development process also facilitates review at a detailed level.

The integration of the models serves two primary goals. The first is to provide a capacity to be able to operate at a level of conservation of carbon at a site or other specified area. This includes all carbon pools and transfers (net of atmospheric uptake and emissions) between pools to ensure that there are no instances of double counting or omissions in accounting. Potentially, this could occur if any of the dominant carbon pools

– soil carbon, biomass and litter – were considered independently. The second is to provide the capacity to run the model continentally as a fine resolution grid-based spatial, multi-temporal application. A single efficient model is required to analyse the requisite large input data sets in a spatial context.

Model calibration includes the collation of a series of previous (quality audited) site measurements and the undertaking of additional field work and laboratory analyses. Independent data sets are maintained for the model calibration and verification of model results. The application of calibrated models in the spatial version of *FullCAM* will rely on interpolation across a range of spatially continuous input data layers. This includes data such as that on climate and soil type.

The following describes the *CAMFor* and *CAMAg* models. The other model components of *FullCAM*, *3PG*, *Roth C* and *GENDEC* are individually described elsewhere in the report.

### CAMFor

*CAMFor* has its origins in the *CO<sub>2</sub> Fix* model of Mohren and Goldewijk (1990). The published Fortran code for this model was converted to an Excel spreadsheet (sheet based, formula driven) format as reported in Richards and Evans (2000a). A series of modifications were made to the original model including:

- introduction of an inert soil carbon pool recognising the nature of carbon in Australian mineral soils, the high charcoal content and the potential long term protection of fine organic matter through encapsulation and absorption by clays;
- addition of a fire simulation capacity that could deal with stand replacing and/or regenerating fires, being either forest floor fires largely removing litter or crown fires affecting the whole tree;
- modification of wood product pool structures and lifecycles to reflect those cited in Jaakko Pöyry (1999);
- improved resolution of component distinctions of the standing tree material, splitting coarse and fine roots, branch and leaf material;
- potential to override the soil carbon model component by directly entering either field data or externally modelled inputs, and
- an added capacity to account from a primary data input of above-ground mass increment as an alternative to stem volume increment.

Within *FullCAM*, the *CAMFor* sub-component can take its growth information from any one of three sources:

- net primary productivity (NPP) derived from *3PG* with feedback from management actions (thinnings, etc.) specified in *CAMFor*;
- information entered from external models; and
- measures of either above-ground mass increment or stem volume increment.

Material entering the debris pool (that is the above-ground coarse and fine litter) and the decay (the root material below ground shed by live biomass) is accounted in either a decomposable or resistant fraction, with the potential to apply separate decomposition rates to each.

The information flowing from *3PG* to *CAMFor* is the total NPP, as reflected in whole tree productivity/growth. Rules for the allocation to various tree components and for the turnover rates that will affect the standing mass increment at any one time (change in mass as opposed to a total productivity change) are specified within a *CAMFor* table.

Neither *CAMFor* nor *3PG* (in this form) deal with a number of stems, but work on proportional change to mass per unit area. Thinning activities, such as harvest or fire, which are specified in *CAMFor* are treated as a proportional decrease of biomass and are reflected as an equivalent proportional decrease in canopy cover within *3PG*. For deforestation, the same applies, but with

a large residual of decomposing woody material being the primary change remaining within *CAMFor*.

## CAMAg

Within *FullCAM*, *CAMAg* serves the same roles for cropping and grazing systems as *CAMFor* does for forests. The *CAMAg* model reflects the impacts of management on carbon accumulation and allocates masses to various product pools within plants and to decomposable and resistant organic residues. Yields may be entered in the model in a variety of ways including above-ground, total or product mass, along with above- and belowground turnover rates. The principal human activities that drive transfers of material in *CAMAg* are ploughing, herbicide application, harvest, fire and grazing (with manure return).

With both *CAMFor* and *CAMAg* embedded within *FullCAM*, it is possible to represent the transitional afforestation, reforestation and deforestation (change at one site) or mix of agricultural and forest systems (discrete activities at separate sites). Under afforestation and reforestation there is a gradual change from the characteristics of the original pasture or cropping system, with the mass of organic matter derived from those systems decomposing and decreasing with declining input. For deforestation, the same applies, but with a large residual of decomposing woody material being the primary change remaining within *CAMFor*.

Within *FullCAM*, *CAMFor* and *CAMAg* can be proportionally represented (as under afforestation, reforestation and deforestation) according to the relative proportions of canopy cover for each of the woody (*CAMFor*) and non-woody (*CAMAg*) categories. This also provides capacity for modelling ongoing mixed systems such as agroforestry.

## MODEL INTEGRATION

The initial integration of the *FullCAM* was performed on a Microsoft Excel developmental version of the forest component of *FullCAM* and linked with the Excel versions of the models *3PG*, *CAMFor*, *GENDEC* and *Roth C*. The resultant developmental model, named *GRC3*, was used to test and refine the linkages between the models. It formed a 10-megabyte Excel workbook, which could be used for developmental purposes, but was not a realistic option for general or routine application.

The C code based application of *FullCAM* is a far more efficient and transportable (e.g., Mac, PC or Unix environments) format, with run speeds capable of continental scale application at fine spatial (using ArcBinary file format) and temporal resolution.

The linkages between models are sequential, from growth estimation (*3PG* for forests only) to management (*CAMFor* and *CAMAg*), decomposition (*GENDEC*) and soils (*Roth C*). The key linkages are as follows:

*3PG* to *CAMFor*: is achieved by inputting the total biomass increment from the *3PG* output to the *CAMFor* biomass table. Allocation of this material to various tree components (above- and belowground) will be as per the *CAMFor* mass distribution table.

*CAMFor* to *GENDEC*: is a transfer of the above-ground debris pools, splitting the decomposable and resistant material described in *CAMFor* between the soluble, cellulose and lignin plant input pools of *GENDEC*. When operated in conjunction, the *CAMFor* breakdown rates for this material act as a 'flow' mechanism to introduce material to the *GENDEC* model. The above-ground debris pools of *CAMFor* thus become holding pools of material which can flow to *GENDEC*. Belowground material is treated independently of *GENDEC* and is either transferred directly to the RPM and DPM pools of *Roth C* from *CAMFor*, or, if *Roth C* is not being implemented, given an empirical decay within the *CAMFor* 'Active' soils pools.

*CAMFor* to *Roth C (direct)*: if *CAMFor* and *Roth C* are in use (without *GENDEC*) the function of the 'breakdown' rates in *CAMFor* is used to decompose above-ground litter (unless ploughed in) which is then (minus losses to the atmosphere) placed in the *Roth C* 'HUM' (humified organic matter) belowground pool. Root material is transferred to the *Roth C* DPM and RPM pools.

*CAMAg* to *GENDEC*: the interaction between *CAMAg* and *GENDEC* mirrors that of *CAMFor* and *GENDEC*. Again *GENDEC* only operates on the pool of above-ground litter.

*CAMAg* to *Roth C (direct)*: the transfers of material when *CAMAg* and *Roth C* are run together (without *GENDEC*) are the same as for *CAMFor* to *Roth C*. Belowground material (and above-ground material 'ploughed in') is dealt with in the DPM and RPM pools of *Roth C*.

While the model is capable of being run at daily, weekly, monthly and annual time steps, the NCAS will generally operate the model at monthly time steps. The choice of time step for any operation will largely depend on the temporal variability of the system being modelled and the temporal resolution of the available data.

The principal testing of *FullCAM* was carried out on *GRC3*, the developmental Excel version, providing maximum transparency

and therefore an ability to track iterations of the spreadsheet formula. Another advantage was an ability to attach the @Risk add-on (Palisade 1997). Among other things, @Risk provides a capacity to implement sensitivity analyses within the Excel model given specified correlations between the various input variables. Each specified output is assessed for its sensitivity to each input variable. Correlations between input variables can be specified and *Monte Carlo* analyses run to enable uncertainty analyses given specified variability. @Risk can also interact with the FullCAM code version and will be implemented within developer's versions of the model.

A range of activities are underway within the NCAS that provide required calibrations for the various components of the *FullCAM* model. Much of this activity was initiated upon selection of the various component models for independent programs. Each of these programs provides for ongoing model testing.

## G'DAY

G'DAY, a **Generic Decomposition And Yield** model, simulates the cycling of carbon (C), nitrogen (N) and water in plant and soil. The model's general structure is shown in Figure 5. The plant sub-model simulates the C and N contents of leaves, fine roots, and wood. The soil sub-model predicts C and N in plant litter and soil organic matter pools (as in the CENTURY model - see CENTURY in this volume) and water storage in the rooting zone. Processes represented include plant photosynthesis and respiration, plant water and N uptake, tissue growth and senescence, litter and soil decomposition, net soil N mineralisation, N input by atmospheric deposition and biological fixation, and N loss by leaching and gaseous emission (Fig. 5). Photosynthetic rates depend on [CO<sub>2</sub>] and temperature, respiration depends on temperature and decomposition depends on soil temperature and moisture content. G'DAY has been used to investigate effects of altered climate and land use on forest ecosystems in tropical, temperate, mediterranean and boreal environments and on temperate grasses.

A time step of one day is used in the daily version of G'DAY. Carbon gain (denoted assimilation in Figure 5) is a function of absorbed light, leaf nitrogen, temperature, soil moisture and autotrophic respiration. The latter is a carbon loss that is usually represented as a constant fraction of gross primary productivity but can also be represented as a function that is proportional to plant non-structural N content (Ryan 1991) and temperature (Medlyn *et al.* 2000). Allocation of net primary produce (NPP) to foliage, fine roots and wood (stem, branches and coarse roots) is constant. The water balance is calculated using either the

Penman-Monteith equation or the RESCAP model as specified in Dewar (1997). Allowance is made for water intercepted by the canopy, runoff and drainage, and evaporation from a top soil layer to obtain effective rainfall (infiltration) before transpiration is calculated. Nitrogen inputs include atmospheric decomposition, biological fixation and fertilisation. Nitrogen losses represent N emissions and leaching as well as the removal of wood and other plant debris. Decomposition and mineralisation are represented by CENTURY and are based on functions of soil moisture, soil temperature, and litter quality (nitrogen and lignin contents). Daily inputs to G'DAY include total solar radiation (or PAR), maximum and minimum temperature, and precipitation. G'DAY also requires a range of site specific parameters, either sourced from empirical studies or estimations.

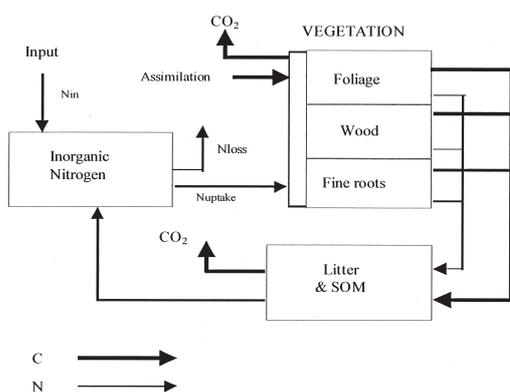


Figure 5: Pools and fluxes of C and N in G'DAY.

G'DAY is fully described in Comins and McMurtrie (1993) and modifications to the plant sub-model is fully described in Medlyn *et al.* (2000) and RESCAP in Dewar (1997). For the CENTURY decomposition sub-model see Parton *et al.* (1987) for a detailed description, and modifications are described in Parton *et al.* (1993).

## GENDEC

GENDEC predicts litter mass loss during decomposition. It does this by combining elements of microbial physiology and population dynamics with empirical observations of C and N pool dynamics, litter mass loss and changing C:N ratios (Moorhead and Reynolds 1991).

Although GENDEC was originally developed to predict litter decomposition in the northern Chihuahuan Desert of southern New Mexico (Moorhead and Reynolds 1991), it has been more recently applied to decomposition of Arctic tussock tundra (Moorhead and Reynolds 1993) and deciduous tree litter

(Moorhead *et al.* 1999, Moorhead and Sinsabaugh 2000). The version of GENDEC shown in Figure 6 was derived from that used by Moorhead and Sinsabaugh (2000).

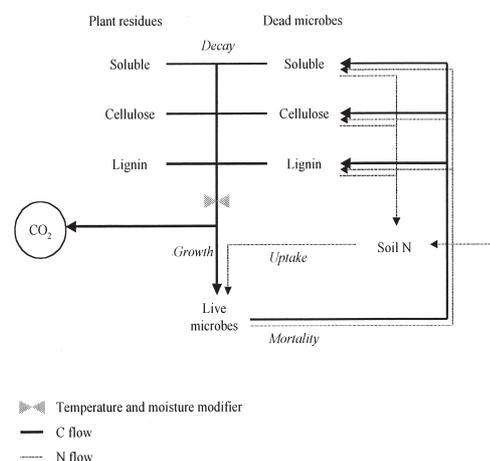


Figure 6: Basic structure and flows of carbon and nitrogen in GENDEC.

Various pools are used in GENDEC, representing dead organic matter (plant residues and dead microbes), living biomass and soil N (Figure 6). There are three pools of dead microbes and three pools of plant residues. Each of these six dead organic matter pools has a different decomposition rate. These rates are modified in accordance with moisture and temperature conditions and N limitation.

Flows between pools are driven by empirical relationships according to characteristics of the microbial community. Microbial growth and respiration are driven by total C losses from dead organic matter, assuming a microbial C assimilation efficiency. A microbial death rate is also inherent in the model. Nitrogen flows are assumed to balance calculated C flows, given assumed N:C ratios of live and dead microbial material. Nitrogen inputs to the soil can also be incorporated in the model.

Inputs required for GENDEC include:

- Microbial assimilation efficiency
- Microbial cell wall fraction
- Microbial cellulose fraction
- Microbial turnover rate
- Monthly limitations of temperature and water availability on decomposition (0 to 1)
- Initial C mass of the live microbes
- Initial C mass of the six dead organic matter (litter) pools

- Initial mass of available N and monthly input of N into the soil

When compared to CENTURY, GENDEC was found to be less sensitive to site conditions (i.e. temperature and moisture) but more sensitive to litter quality and soil nitrogen availability (Moorhead *et al.* 1999).

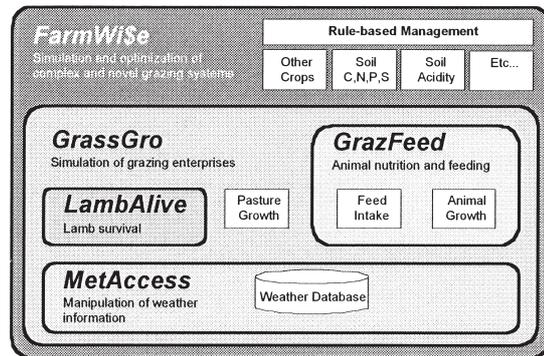
## GRAZPLAN

The GRAZPLAN suite of models has been developed as part of a decision support project for temperate Australian grazing lands. The models are configured in different ways to meet particular purposes. For the purposes of the workshop, the key models are the ruminant biology model (Freer *et al.* 1997), the soil moisture budget and pasture growth model (Moore *et al.* 1997) and our unpublished soil nutrient cycling model. Together these models represent the cycling of C, N, P and S in the soil-plant-atmosphere-animal system. The models operate at a daily time step. They take precipitation, maximum and minimum air temperature, solar radiation, potential evapotranspiration and wind speed as driving variables (PET is usually estimated from pan evaporation).

The soil water budget is based on that of Williams *et al.* (1985). It includes a term for interception of water on herbage and its subsequent evaporation. Sub-daily time steps may be used in simulating percolation. Evaporation from bare soil and transpiration are modelled as parallel processes.

The pasture model distinguishes multiple species growing together, and within each species keeps track of tissue pools classified as seedling/established and leaf/stem/root/seed. For shoots live/dead/litter pools and five digestibility classes are also followed. Phenology of each species is followed, including dormant stages. Net assimilation is estimated as a function of radiation amount and intensity, temperature, soil moisture, PET and soil solution nutrient contents; it is computed as the product of radiation receipt and RUE, modified by growth-limiting factors.

The nutrient (N, P and S) economy of plants is modelled using a demand and supply approach. Uptake of nutrients is modelled using the approach of de Willigen and van Noordwijk (1994); biological N-fixation and internal recycling of nutrients are also modelled. Allocation of assimilate follows a functional equilibrium approach and depends on species, phenological stage and light regime. Tissue death, litter fall and changes in digestibility depend on phenological stage, soil moisture and temperature. Processes of seed dormancy, germination and seeding establishment are simulated.



The GRAZPLAN Suite of Models

The ruminant biology model is a development from the Australian feeding standard (SCA 1990). It may be applied to any breed of sheep or cattle. Potential intake of animals is a function of their size; their actual intake is estimated as a fraction of potential intake by considering the amount and quality of pasture available to the stock (animals select a diet of higher quality than that which is on offer). Intake may be influenced by the availability of supplementary feeds. Maintenance requirements for energy and protein are estimated from the breed and weight of the animal and its level of intake. Utilization of protein depends on the amount of digestible protein leaving the stomach, including bypass protein and microbial crude protein. Requirements for pregnancy, lactation and wool growth are estimated where appropriate. Once all other uses of energy and protein have been estimated, the balance is used to estimate the weight change of the stock. Faecal and urinary outputs of carbon and nutrients are predicted, as are methane emissions from livestock.

The soil nutrient cycling model has not yet reached a stable form. The current version has four SOM pools and follows profiles of inorganic nitrate, ammonium, urea, phosphates and sulphate. Separate "fixed" and "available" phosphate pools are simulated. Solution concentrations of the nutrients are estimated from available concentrations using a range of sorption functions. SOM decomposition is predicted using first-order equations for each pool, modified by soil temperature, moisture and pH; constant efficiencies of microbial synthesis and humification rates are assumed for each pool. The C:nutrient ratio of the biomass pool depends on external nutrient concentrations, while the C:nutrient ratio of humus is fixed. Transformations between N forms are simulated, as are inputs of excreta (taking spatial heterogeneity into account) and the application and breakdown of fertilizers. The model may be linked to a simple process model of soil acidification.

These models form the basis of the GRAZPLAN suite of decision support tools. In particular, the ruminant biology model underpins the successful GrazFeed decision support tool, which provides hundreds of users across southern Australia with tactical advice about livestock nutrition; and the pasture, soil water and ruminant models are distributed to users in the GrassGro decision support tool for analyzing grazing systems.

## GRASP

GRASP is a 'pasture growth' model which combines a soil water model and a model of above-ground dry-matter flow. It has been built to meet specific objectives relating to grazing management of Australian rangelands:

- objective assessment of drought and degradation risk in near-real time (Carter *et al.* 2000);
- simulation of grazing management options including seasonal forecasting (Ash *et al.* 2000, McKeon *et al.* 2000, Stafford Smith *et al.* 2000);
- assessment of safe carrying capacity (Johnston *et al.* 1996, Hall *et al.* 1998);
- evaluation of impact of climate change and CO<sub>2</sub> increase (Hall *et al.* 1998, Howden *et al.* 1999);
- reconstruction of historical degradation episodes (Carter *et al.* 2000).

GRASP has been developed incrementally since 1978 in parallel with application studies and field trials. Thus the model has been under constant critique/review in terms of development, parameterisation, validation and usefulness to client needs. Currently GRASP is being developed to address issues of deep drainage, tree growth and death, and grazing land degradation. Each relationship in the model is described in Littleboy and McKeon (1997), and a critique of model limitations is given in Day *et al.* (1997).

### Soil water balance

The soil water balance in GRASP simulates, on a daily time step, the processes of soil evaporation, pasture transpiration (Rickert and McKeon 1982), tree transpiration (Scanlan and McKeon 1993), run-off, and through drainage. Four soil layers are simulated on a daily time step (0-10cm, 10-50cm, 50-100cm, >100cm). Soil evaporation occurs from top 50cm, grass transpiration from top 100cm and tree transpiration from all four layers. Initially an empirical runoff model has been used (Scanlan *et al.* 1996) with run-off calculated as a function of surface cover, rainfall intensity and soil water deficit. A more standard hydrological approach (curve numbers linked to cover) has also been implemented (Yee Yet *et al.* 1999). Potential

evaporative demand is input as Class A Pan or calculated from vapour pressure deficit (VPD) and solar radiation.

### Dry matter flow

The above-ground pasture processes of growth, senescence of green tissue, detachment of standing dead, litter decomposition, animal trampling and consumption are modelled at a daily time step. Five pasture dry matter pools are represented: green leaf; green stem; standing dead leaf; standing dead stem; and surface pasture litter. Plant growth is calculated as a function of solar radiation interception, air temperature, VPD, soil moisture or grass transpiration, and available nitrogen. Growth parameters can be changed for different levels of CO<sub>2</sub>. Senescence is a function of frost, soil water deficit and age. Detachment is a function of season and rainfall. Litter decomposition is a function of temperature and surface moisture. Trampling and consumption are functions of stocking rate (beasts/ha) and pasture availability. Pasture burning is also simulated by resetting dry matter pools. Daily climate data are used as inputs and surfaces of daily climate data (Jeffrey *et al.* 2000) have been developed to support application at a national level.

Nitrogen uptake is calculated as a function of transpiration accumulated from the start of the growing season in each year. Potential annual nitrogen uptake is a key parameter as nitrogen limits pasture growth in wetter years (Mott *et al.* 1985). Parameters have been derived from data collected in field studies (>100 sites) specifically designed to measure as many of the functional parameters (e.g. peak nitrogen yield) as possible (McKeon *et al.* 1990, Day *et al.* 1997). The project has been generously supported since 1986 by the goodwill of many pasture scientists in northern Australia. Calibration is usually restricted to a limited number of parameters (e.g. above-ground transpiration efficiency, nitrogen uptake per mm of transpiration, potential regrowth rate after defoliation or burning). Spatial versions of the model have allowed parameterisation using (1) extensive ground truthing measurements of above-ground standing dry matter (>200,000 observations in Queensland, Hassett *et al.* 2000); and (2) time series of remotely sensed green cover (NDVI, Carter *et al.* 2000). Animal production (annual steer live weight, wool cut) is calculated at an annual time step from simulated variables such as percent utilisation, number of green or growing days (Hall *et al.* 1998, McKeon *et al.* 2000).

## Grazing effects

The various effects of grazing on pastures have been simulated with sub-models of:

- perennial grass basal cover which drives potential regrowth rate;
- pasture composition which changes species parameters (e.g. nitrogen use efficiency, detachment rates);
- effects of grazing on plant functioning (water and nitrogen uptake); and
- soil loss affecting available water range and nutrient availability.

## Tree/shrub effects

The representation of tree/shrub effects has concentrated on the dominating competitive effect of trees/shrubs for water and nitrogen (e.g. Scanlan and McKeon 1993, Cafe *et al.* 1999). Sub-models of the effects of tree/shrub cover on pasture microclimate, pasture species composition, and water, nitrogen and litter flow are now being developed. J.O. Carter (unpublished) is developing a tree growth model in GRASP for rangelands.

### LINKAGES

LINKAGES is a simulation model of linked carbon and nutrient cycles developed to simulate forest growth and long term community dynamics in northeastern USA. The basic structure of the model consists of a set of three sub-models (TEMPE, MOIST, DECOMP) that determine site conditions and a set of three demographic sub-models (BIRTH, GROW, KILL) that calculate tree growth and population dynamics (Figure 7). These two set of sub-models are linked with GMULT sub-model that estimates growth multipliers.

LINKAGES represents effects of climate, soil N and water availability on growth of different tree species, and feedbacks between species chemistry, N availability, and forest production that may control species composition. It requires a relatively simple set of calibration data, and can simulate the development of both even-aged, single species, and mixed-age, mixed-species stands. It has been used in other forest types and conditions ; .

Production is simulated using the single-tree, non-spatial 'gap' model construct ; . Simulated plot size can vary depending on the stature of the forest. Individual trees of each species are established (with a dbh between 1 and 3 cm chosen stochastically) at a user-specified rate, if light and moisture conditions are suitable for the species. These established individuals increment in diameter on an annual time-step.

Growth rate is a proportion of potential maximum diameter increment under optimal conditions (essentially a function of the maximum age and maximum diameter of each species), and modified according to the simulated availability of light, water and N, and varying species response to the availability of these different resources. Mortality is simulated in two ways: (i) exogenous mortality is simulated by killing a small proportion of trees each year, so that 1% of trees reach the potential maximum age for their species; and (ii) within stand competition is simulated by increasing the probability of death for trees that grow slowly due to lack of available resources.

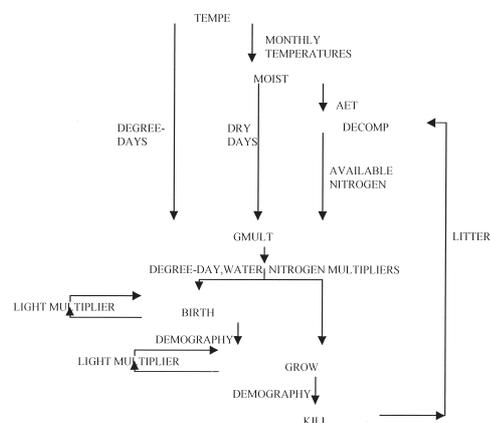


Figure 7: Schematic flow diagram of the Linkages.

Light at any level in the canopy is a function of the foliage biomass (determined from allometric relationships between diameter and foliar biomass) above that level, assuming all foliage for an individual is situated at the top of the tree, and spread across the entire plot. Available moisture is calculated from climate and soil texture. The mean and the standard deviation of monthly temperature and precipitation for the study area are input, and normally-distributed, random values are selected to simulate an annual climate. Thornthwaite and Mather's monthly actual evapotranspiration (AET) is calculated according to an approximation function (Pastor and Post, 1984), and combined with soil moisture-holding capacity (from soil texture) to determine the proportion of the growing season that soil moisture falls below field capacity. This value is used to reduce diameter growth. Foliar, root and twig litterfall are calculated for each year from foliar biomass and foliage retention time. Coarse woody litter is a function of mortality.

N is assumed to be limiting tree growth and N availability is calculated in the decomposition component. Litter mass loss is

a function of litter quality (lignin:N) and AET. The model accounts for annual litter cohorts of each species and litter type (leaves, roots, twigs and logs). N dynamics is simulated for each cohort using a linear relationship between the mass remaining and the N concentration in the remaining material : The coefficients of this relationship are specified as input for each litter type. Woody litter cohorts lose mass at user-specified annual rates. Lignin dynamics are simulated in a similar way. Lignin:N ratio for each cohort is updated annually for each cohort, which affects mass loss for the following year. Depending on the slope of the relationship between %OM remaining and %N, and the proportion of mass remaining, the model simulates either nitrogen immobilisation or release. Some immobilisation is satisfied by N in throughfall, external inputs, and biological fixation, the remainder from N mobilised from other cohorts. When litter reaches a certain percent N remaining when it is transferred to the humus or well-decayed wood pools that lose mass, and N, at a constant rate (1-2% per year).

The model code is in FORTRAN (a C version has also been produced) and is structured to run over long time periods (50-1000 years or more). Up to 100 plot replications can be simulated to assess the variation associated with stochastic processes such as climate, regeneration and mortality. Outputs include above ground biomass and number of stems by species, NPP, litterfall, N mineralisation, and CO<sub>2</sub> evolution.

## ProMod – A SITE PRODUCTIVITY MODEL

ProMod is intended primarily for screening prospective plantation sites. It focuses on the period following canopy closure, and provides a prediction of the closed-canopy leaf area index (LAI), annual net primary production (NPP), and water use by the stand, and available soil water (ASW). ProMod is calibrated to predict measures of site productivity of specific interest to forest managers, e.g. peak mean annual stem-volume increment of a plantation. It is used in combination with a conventional empirical model to predict stand development.

ProMod has its roots in a workshop ("FORMOD95: a Tree and Forest Growth Modelling Workshop", Sands 1995a) that brought together modellers and representatives from forest industries to assess if and how process-based models could provide tools for plantation management. Little specific interest was expressed in detailed predictions of biomass partitioning, so a pragmatic approach to the development of a model predicting site productivity was adopted: empirical expressions were developed for several key relationships that are other-wise difficult to model, and used in conjunction with a realistic, physiologically-based model for NPP.

A simple empirical submodel for the closed-canopy LAI was based on long-term climatic factors, drawing on the observation that LAI varies only slowly with long-term conditions following canopy closure. Daily canopy water-use

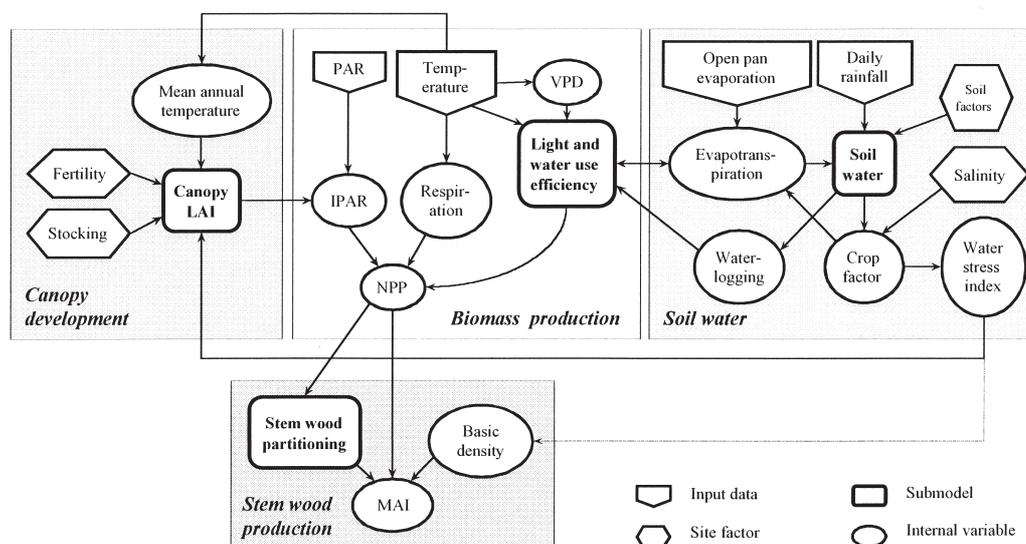


Figure 8: A simple representation of the structure of ProMod, and its input and output data.

efficiency is a function of vapour pressure deficit (VPD), and the crop factor, or ratio of actual transpiration to open-pan evaporation, depends only on relative ASW. However, development of ProMod was also physiologically realistic as ASW is modelled using a daily water-balance model (McAlpine 1970), and the heart of ProMod is a model of canopy photosynthesis (Sands 1995b, 1996) soundly based on physiological principles and parameterised from the results of physiological experiments. Production is calculated daily, taking limitations due to water stress or VPD into account, and summed to give annual NPP. Predicted NPP is converted to measures of site productivity through an empirical calibration based on a comparison of predicted NPP with observed measures of site productivity frequently used by forest managers.

ProMod was parameterised for *E. globulus* using data from 9 research plots in Tasmania and Western Australia, and validated against 19 *E. globulus* plots in N Tasmania. Full details of the development, structure, parameterisation and validation of ProMod are in Battaglia and Sands (1997), and its structure, input data and outputs are summarised in Figure 8. ProMod has since been parameterised for *E. nitens* and *Pinus radiata* and applied to various management-related problems (Sands 2000, Mummery and Battaglia 2001, Battaglia *et al.* 2001).

The input data required by ProMod are of a quality and quantity that forest managers can readily and cheaply obtain. The site factors are site latitude; measures of soil texture, stoniness, depth and drainage, including the presence or absence of a hard pan or other features that impede root growth; a measure of salinity; an index of the site's capacity to supply the nutrients necessary for growth; and the depth to any watertable. These can often be obtained from local knowledge and soil-data map sheets. The climatic factors are the monthly mean values of daily maximum & minimum temperatures, radiation, rainfall, pan evaporation and number of rain days. These can all be obtained from a bioclimatic package such as Esoclim, or from historical meteorological bureau data. ProMod can also be run using actual daily meteorological data.

The primary output from ProMod is NPP, an unequivocal measure of the productive potential of a site. However, as this is of little interest to a manager, NPP was calibrated against observed measures of stem volume production to provide practical measures of productivity. Other outputs include LAI, canopy water use, available soil water, and light use efficiency. ProMod can be used to infer the extent to which factors such as temperature, soil-water and site fertility are limiting

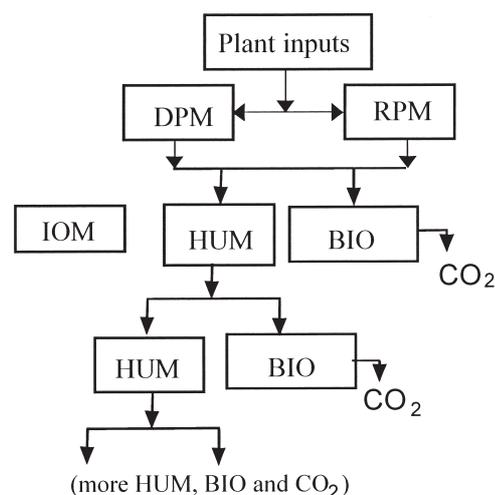
production (Battaglia and Sands 1997). The measures of productivity predicted by ProMod can be used to drive conventional empirical stand development models, e.g. the hybrid of ProMod and NitGro predicts the age variation of mean dominant height, stand basal area, stem volume and MAI (Battaglia *et al.* 1999).

ProMod has been implemented as Visual Basic macros running behind Excel spreadsheets, and as a stand-alone package. The Excel version provides a convenient, flexible development tool, even though execution speeds are slow. The stand-alone program has a simple, user-friendly interface, and site and climatic data can be provided as a text file, or entered directly and edited using a data-entry form as part of the user interface. This implementation was subsequently included on a CD of software tools for use by farm foresters (Private Forests Tasmania 1999).

### ROTH-C

The Rothamsted soil carbon turnover model (Jenkinson 1990) was initially developed for grassland, forest, pasture and crops under temperate European conditions. Figure 9 shows the model where plant material enters the soil environment and undergoes decomposition through the soil microbial biomass to form a number of well defined pools with the emission of CO<sub>2</sub>. These pools have varying resistance to degradation, ranging from highly labile through to inert material.

### The Rothamsted Model



The model essentially consists of a five-compartment system with separate organic carbon pools:

- inert organic matter (IOM)
- easily decomposable plant material (DPM)
- resistant plant material (RPM)
- microbial biomass (BIO)
- humified organic matter (HUM)

Both DPM and RPM decompose to form CO<sub>2</sub>, BIO and HUM, with subsequent further decomposition of the BIO and HUM to more CO<sub>2</sub>, BIO and HUM. The amount and nature of plant material, clay content, rainfall, pan evaporation, soil temperature and the rate constant for each pool affect the rate of carbon decomposition and thus determine the carbon balance in the soil. Plant residue inputs are either measured directly or are estimated from crop yield data. Different qualities of plant input material (eg different N contents) are handled through varying the DPM/RPM ratio. The model runs on a monthly time step.

In Australia, the model has been calibrated and tested against a number of long-term field trials for depths between 10 and 30 cm using particulate organic carbon (POC) and charcoal-C as surrogates for the RPM and IOM pools respectively. The HUM pool is determined by difference. The model performs well under these conditions with a slowing of the RPM pool rate the only modification required.

## SOCRATES

SOCRATES (**S**oil **O**rganic **C**arbon **R**ates **a**nd **T**ransformations in agro-**E**cosystems) (version 3.00b) is a simulation model developed in Australia to estimate changes in SOC, as influenced by crop and pasture rotation, N fertilizer addition, disease, grazing intensity and climate. It was originally developed as a simple, less-data intensive alternative to the more complex CENTURY (Parton *et al.* 1987) and Rothamsted C models (Jenkinson 1990). The main considerations in the development of SOCRATES was that the input data could be easily and rapidly measured in the laboratory and the model was as widely applicable as both the CENTURY and Rothamsted C models. SOCRATES uses a weekly time step, however the driving variables include, annual or monthly precipitation (mm), mean annual temperature (°C), soil clay content (%) or CEC (mmol kg<sup>-1</sup>) and initial soil organic C (%).

The carbon model consists of 5 components. Plant material entering the soil matrix is divided into decomposable (sugars and carbohydrate), and resistant material (lignin and cellulose)

and the soil components consists of microbial biomass and humus. The microbial fraction is further divided into a transient unprotected fraction, which is involved in the initial stage of crop residue decomposition and a protected fraction that is actively involved in the decomposition of native humus and microbial metabolites (Ladd *et al.* 1995). When initialising the model, 2% of the measured SOC store is considered to be protected microbial biomass, with the remaining 98% being stable humus.

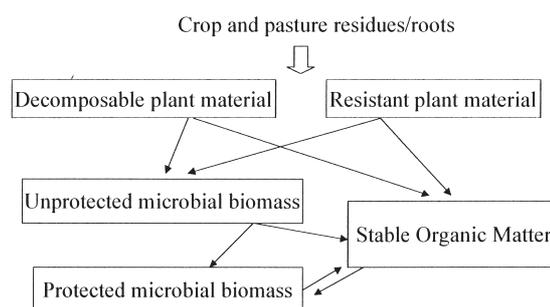


Figure 10: Compartmentalization of plant and soil components in the SOCRATES simulation model (v3.00b). Arrows indicate flow of organic C in the model structure.

The decomposition process in the model produces microbial material, humus and carbon dioxide (Fig. 10) in proportions which are dependent on soil texture, or more specifically the CEC of a soil (Amato and Ladd 1992).

The proportioning of C flows to the microbial biomass, humus and carbon dioxide, and the specific decay rates for each component of the model were initially calibrated using <sup>14</sup>C data of Ladd *et al.* (1995). The maximum first order decay rates currently used in the model are 0.84 w<sup>-1</sup> for decomposable plant material, 0.06, 6.65, 0.055 and 0.0009 w<sup>-1</sup> for resistant plant material, unprotected and protected microbial biomass and stable organic matter, respectively. The decay rate for the resistant plant fraction in SOCRATES is significantly faster than those specified in the CENTURY and Rothamsted C models, because by definition this material is considered to be recognizable light fraction which is capable of being removed prior to a SOC analyses being performed. The effect of temperature on decomposition is based on a Q<sub>10</sub> relationship of 2. With respect to soil water calculations, the model has been simplified by considering them to be based on a consistent seasonal cycle. The decay rates are set at 26% of the optimal rate when growing cereal crops and 90% of the optimal rate for fallows (where water is plentiful). For pasture, because additional root production may extract more water, the value used to modify the rate (16%) is lower than the value used for

cereals. A more detailed water balance model based on the potential evapotranspiration approach of Thornthwaite and Mather (1957) has been incorporated in later versions.

The model also contains a simple plant growth sub-model if required by the user. This sub-model is essentially a means of producing either leguminous or non-leguminous dry matter to be used in the SOC decomposition model. The user has the option to input actual yield data if available. Plant production is based on the relationship between growing season rainfall and stored soil water at sowing, and productivity, after adjustments are made for the water use efficiency of the system, which is similar to the approach used by French and Schultz (1984). A linear regression is specified for each crop or pasture for the potential yield in a certain environment and the yield is then adjusted using a water availability index (WAI) which also incorporates runoff and evaporation (Fig. 11).

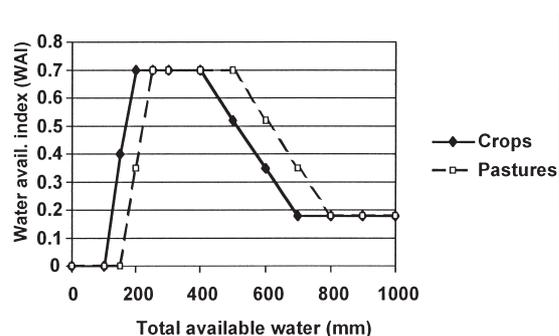


Figure 11: Relationship between total available water (seasonal rainfall and stored water) and the soil water availability index (WAI) for calculating aboveground plant production in SOCRATES v3.00b.

As a strong relationship exists between C accumulation, aggregate stability and infiltration (Tisdall and Oades, 1982), the WAI in the model will also change in response to fluctuations in annual C stores. The individual crops considered in the model are canola, barley, wheat, oats and grain legumes.

The model can also estimate grass and legume pasture productivity and is easily adapted for other crops (e.g. sorghum, millet, maize) through the generic plant growth sub-model. The plant production sub-model also responds to N fertilizer addition and the residual effect of N from grain and pasture legumes. Whilst the original version of SOCRATES does not explicitly simulate N mineralization, the partitioning of plant materials into decomposable and resistant fractions is based on their nitrogen content (i.e. cereals vs legumes). Mineralisation is explicitly outlined in later versions of SOCRATES with a linked soil C/N routine and modifications to simulate conservation

tillage strategies. A complete array of plant materials across all biomes can also be simulated in later versions.

The original model was field calibrated using a selection of yield and SOC data from the Permanent Rotation Trial at the Waite Agricultural Research Institute (Grace *et al.*, 1995) and has been found to be accurate in a wide range of semi-arid systems in South Australia, Victoria and Western Australia (RIRDC, unpublished report).

SOCRATES has been recognised as a model of global significance. Izaurradle *et al.* (1996) selected SOCRATES after testing it against five other SOC models (CENTURY, RothC 26.3, DNDC version 4.3, EPIC 5125 and ECOSYS). They selected SOCRATES for an agroecosystem carbon aggregation experiment for cropped and grassland soils in Canada because it reproduced soil organic carbon dynamics best in a series of long-term studies and met both strict statistical and practical criteria (Post *et al.*, 1999). Grace *et al.* (2001) also found it to be superior to the CENTURY model in simulating changes in SOC in semi-arid cropping systems in southern Australia and the model has been used in Ethiopia (Georgis *et al.*, 2001) for C management and as a teaching tooling the Midwest USA (G.P. Robertson, pers. comm.). SOCRATES has also been used in a continental assessment of soil C stocks of Australia in response to a range of climate change scenarios (Grace *et al.*, 1996; 2001)

### 3-PG

3-PG is a generalised stand model (i.e. it is not site or species-specific, but needs to be parameterised for individual species) applicable to plantations or even-aged, relatively homogeneous forests, which was developed in a deliberate attempt to bridge the gap between conventional, mensuration-based growth and yield, and process-based carbon balance models (Landsberg and Waring 1997). The model consists, essentially, of two sets of calculations: those that lead to biomass values, and those that distribute biomass between various parts of the trees, and hence determine the growth pattern of the stand (Fig. 12). It includes water use and soil water balance calculations. Time step is a month and the state of the stand is updated each month.

The input data required by the model are monthly average values of solar radiation, atmospheric vapour pressure deficit (VPD), rainfall, frost days per month and average temperature, soil water holding capacity in the root zone ( $q$ , mm depth equivalent), initial stem number ( $n_{st}$ ), initial total stem, foliage and root mass ( $w_s$ ,  $w_f$  and  $w_r$ , Mg ha<sup>-1</sup>), and an (index) value

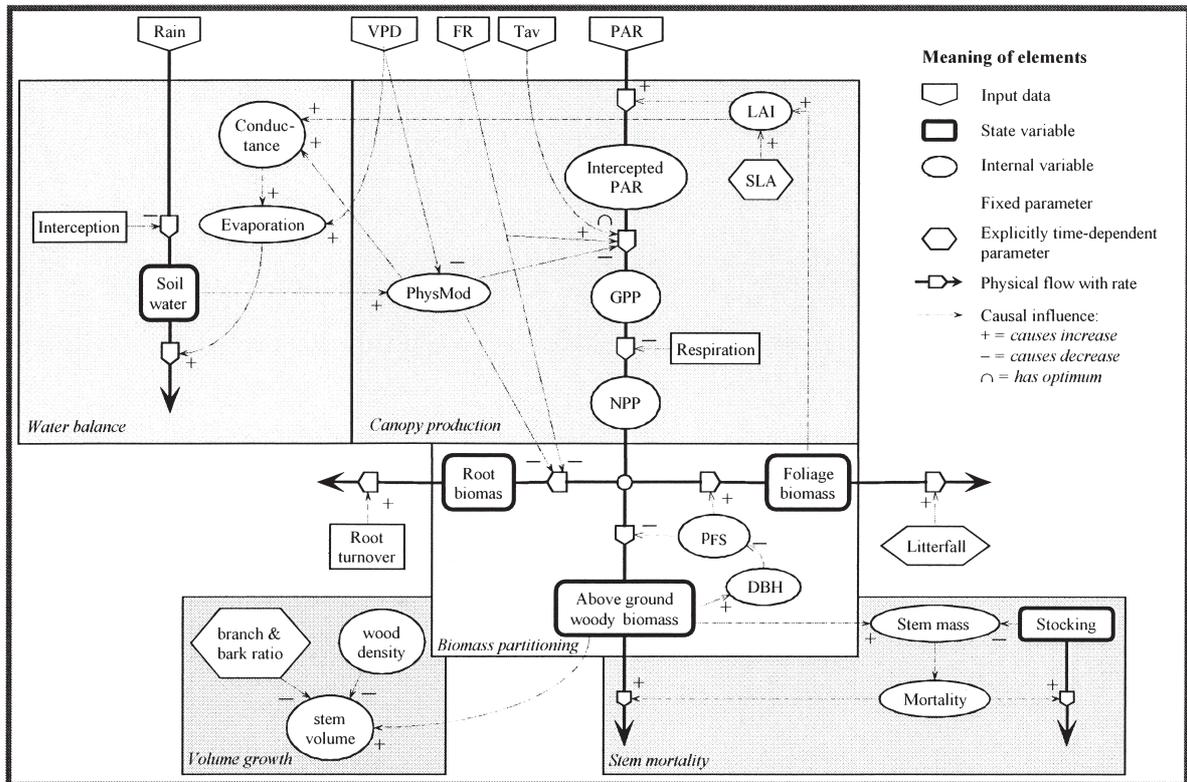


Figure 12: Flow diagram for 3-PG showing model structure, causal influences and interactions. (Diagram developed by Peter Sands)

for soil nutrient status (the fertility rating, FR). FR takes values between 0 (very poor nutrition) and 1 (optimum nutrition). Parameter values needed are the constants ( $a_i$ ) and coefficients ( $n_i$ ) of the allometric equations ( $w_i = a_i B^{n_i}$ ), specific leaf area (SLA), cardinal temperatures (see below), litterfall rate, maximum stomatal conductance and, the most important, canopy quantum efficiency (QE).

Output variables are those of interest to forest managers: monthly or annual values of Leaf Area Index ( $L^*$ ), stem mass and volume, stem growth rate, Mean Annual (volume) Increment (MAI), stem basal area and stem number. Litterfall (mass), and root turnover are calculated from input rates. Stand transpiration and evaporation of intercepted water are calculated producing monthly soil water balance values.

Gross Primary Production (GPP) is the product of Absorbed Photosynthetically Active Radiation (APAR) and QE, which is modified by correcting for the effects of soil drought, atmospheric vapour pressure deficits and temperature. Stomatal conductance is affected by VPD; it influences QE and the values are also used in the calculation of transpiration

(Ewers *et al* 2001). QE ( $a_c$ ) is also assumed to be linearly dependent on nutrition:

$$a_c = a_0(fN_0 + (1 - fN_0)FR)$$

where  $a_0$  is the maximum (unconstrained) value of QE. We originally used a default value of  $0.03 \text{ mol C (mol quanta)}^{-1}$  (equivalent to  $1.65 \text{ g C MJ}^{-1} \text{ APAR}$ , assuming  $0.5 \text{ g C (g dry biomass)}^{-1}$ ). Values of 0.04 and 0.05 have been obtained from work in the USA (Law *et al.* 1999), and studies on fast-growing eucalypts indicate a maximum  $a_0$  value of  $0.07 \text{ mol C (mol quanta)}^{-1}$ . We use  $a_0 = 0.05$  for conifers and 0.065 for broadleaved species.  $fN_0$  is usually taken as 0.6 or 0.55. Evidence for these values is not strong, but some exists.

The NPP:GPP ratio is assumed constant, eliminating the need to calculate respiration. Carbohydrates are allocated to roots first, the proportion of monthly NPP going to roots increases under poor nutritional conditions and is increased by water stress. Allocation to stems and foliage is on a single-tree basis and relies on the ratio of the derivatives ( $p_{f,S}$ ) of the allometric equations describing leaf ( $w_f$ ) and stem ( $w_s$ ) mass in terms of stem (bole) diameter at 'breast' height (B). The procedure is dynamic and self-regulating. The equations are

$$p_{f,S} = (dw_f/dB)/(dw_g/dB) = a_f n_f B_f^{(n_f-1)} / a_S n_S B_S^{(n_S-1)} \int a_p B_p^n \quad (1)$$

$p_{f,S}$  affects the carbon allocation coefficients for foliage ( $h_f$ ), roots ( $h_r$ ) and stems ( $h_s$ ) - which must sum to unity - through the relations

$$h_s = (1 - h_f)/(p_{f,S} + 1) \text{ and } h_f = 1 - h_r - h_s. \quad (2)$$

$L^*$  is calculated from SLA, foliage mass/stem and stem number.

Mass losses through litterfall and root turnover can be used as inputs to stand carbon balance calculations.

Stem size is calculated by inversion of the allometric equation; stand volume comes from stem mass, wood density and stocking (stem number per hectare).

Stem mortality is governed by the  $-3/2$  power 'law'; the point where mortality starts is set by a stem mass value. This works well when natural mortality is the main mechanism, although the start of stem mortality tends to be too abrupt. 3-PG includes a thinning routine.

3-PG is being evaluated in many countries, including Australia (Coops *et al.* 1998; Tickle *et al.* 2000; Sands and Landsberg 2001), New Zealand (Coops *et al.* 1998a; White 2000; Whitehead *et al.* 2001), the USA (Coops *et al.* 2000b; Landsberg *et al.* 2000; Coops and Waring 2001a, b), South Africa (Dye 2001), Brazil, Chile, the UK (Waring 2000), Denmark, Sweden. It has been adopted as an operational tool by a major forestry company (Aracruz Celulose SA) in Brazil, where it will be implemented in a GIS, in association with calibration plots and fertilisation experiments. In that application stem number and volume outputs will be analysed using conventional forestry product models. It has also been combined with satellite measurements to give remotely sensed input information into important physiological driving variables in the model (Coops *et al.* 1998b; Coops 1999).

EXCEL/Visual Basic software for the 3-PG model has been developed by Dr Peter Sands (CSIRO DFFP, Hobart) and another version of the code (produced by Dr Nicholas Coops and Andrew Loughhead, CSIRO DFFP) is available in C++. This allows spatial ARC/INFO coverages to be input and spatial estimates of parameters to be produced. Both of these versions of the code are available at [www.landsberg.com.au](http://www.landsberg.com.au) and mirrored at CSIRO FFP WWW site ([www.ffp.csiro.au](http://www.ffp.csiro.au)). Peter Sands' software is accompanied by a Technical Report on the model (Sands 2001).

## References

- Aber, J.D. and Melillo, J.M. (1980). Litter decomposition: measuring relative contribution of organic matter and nitrogen to forest soils. *Canadian Journal of Botany* **58**: 416-421.
- Amato, M. and Ladd, J.N. (1992). Decomposition of  $^{14}C$ -labelled glucose and legume materials in soils: Properties influencing the accumulation of organic residue C and microbial biomass C. *Soil Biology Biochemistry* **24**: 455-464.
- Ash, A.J., O'Reagain, P.J., McKeon, G.M. and Stafford Smith, M. (2000). Managing climate variability in grazing enterprises: A case study of Dalrymple Shire, north-eastern Australia. 'Applications of Seasonal Climate Forecasting in Agricultural and Natural Ecosystems - the Australian Experience'. (Eds G. Hammer, N. Nicholls and C. Mitchell.) Kluwer Academic Press: Netherlands. p 253-270.
- Battaglia, M., Mummery, D. and Smith, A. (2001). Economic analysis of site survey and productivity modelling for the selection of plantation areas. *Forest Ecology and Management* (In press).
- Battaglia, M. and Sands, P.J. (1997). Modelling site productivity of *Eucalyptus globulus* in response to climatic and site factors. *Australian Journal of Plant Physiology* **24**: 831-850.
- Battaglia, M., Sands, P.J. and Candy, S.G. (1999). Hybrid growth model to predict height and volume growth in young *Eucalyptus globulus* plantations. *Forest Ecology and Management* **120**: 193-201.
- Botkin, D.B. (1993). *Forest Dynamics*. Oxford Univ. Press, Oxford.
- Cafe, L.M., McKeon, G.M., Dyer, R.M. and Heywood, J.M. (1999). Trees compete with pastures in the semi-arid tropics of the Northern Territory. VIth International Rangeland Congress Proceedings Vol. 1. pp. 291-292.
- Carter, J.O., Hall, W.B., Brook, K.D., McKeon, G.M., Day, K.A. and Paull, C.J. (2000). Aussie GRASS: Australian grassland and rangeland assessment by spatial simulation. In 'Applications of Seasonal Climate Forecasting in Agricultural and Natural Ecosystems - the Australian Experience'. (Eds G. Hammer, N. Nicholls and C. Mitchell.) Kluwer Academic Press: Netherlands pp. 329-350.
- Comins, H.N. and McMurtrie, R.E. (1993). Long-term response of nutrient-limited forests to  $CO_2$ -enrichment; equilibrium

- behaviour of plant-soil models. *Ecological Applications* **3**: 666-681.
- Coops, N.C. (1999). Linking multi-resolution satellite-derived estimates of canopy photosynthetic capacity and meteorological data to assess forest productivity in a *Pinus radiata* (D. Don) stand. *Photogram. Eng. Remote Sen.* **65**: 1149-1156.
- Coops, N.C. and Waring, R.H. (2001a). Estimating maximum potential site productivity and site water stress of the Eastern Siskiyou Mountains of southwestern Oregon using a satellite driven process model, 3-PGs. *Can. J. For. Res.* **31**: 143-154.
- Coops, N.C. and Waring, R.H. (2001b). Assessing forest growth across southwestern Oregon under a range of current and future global change scenarios using a process model, 3-PG. *Global Change Biology* **7**: 15-29.
- Coops, N.C., Waring, R.H., Brown, S. and Running, S.W. (2000a). Predictions of net primary production and seasonal patterns in water use with forest growth models using daily and monthly time-steps in south-eastern Oregon. *Ecological Modelling* (in press).
- Coops, N.C., Waring, R.H., Landsberg, J.J. (1998a). Assessing forest productivity in Australia and New Zealand using a physiologically-based model driven with averaged monthly weather data and satellite-derived estimates of canopy productivity. *For. Ecol. and Manage.* **104**: 113-127.
- Coops, N.C., Waring, R.H. and Landsberg, J.J. (1998b). The development of a physiological model (3-PG S) to predict forest productivity using satellite data. In: G. Nabuurs, T. Nuutinen, H. Bartelink, & M. Koorhonen, eds. *Forest scenario modelling for ecosystem management at landscape level*. EFI Proceedings, pp. 173 -191.
- Coops, N.C., Waring, R.H. and Landsberg, J.J. (2000b). Estimation of potential forest productivity across the Oregon transect using satellite data and monthly weather records. *Int.J. Remote Sens.* (in press).
- Day, K.A., McKeon, G.M. and Carter, J.O. (1997). Evaluating the risks of pasture and land degradation in native pasture in Queensland. Final report for Rural Industries and Research Development Corporation project DAQ124A.
- Dewar, R.C. (1997). A simple model of light and water use evaluated for *Pinus radiata*. *Tree Physiology* **17**: 259-265.
- de Willigen P. and van Noordwijk, M. (1994). Diffusion and mass flow to a root with constant nutrient demand or behaving as a zero-sink. *Soil Science* **157**: 171-175.
- Dye, P.J. (2001). Modelling growth and water use in four *Pinus patula* stands with the 3-PG process-based model. *South African For. Jnl.* (In press).
- Ewers, B.E., Oren, R., Johnsen, K.H. and Landsberg, J.J. (2001). Estimating maximum mean canopy stomatal conductance for use in models. *Can. J. For. Res.* **31**: 198-207.
- Freer, M., Moore, A.D. and Donnelly, J.R. (1997). GRAZPLAN: decision support systems for Australian grazing enterprises. II. The animal biology model for feed intake, production and reproduction and the GrazFeed DSS. *Agric. Systems* **54**: 77-126.
- French, R.J. and Schultz, J.E. (1984). Water use efficiency in wheat production in a Mediterranean type of environment. I. The relationship between yield, water use and climate. *Australian Journal of Agricultural Research* **35**: 743-764.
- Georgis, K., Grace, P.R., Reeves, T.G. and Alston, A.M. (2001). Management options to sustain soil organic matter and productivity in cropping systems of semi-arid Ethiopia. *Agriculture, Ecosystems and Environment*.
- Grace, P.R., Bryceson, K., Hennessy, K. and Truscott, M. (1996). Climate change and soil carbon resources. In *Land use in a changing climate*, Maurice Wyndham Series, University of New England Press, Armidale, pp. 19-32.
- Grace, P.R., Bryceson, K., Hennessy, K., Truscott, M. and Post, W.M. (2001). The potential impact of climate change on Australia's soil organic carbon resources. *Agriculture, Ecosystems and Environment* (submitted).
- Grace, P.R., Georgis, K., Reeves, T.G., Alston, A. (2001). Simulating changes in soil organic carbon in cropping systems of the semi-arid Mallee region of Australia. *Agricultural Systems* (submitted).
- Grace, P.R., Oades, J.M., Keith, H. and Hancock, T.W. (1995). Trends in wheat yields and soil organic carbon in the Permanent Rotation Trial at the Waite Agricultural Research Institute, South Australia. *Australian Journal of Experimental Agriculture* **35**: 857-864.
- Hall, W.B., McKeon, G.M., Carter, J.O., Day, K.A., Howden, S.M., Scanlan, J.C., Johnston, P.W. and Burrows, W.H. (1998). Climate change and Queensland's grazing lands: II. An assessment of the impact on animal production from native pastures. *Rangeland Journal* **20**, 174-202.
- Hassett, R.C., Wood, H.L., Carter, J.O. and Danaher, T.J. (2000). A field method for statewide ground-truthing of a spatial pasture growth model. *Australian Journal of Experimental Agriculture*, **2000**, **40**: 1069-1079.

- Howden, S.M., McKeon, G.M., Walker, L., Carter, J.O., Conroy, J.P., Day, K.A., Hall, W.B., Ash, A.J. and Ghannoum, O. (1999). Global change impacts on native pastures in south-east Queensland, Australia. *Environmental Modelling and Software* **14**, 307-16.
- Izaurrealde, R.C., McGill, W.B., Jans-Hammermeister, D.C., Haugen-Korzyra, K.L. and Hiley, J.C. (1996). Development of a technique to calculate carbon fluxes in agricultural soils at the ecodistrict level using simulation models and various aggregation methods. Interim Report, Submitted to the Scientific Authority of the Agriculture and Agri-Food Canada Greenhouse Gas Initiative, University of Alberta, Edmonton, AB,
- Jaakko Pöyry (1999). Usage And Life Cycle Of Wood Products. National Carbon Accounting System Technical Report No. 8. November 1999.
- Jeffrey, S.J., Carter, J.O., Moodie, K.B. and Beswick, A.R. (2001). Using spatial interpolation to construct a comprehensive archive of Australian climate data. *Environmental Modelling and Software* (in press).
- Jenkinson, D.S. (1990). The turnover of organic C and N in soil. *Philosophical Transactions. Royal Society London* **B329**: 361-368.
- Jenkinson, D.S., Adams, D.E., Wild, A. (1991). Model estimates of CO<sub>2</sub> emissions from soils in response to global warming. *Nature* **352**: 304-306.
- Jenkinson, D.S., Hart, P.B.S., Rayner, J.H. and Parry, L.C. (1987). Modelling the turnover of organic matter in long-term experiments at Rothamsted. *Intercol Bulletin* 15: 1-8.
- Johnston, P.W., McKeon, G.M. and Day, K.A. (1996). Objective "safe" grazing capacities for south-west Queensland Australia: development of a model for individual properties. *Rangeland Journal*. **18**: 244-258.
- Keenan, R.J., Kimmins, J.P. and Pastor, J. (1995). Modelling ecosystem-level carbon and nutrient dynamics in western red cedar and western hemlock forests. In J. M. Kelly and W. W. McFee, ed. *Carbon Forms and Functions in Forest Soils*. Soil Science Society of America, Madison, pp. 547-568.
- Kellomäki, S. and Kolstrom, M. (1992). Simulation of tree species composition and organic matter accumulation in Finnish boreal forests under changing climatic conditions. *Vegetatio* **102**: 47-68.
- Kirschbaum, M.U.F. (1999a). CenW, a forest growth model with linked carbon, energy, nutrient and water cycles. *Ecological Modelling* **181**: 17-59.
- Kirschbaum, M.U.F. (1999b). The effect of climate change on forest growth in Australia. In: *Impacts of global change on Australian temperate forests*. (Howden, S.M. and Gorman, J.T., eds.), Working Paper Series, 99/08, pp. 62-68.
- Kirschbaum, M.U.F. (1999c). Modelling forest growth and carbon storage with increasing CO<sub>2</sub> and temperature. *Tellus* **51B**: 871-888.
- Kirschbaum, M.U.F. (2000). CenW: a generic forest growth model that links carbon, nutrient and water cycles. *New Zealand Journal of Forestry* **45**: 15-19.
- Ladd, J.L, Amato, M., Grace, P.R. and Van Veen, J.A. (1995) Simulation of <sup>14</sup>C turnover through the microbial biomass in soils incubated with <sup>14</sup>C-labelled plant residues. *Soil Biology Biochemistry* **27**: 777-783.
- Landsberg, J.J., Johnson, K.H., Albaugh, T.J., Allen, H.L. and McKeand, S.E. (2000). Applying 3-PG, a simple process-based model designed to produce practical results, to data from loblolly pine experiments. *Forest Science*. (In press)
- Landsberg, J.J., Waring, R.H. (1997). A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance, and partitioning. *Forest Ecology and Management* **95**: 209-228.
- Law, B.E., Waring, R.H., Anthoni, P.M., Aber, J.D. 1999. Measurements of gross and net ecosystem productivity and water exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biology* **5**: 1-15
- Littleboy, M. and McKeon, G.M. (1997). Subroutine GRASP: Grass Production Model. Documentation of the Marcoola Version of Subroutine GRASP. Appendix 2 of "Evaluating the risks of pasture and land degradation in native pasture in Queensland". Final Project Report for the Rural Industries Research and Development Corporation DAQ124A, pp. 76.
- McAlpine, J.R. (1970). Estimating pasture growth periods and droughts from simple water balance models. In 'XI International Grasslands Congress', Surfers Paradise, Queensland (Ed. M. J. T. Norman) pp. 484-487.
- McCown, R.L, Hammer, G.L, Hargreaves, J.N.G., Holzworth, D.L and Freebairn, D.M. (1996). APSIM: a novel software system for model development, model testing, and simulation in agricultural systems research. *Agricultural Systems* **50**: 255-271.
- McKeon, G.M., Ash, A.J., Hall, W.B. and Stafford Smith M. (2000). Simulation of grazing strategies for beef production in north-east Queensland. 'Applications of

- Seasonal Climate Forecasting in Agricultural and Natural Ecosystems - the Australian Experience' (Eds G. Hammer, N. Nicholls and C. Mitchell.) Kluwer Academic Press: Netherlands. p.227-252.
- McKeon, G.M., Day, K.A., Howden, S.M., Mott, J.J., Orr, D.M., Scattini, W.J. and Weston, E.J. (1990). Northern Australian savannas: management for pastoral production. *Journal of Biogeography* **17**, 355-72.
- Medlyn, B.E., McMurtrie, R.E., Dewar, R.C. and Jeffreys, M.P. (2000). Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO<sub>2</sub> concentration. *Canadian Journal of Forest Research* **30**: 873-888.
- Mohren, G.M.J and Goldewijk, K.C.G.M. (1990). CO<sub>2</sub>Fix: a dynamic model of the CO<sub>2</sub> fixation in forest stands. Rapport 624, De Dorschkamp, Research Institute of Forestry and Urban Ecology, Wageningen, 96pp.
- Moore, A.D., Donnelly, J.R. and Freer, M. (1997). GRAZPLAN: decision support systems for Australian grazing enterprises. III. Pasture growth and soil moisture submodels, and the GrassGro DSS. *Agric. Systems* **55**: 535-582.
- Moorhead, D.L., Currie, W.S., Rastetter, E.B., Parton, W.J. and Harmon, M.E. (1999). Climate and litter quality controls on decomposition: An analysis of modeling approaches. *Global Biogeochemical Cycles* **13**: 575-589.
- Moorhead, D.L. and Reynolds, J.F. (1991). A general model of litter decomposition in the northern Chihuahuan Desert. *Ecological Modelling* **56**: 197-219.
- Moorhead, D.L. and Reynolds, J.F. (1993). Effects of climate change on decomposition in Arctic Tussock Tundra: A modeling synthesis. *Arctic and Alpine Research* **25**: 401-412.
- Moorhead, D.L. and Sinsabaugh, R.L. (2000). Simulated patterns of litter decay predict patterns of extracellular enzyme activities. *Applied Soil Ecology* **14**: 71-79.
- Mott, J.J., Williams, J., Andrew, M.H. and Gillison, A.N. (1985). Australian savanna ecosystems. In 'Ecology and Management of the Worlds Savannas'. (Eds J.C. Tohill and J.J. Mott.) pp. 56-82. (Australian Academy of Science: Canberra.)
- Mummery, D., and Battaglia, M. (2001). Environmental sensitivity analysis as a method of screening for prospective plantation sites: a case study with *E. globulus* in Tasmania. *Forest Ecology and Management* **140**: 51-63.
- Palisade (1997). *@RISK vers. 4 – Advanced Risk Analysis for Spreadsheets*. Palisade corporation, New York.
- Parton, J.W., Schimel, D.S., Cole, C.V. and Ojima, D. S. (1987). Analyses of factors controlling soil organic matter levels in the Great Plains grassland. *Soil Science Society America Journal* **51**: 1173-1179.
- Parton W.J., Scurlock, J.M.O., Ojima D.S., Gilmanov, T.G., Scholes R.J., Schimel D.S., Kirchner T., Menaut J.-C., Seastedt T., Garcia Moya E., Kamnalrut Apinan and Kinyamario J.I. (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles* **7**: 785-809.
- Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Schimel, D.S., Hall, D.O., Coughenour, M.B., Garcia Moya, E., Gilmanov, T.G., Kamnalrut, A., Kinyamario, J.I., Kirchner, T., Kittel, T.G.F., Menaut, J.-C., Sala, O.E., Scholes, R.J., and van Veen, J.A. (1995). Impact of climate change on grassland production and soil carbon worldwide. *Global Change Biology* **1**:13-22. **717**
- Pastor, J. and Post, W.M. (1986). Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* **2**: 3-27.
- Post, W.M., Izaurrealde, R.C., Mann, L.K. and Bliss, N. (1999). Monitoring and verifying soil organic carbon sequestration In *Carbon Sequestration in Soils* (Rosenberg, N.J., Izaurrealde, R.C. and Malone, E.L., eds), Proceeding of the St. Michaels Workshop: 41-66.
- Private Forests Tasmania (1999). "The Farm Forestry Toolbox, an aid to growing trees in Tasmania", Private Forests Tasmania, Kings Meadows, Tasmania, Australia.
- Probert, M.E., Dimes, J.P., Keating, B.A., Dalal, R.C. and Strong, W.M. (1998). APSIM's water and nitrogen modules and simulation of the dynamics of water and nitrogen in fallow systems. *Agricultural Systems* **56**: 1-28.
- Richards, G.P. and Evans, D.W. (2000a). CAMFor User Manual v 3.35 National Carbon Accounting System Technical Report No. 26 (47 pp.), Australian Greenhouse Office.
- Richards, G.P. and Evans, D.W. (2000b). *CAMAg* National Carbon Accounting System, Australian Greenhouse Office, Canberra.
- Richards, G.P. (2001). The *FullCAM* Carbon Accounting Model: Development, Calibration and Implementation for the National Carbon Accounting System. National Carbon Accounting System Technical Report No. 28. Australian Greenhouse Office, Canberra.

- Rickert, K.G. and McKeon, G.M. (1982). Soil water balance model: WATSUP. *Proceedings of the Australian Society of Animal Production* **14**, 198-200.
- Ryan M.G. (1991) Effects of climate on plant respiration. *Ecological Applications* **1**: 157-167.
- Sands P.J. (1995a). Proceedings & Report - ForMod95: a Tree & Forest Growth Modelling Workshop, CSIRO Division of Forestry and CRC for Temperate Hardwood Forestry, Hobart, Australia.
- Sands, P.J. (1995b). Modelling canopy production. II. From single-leaf photosynthetic parameters to daily canopy photosynthesis. *Australian Journal of Plant Physiology* **22**: 603-614.
- Sands, P.J. (1996). Modelling canopy production. III. Canopy light-utilisation efficiency and its sensitivity to physiological and environmental variables. *Australian Journal of Plant Physiology* **23**: 103-114.
- Sands, P.J. (2001). 3PGPJS – a User-Friendly Interface to 3-PG, the Landsberg and Waring Model of Forest Productivity. Tech. Rep. 29(2). CRC for Sustainable Production Forestry and CSIRO Forestry and Forest Products, Hobart, Tasmania.
- Sands, P.J., Battaglia, M. and Mummery, D. (2000). Application of process-based models to forest management: Experience with ProMod, a simple plantation productivity model. *Tree Physiology* **20**: 383-392.
- Sands, P.J. and Landsberg, J.J. (2001) Parameterisation of 3-PG for plantation grown *Eucalyptus globulus*. *For. Ecol. and Manage.* (Submitted)
- SCA (1990). *Feeding Standards for Australian Livestock Ruminants*. Standing Committee on Agriculture and CSIRO, Melbourne, 266 pp.
- Scanlan, J.C. and McKeon, G.M. (1993). Competitive effects of trees on pasture are a function of rainfall distribution and soil depth. Proceedings of the XVII International Grassland Congress, Palmerston North, New Zealand, pp. 2231-2.
- Scanlan, J.C., Pressland, A.J. and Myles, D.J. (1996). Runoff and soil movement on mid-slopes in north-east Queensland grazed woodlands. *Rangeland Journal* **18**, 33-46.
- Shugart, H.H. (1984). *A Theory of Forest Dynamics*. Springer-Verlag, New York.
- Stafford Smith, M., Buxton, R., McKeon, G. and Ash, A. (2000). Seasonal climate forecasting and the management of rangelands: Do production benefits translate into enterprise profits. Applications of Seasonal Climate Forecasting in Agricultural and Natural Ecosystems - the Australian Experience' (Eds G. Hammer, N. Nicholls and C. Mitchell.) Kluwer Academic Press: Netherlands. p. 271-289.
- Thornthwaite, C.W and Mather, J.R. (1957). Instructions and tables for calculating potential evapotranspiration and the water balance. *Publications in Climatology* **10**: 183-311.
- Tickle, P., Coops, N.C. and Hafner, S. (2000). Assessing forest productivity across a native eucalypt forest using a process model, 3-PG SPATIAL. *For. Ecol. Manage.* (In press).
- Tisdall, J.M. and Oades, J.M. (1982). Organic matter and water-stable aggregates in soils. *Journal of Soil Science* **33**: 141-163.
- VEMAP, Melillo, J.M., Borchers, J., Chaney, J., Fisher, H., Fox, S., Haxeltine, A., Janetos, A., Kicklighter, D.W., Kittel, T.G.F., McGuire, A.D., McKeown, R., Neilson, R., Nemani, R., Ojima, D.S., Painter, T., Pan, Y., Parton, W.J., Pierce, L., Pitelka, L., Prentice, C., Rizzo, B., Rosenbloom, N.A., Running, S., Schimel, D.S., Sitch, S., Smith, T., and Woodward, I. (1995). Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO<sub>2</sub> doubling. *Global Biogeochemical Cycles* **9**: 407-437.
- Verburg, K. (Ed), (1996). Methodology in soil water and solute balance modelling: an evaluation of the APSIM-SoilWat and SWIMv2 models. Divisional Report No 131, CSIRO Division of Soils, Canberra, Australia.
- Waring, R.H. 2000. A process model analysis of environmental limitations on growth of Sitka spruce plantations in Great Britain. *Forestry* **73**: 65-79
- White, J.D., Coops, N.C. and Scott, N.A. (2000). Predicting broad-scale forest and scrub biomass for New Zealand: Investigating the application of a physiologically based model. *Ecological Modelling* **131**: 175-190.
- Whitehead, D. *et al.* (2001). Analysis of the growth of rimu (*Dacrydium cupressinum*) in south Westland, New Zealand, using process-based simulation models. *Int. Jnl. Biometeorol.* (Submitted).
- Williams, J.R., Nicks, A.D. and Arnold, J.G. (1985). Simulator for water resources in rural basins. *J. Hydraulic Engineering, American Soc. Civil Engineers* **111**: 970-986.
- Yee Yet, J.S., Silburn, D.M. and McKeon, G.M. (1999). Cover run-off equations which improve the simulation of run-off in pasture growth models. VIth International Rangeland Congress Proceedings Vol. 2. pp. 849-850

# Modelling radiation absorption by plant canopies

Ying Ping Wang  
CSIRO Atmospheric Research

## Introduction

The amount of radiation absorbed by plant canopies is one of the major drivers of photosynthesis, dry matter production and energy exchange between the land surface and the atmosphere. The amount of absorbed radiation depends on the amount of incident radiation and the proportion in direct and diffuse radiation, canopy structure and the optical properties of the plant elements and the underlying soil surface. Many models developed for estimating carbon or energy exchanges between the terrestrial biosphere and the atmosphere include the calculation of the amount of radiation absorbed by plant canopies using Beer's law or the two-stream approximation to the equations of radiative transfer.

I recently surveyed ten terrestrial carbon-exchange models developed in Australia, most of which have been, or can be, applied at continental scales (see Table 1). This did not include many models that were developed for some specific plant systems, such crop models. Apart from G'DAY and the CSIRO Biospheric Model (CBM), none of the other models considered the absorption of diffuse and direct beam radiation separately, nor photosynthetically active radiation (PAR) and near infra-red radiation (NIR). All models except CBM use the simple Beer's law to estimate the amount of radiation absorbed. The plant canopy is represented quite differently among the models. Most models

treat the canopy as a single or as two vertical layers, but LINKAGES model each individual plant in a system.

In this paper I shall review how various models calculate the radiation absorption and why the simple Beer's law is inaccurate for our purpose. I also discuss the differences between the two models of radiative transfer in plant canopies and the implications in the calculated hourly fluxes of net CO<sub>2</sub> and energy exchanges between a plant canopy and the atmosphere using CBM.

## The theory

Most early work has been reviewed by Lemeur and Blad (1974) and summarized in Ross (1981). Some of the concepts in modelling radiative transfer in plant canopies were adapted from models of radiative transfer in the atmosphere, particularly the work of Ross and his colleagues. The radiative transfer equation in a plant canopy is (Ross 1981):

$$-\frac{\partial I}{\partial \xi} = K_b I - \frac{1}{\pi \mu} \int_{4\pi} I \gamma(\theta, \theta^*) d\Omega \quad (1)$$

where  $I$  is the radiation flux density within the canopy,  $\xi$  is the cumulative leaf area index from the canopy top,  $K_b$  is the extinction coefficient, and  $\gamma$ , the scattering phase function, defines the fraction of total scattered radiation that is scattered in the direction of  $\theta^*$  to a unit solid angle;  $\mu$  is the cosine of the zenith angle of the incident radiation. The first and second terms on the right-hand side of eqn (1) describe the absorption and scattering loss of the incident radiation, respectively. Eqn

Model	Direct beam/diffuse PAR/NIR	Canopy	Radiative transfer theory
CBM	yes	one-layer	Goudriaan's theory
CENTURY	no	one-layer	Beer's law
CENW	no	one-layer	Beer's law
FullCAM	no	one-layer	Beer's law
G'DAY	yes	one-layer	Beer's law
Gendec	no	one-layer	Beer's law
GrazPlan	no	multi-layer	Beer's law
Linkages	no	individual trees	Beer's law
Promod	no	one-layer	Beer's law
3PG	no	one-layer	Beer's law

Table 1. Survey of results of the representation of canopy structure, incident solar radiation and the theory of radiative transfer used in ten terrestrial models developed in Australia.

(1) can be applied to both direct beam and diffuse radiation. The solution to eqn (1) can only be obtained analytically for some special cases (see Ross 1981). In the case of isotropic scattering, the two-stream approximation can be used to model radiative transfer in plant canopies. One form of the two-stream theory was proposed by Dickinson (1983). That is

$$-\mu \frac{di_u}{d\xi} + [1 - (1 - \beta)\omega]i_u - \omega\beta i_d = \omega\mu K\beta_0 \exp(-K_b^*\xi) \quad (2)$$

$$\mu \frac{di_d}{d\xi} + [1 - (1 - \beta)\omega]i_d - \omega\beta i_u = \omega\mu K(1 - \beta_0) \exp(-K_b^*\xi) \quad (3)$$

where  $i_u$  and  $i_d$  are the upward and downward radiative fluxes normalised by the incident radiation flux density  $I_0$ , respectively.  $\bar{\mu}$  is the average inverse diffuse optical depth per unit leaf area,  $\beta$  and  $\beta_0$  are the upscatter parameters for the diffuse and direct beam radiation, respectively, and  $\omega$  is the leaf scattering coefficient. Eqns (2) and (3) have to be applied to direct beam and diffuse radiation separately. For diffuse radiation, the terms on the right-hand side of both equations are set to zero. An analytic solution to eqns (2) and (3) was obtained by Sellers (1985). The radiation absorbed per unit leaf area within the canopy by shaded ( $Q_{shade}$ ) or sunlit ( $Q_{sun}$ ) leaves is:

$$Q_{shade}(\xi) = \frac{I_0 d(i_u - i_d)}{d\xi} \quad (4)$$

$$Q_{sun}(\xi) = (1 - \omega)K_b^* f_b I_0 + \frac{I_0 d(i_u - i_d)}{d\xi} \quad (5)$$

where  $K_b^*$  is the direct beam extinction coefficient and  $f_b$  is the beam fraction of incident radiation above the canopy.

Over 80% of intercepted PAR is absorbed by plant leaves. If scattering is ignored, the solution of eqn (1) is

$$i_d = \exp(-K_b^*\xi) \quad (6)$$

This is the Beer's law, and has been used in many models for estimating the amount of radiation absorbed. If Beer's law is applied to direct beam and diffuse radiation separately, the radiation flux density within the canopy,  $i$ , is calculated as

$$i = f_b \exp(-K_b^*\xi) + f_d \exp(-K_d^*\xi) \quad (7)$$

Goudriaan (1977) proposed an alternative to the two-stream approximation. Because of scattering, the transmittance of incident radiation within a canopy with non-black leaves is higher and the effective radiation extinction coefficient is less, than those of a canopy with black leaves. Based on the analytic solution to the equations of radiative transfer for a canopy with horizontal leaves ( $K=1$ ) (the Suits radiation model), the effective canopy extinction coefficient is equal to  $\sqrt{1-\omega}$  if the scattered radiation is isotropic ( $\rho = \tau = \omega/2$ ). He also found that the reduction in  $K$  for a horizontal canopy by a factor of  $\sqrt{1-\omega}$  is a very good approximation to any non-horizontal canopy. In the

approximation, Goudriaan and van Larr (1994) used a single exponential function of diffuse radiation within the canopy, and treated the direct beam and scattered beam separately. To conserve the total amount of radiative energy absorbed by the canopy, the absorbed direct beam or diffuse radiation is modified by the effective canopy reflectance. The amount of absorbed radiation per unit leaf area within the canopy is:

$$Q_{shade}(\xi) = (1 - \alpha_{c,d})K_d f_d I_0 \exp(-K_d \xi) + (1 - \alpha_{c,b})K_b f_b I_0 \exp(-K_b \xi) - (1 - \omega)K_b^* f_b I_0 \exp(-K_b^* \xi) \quad (8)$$

and

$$Q_{sun}(\xi) = (1 - \omega)K_b f_b I_0 + Q_{shade} \quad (9)$$

where  $f_d$  is the fraction of diffuse radiation of the incident radiation above the canopy ( $=1 - f_b$ ). The sum of the last two terms on the right-hand side of equation (8) is the amount of scattered direct beam radiation absorbed by the leaves within the canopy.

## Results

A fraction of intercepted radiation  $\omega$  is not absorbed by the leaves. In calculating canopy photosynthesis or energy balance, we should use the amount of absorbed rather than intercepted radiation. The difference between absorption and interception has been discussed previously using a simple model (Russell, Jarvis and Monteith 1989). The amount of intercepted radiation is usually calculated as the difference in the downward flux density of radiation above and below the canopy, whereas the total amount of absorbed radiation is calculated by integrating eqns (4) and (5) over the whole canopy. For a canopy with spherical leaf angle distribution, we found that only 75% and 94% of the intercepted PAR is absorbed by canopies with leaf area index of 1 and 6, respectively.

As compared with the Goudriaan radiation model, the Beer's law model can provide a good approximation for calculating the absorption of PAR if the extinction coefficients, and are substituted with  $K_b$  and  $K_d$ , respectively, provided that the amount of absorbed scattered direct beam radiation is negligible. Therefore eqn (7) is a good approximation for PAR, or for NIR when  $f_b$  is small ( $< 0.1$ ). However, Beer's law is very inaccurate for calculating the amount of NIR absorbed if the direct beam fraction is substantial ( $> 0.1$ ). The error can be as large as 100%, and is larger for a denser canopy, and is larger for NIR than for PAR because of stronger scattering.

It is also important to calculate the absorption of direct beam and diffuse radiation separately. For a spherical leaf angle

distribution,  $K_d$  is about 0.72 for PAR, whereas  $K_b$  varies from 0.45 to infinity. Models that do not consider the absorption of direct beam and diffuse radiation separately will give biased estimates of the amount of radiation absorbed.

In Goudriaan's model, upward and downward scattering is not considered separately, and only the absorption of the scattered direct beam radiation is explicitly considered. The absorption of scattered diffuse radiation is included by substituting the leaf scattering coefficient with the canopy albedo for diffuse radiation. Therefore, the total amount of absorbed diffuse radiation calculated by Goudriaan's model and the two-stream theory is equal if the canopy albedos given by the two models are also equal. However the vertical profile of absorbed diffuse radiation predicted by the two models is different. As compared with the two-stream theory, the Goudriaan model overestimates the amount of absorbed PAR near the top of the canopy, and the amount of absorbed NIR near the bottom of the canopy, because the vertical profile of radiation flux density as calculated by the Goudriaan model is more uniform than that calculated by the two-stream theory.

It has been shown that canopy photosynthesis and energy exchange can be accurately calculated using two big leaves, sunlit and shaded (de Pury and Farquahr 1997; Wang and Leuning 1998). Wang and Leuning (1998) used the Goudriaan radiation model to estimate the amount of PAR and NIR absorbed by the two big leaves. Using the CBM, I compared the calculated fluxes of net CO<sub>2</sub>, latent and sensible heat fluxes for wheat crops at Wagga Wagga as did Leuning *et al.* (1998) using the absorbed radiation estimated by the Goudriaan radiation model with that by the two-stream theory. I found that the differences in the estimated fluxes were not significantly different (< 5%).

The Goudriaan model is simpler than the two-stream theory, and can be more easily implemented in most models of terrestrial biosphere that require the amount of absorbed radiation to be calculated. Because of some empirical elements, the Goudriaan model should be tested against more field data. As compared with the two-stream theory, the accuracy of Goudriaan model depends on the accuracy of the estimated canopy albedos for direct beam and diffuse radiation. A study is in progress on comparing the canopy albedo predicted by Goudriaan model with the field measurements.

## Conclusions

We can draw the following conclusions from this study:

- processes of photosynthesis and energy exchange in plant canopies are directly related to the absorbed, rather than the intercepted amount of radiation. The amount of absorbed radiation can be significantly less than the amount of intercepted radiation;
- the two-stream theory or Goudriaan radiation treatment should be used in estimating the amount of radiation absorbed by plant canopies, particularly in the NIR region when a significant fraction of the incident radiation is direct beam.

## References

- De Pury, DGG and Farquhar, GD (1997). Simple scaling of photosynthesis from leaves to canopies without errors of big-leaf models. *Plant, Cell and Environment*, **20**:537-557.
- Goudriaan, J. (1977). *Crop micrometeorology: a simulation study*. PUDOC, Wageningen.
- Goudriaan, J. and van Laar, HH (1994). *Modelling potential crop growth processes*. Kluwer Academic Publishers, Dordrecht.
- Lemueur, R and Blad, BL (1974). A critical review of light models for estimating the shortwave radiation regime of plant canopies. *Agricultural Meteorology*, **14**:255-286.
- Leuning, R., Dunin, FX and Wang, YP (1998). ). A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. II. Comparison with measurements. *Agricultural and Forest Meteorology*, **91**:113-125.
- Ross, J (1981). *The radiation regime and architecture of plant stands*. Dr W Junk Publishers. The Hague.
- Russell, G, Jarvis, PG and Monteith, JL (1989). Absorption of radiation by canopies and stand growth. In *Plant canopies: their growth, form and function*. Eds G. Russell, B. Marshall and PG Jarvis. Society for Experimental Biology, Seminar Series 31. Cambridge University Press.
- Sellers, PJ (1985). Canopy reflectance, photosynthesis and transpiration. *International Journal of Remote Sensing*, **6**:1335-1372.
- Wang, YP and Leuning, R (1998). A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. I. Model description. *Agricultural and Forest Meteorology*, **91**:89-111.

# Radiation Conversion

*Belinda Medlyn, University of New South Wales*

*With contributions from:*

*Damian Barrett, John Carter, Rod Keenan,  
Miko Kirschbaum, Joe Landsberg, Andrew Moore,  
Mike Raupach, Peter Sands, Richard Simpson,  
Ying Ping Wang*

The conversion of radiation into photosynthate at leaf scale is perhaps the most studied of all plant physiological processes and hence is relatively well-understood. One outstanding major scientific issue with modelling this process is the question of how to scale up to large, heterogeneous areas. This paper will also discuss issues of scaling and large-scale parameterisation and validation of models.

## Introduction

At the core of most models of plant production there is a calculation of photosynthate production. In general, the major driving factor in this calculation is the radiation intercepted by the plant. This review summarises the alternative methods used to calculate conversion of intercepted radiation into photosynthate.

It should be noted that in Australian conditions the most limiting resource to photosynthesis is often not light but water availability. In some models, water availability is treated as one of a number of factors modifying the rate of radiation conversion, but in other models the water limitation is implemented in a 'minimum limiting factor' approach, implying that radiation interception becomes irrelevant for production if water availability is low. These alternative approaches will be discussed briefly.

## Overview of modelling approaches in Australian models

Table 1 gives details of the models considered in this review. Four different types of "radiation conversion" model can be distinguished. These are, in order of increasing complexity, maximum productivity, radiation-use efficiency, big-leaf and sun-shade models. More information on these approaches is given below. The water limitation to productivity may be incorporated by either (1) taking the minimum of radiation- and water-limited production or (2) multiplying radiation-limited production by a modifying factor dependent on available water. In the first approach, water-limited productivity is generally calculated using a water-use efficiency model, described briefly below. In the second approach, several

Model	GPP / NPP	Radiation	Water	Ecosystems	Timestep
Century	GPP	Max. prod.	Modifier	All (Grass)	Month
Linkages	NPP	Max. prod.	Modifier	Forests	Month
3PG	GPP	RUE	Modifier	Forests	Month
APSIM	NPP	RUE	WUE	Crops	Day
GRASP	NPP	RUE	WUE	Pasture	Day
VAST	GPP	RUE	Modifier	All	Month
GrazPlan	NPP	Modified RUE	Modifier	Pasture	Day
CENW	GPP	Big-leaf	Modifier	Forests	Day
Promod	GPP	Big-leaf	WUE	Forests	Day
G'DAY	GPP	Sun-shade	WUE	All (Forests)	Day
Wang & Leuning	GPP	Sun-shade	Modifier	All	Hour

*Table 1: Models included in this overview. Note: the FullCAM model, also included in the survey, uses 3PG logic for above-ground production. Key references: 3PG: Landsberg & Waring (1997); APSIM: Meinke et al. (1997); CENTURY: Parton et al. (1993); CENW: Kirschbaum (1999); G'DAY: Medlyn et al. (2000); GRASP: Littleboy & McKeon (1997); GrazPlan: Moore et al. (1997); Linkages: Pastor & Post (1986); PROMOD: Sands (1995); VAST: DJ Barrett, pers. comm.; Wang & Leuning (1998).*

alternative forms are used for the modifying factor. These functions are not further discussed here; nor are the effects of other environmental factors, such as nutrient availability, air temperature, and plant age, which will be addressed by other contributors.

Note that some of the models explicitly calculate both gross primary productivity (GPP) and respiration, whereas others only calculate net primary production (NPP). The more mechanistic big-leaf and sun-shade approaches are used only to calculate GPP, but the maximum productivity model and the radiation use efficiency approach are used to calculate both GPP and NPP in different models. Importantly, the logic is identical whether GPP or NPP is being calculated; only parameter values differ.

### Maximum productivity model

The simplest method of calculating photosynthate production is adopted in both the CENTURY and LINKAGES models. With this approach, maximum productivity for a given species is specified as a parameter to the model. Productivity is then assumed to be reduced below this maximum by environmental factors such as radiation, temperature and water and nutrient availability. In CENTURY, the influence of radiation interception is incorporated (for forests only) by a modifying factor that depends exponentially on leaf area index (NREL 2000). In LINKAGES, the same effect is represented by a non-linear function of the percentage of full sunlight absorbed (Pastor & Post 1986).

This approach can be criticised for being too simple. In the case of LINKAGES, it is used because the model attempts to simulate mixed-species forests, for which it is extremely difficult to model radiation interception simply. The CENTURY model uses the maximum productivity approach because its major focus is on belowground processes. A known limitation to the CENTURY implementation of this approach is that effects of incident radiation are not taken into account. The model performs adequately in current conditions because of the strong correlation between radiation and temperature, but this correlation may not hold in future conditions (e.g. increased cloudiness) (Parton *et al.* 1993).

### Resource use efficiency models

The radiation use efficiency approach is formulated simply as

$$G = \epsilon I_{\text{abs}} \quad (1)$$

where  $G$  is production (GPP or NPP),  $I_{\text{abs}}$  is absorbed radiation, and  $\epsilon$  is a constant, known as the radiation use efficiency (RUE) (Monteith 1977). It has been suggested that the relation

between  $G$  and  $I_{\text{abs}}$  is not strictly proportional, as in eqn (1), but that the RUE is higher at low radiation levels. Some models take this into account by adding a modifying factor to increase  $\epsilon$  at low  $I_{\text{abs}}$  (e.g. GrazPlan, Moore *et al.* 1997).

The water use efficiency approach is similar:

$$G = q T \quad (2)$$

where  $T$  is plant transpiration and  $q$  is the water-use efficiency (WUE), which is generally assumed to depend inversely on atmospheric vapour pressure deficit (e.g. RESCAP, Monteith *et al.* 1989; applied to *Pinus radiata* by Dewar 1997).

The resource-use efficiency approach has been extremely widely adopted. It is appealingly simple. The radiation-use efficiency, in particular, is readily applied to remotely-sensed data of radiation interception. Critics of this model question how linearity could arise from an essentially non-linear process (photosynthetic response to light) (e.g. Medlyn 1998); it has been suggested that linearity could arise through an optimisation process (Goetz & Prince 1999). The model has also been criticised on the grounds of auto-correlation in the estimation of the resource-use efficiency parameter (Demetriades-Shah *et al.* 1992). Regardless of these criticisms, many modellers have found that this approach performs adequately when model output is tested against observations of growth (e.g. Landsberg & Waring 1997, Clark *et al.* 2000).

### Big-leaf model

A major difficulty in scaling photosynthesis rates from leaves to canopies is the non-linearity of the light response of leaf photosynthesis. This difficulty is overcome in the big-leaf model by assuming that the maximum rate of leaf photosynthesis ( $A_{\text{max}}$ ) is proportional to the fraction of intercepted radiation throughout the canopy. This assumption essentially allows equations for leaf photosynthesis to be applied to the canopy as a whole. The two models using this approach in this survey (CENW and PROMOD) use the version of the big-leaf model proposed by Sands (1995), in which instantaneous canopy photosynthesis is integrated over the day. The advantage of the big-leaf model is that it is mechanistic but swift at the same time.

### Sun-shade model

In order to overcome the problem of scaling the non-linear light response of photosynthesis, highly detailed models of canopy photosynthesis generally divide the canopy into a large number of sections with similar incident radiation and calculate the photosynthetic rate in each section. However, experiments with

such models suggest that canopy photosynthesis can be accurately modelled with a division into just two sections: sunlit and shaded (e.g. Reynolds *et al.* 1992). The sun-shade model approach is based on this observation: canopy photosynthesis is calculated as the sum of components from sunlit and shaded foliage, each of which is determined following the big-leaf approximation (Wang & Leuning 1998, Medlyn *et al.* 2000). As with the big-leaf model, this model has the advantage of being mechanistic, but is somewhat more complex to implement.

### *Comparison of different approaches*

The maximum productivity and resource-use efficiency models are simple, empirical approaches, easy to understand and computationally swift. The big-leaf and sun-shade approaches are more complex but have a stronger mechanistic basis. More detailed models of radiation conversion are also available, such as those assuming heterogeneous canopies, but these are generally regarded as inappropriate for modelling on large spatial scales.

There have been several papers showing why sun-shade models should theoretically perform better than big-leaf models (de Pury & Farquhar 1997); however, the difference between the models is quite small relative to the errors involved in parameter estimation. There are also good theoretical reasons for expecting that the big-leaf and sun-shade models should perform better than the simpler resource-use efficiency model but I am not aware of any work in which a direct comparison has been performed. Certainly, proponents of both approaches have been successful in modelling NPP at both point and regional scale (e.g. Coops *et al.* 1998, Sands *et al.* 2000). For example, the Potsdam NPP Model Intercomparison project (Cramer *et al.* 1999) compared estimates of global NPP from models utilising a range of radiation conversion approaches, including resource-use efficiency and big-leaf models. Differences between model estimates could not be attributed to differences in modelling strategy. Similarly, there is little evidence to demonstrate which is the better of the two approaches to water limitation, the minimum-limitation or modifying-factor approach.

### *Modelling the Australian continent: issues of scaling, parameterisation, and validation*

Broadly speaking, we have a good scientific understanding of the processes involved in conversion of radiation to photosynthate and can fairly confidently model these processes at leaf and canopy scales. An outstanding issue, however, is how

to extend our modelling to large scales. This issue of course concerns all processes, not just radiation conversion, but since we are here considering core model structure it is appropriate to address scaling in this paper. Scaling up from stand to regional scales is generally achieved by applying a stand-scale model with parameters appropriate to the region. Two issues are particularly of concern with this scaling up: the choice of appropriate parameters, and the validation of model outputs at regional scale.

### *Parameterisation*

At the stand scale, parameterisation of the big-leaf or sun-shade models is relatively straightforward because the main parameters can be related directly to simple physiological measurements. It is somewhat more difficult to determine the maximum productivity or radiation-use efficiency parameters. Two alternative methods are commonly used to obtain these parameters: they may be estimated from laborious stand-scale measurements of productivity; or they may be derived from more complex physiologically-based models.

At regional scale, point to point variation is a problem for parameterising all types of models. In general, the methodology used to scale from stands to regions involves applying the same model repeatedly to a series of grid squares that make up the region. Parameter values are selected to represent each grid square. A common approach is to classify the vegetation type of each grid square and then choose parameter values typical for each vegetation type. The required spatial information on vegetation characteristics may be available from existing maps or from remotely-sensed data (Cramer *et al.* 1999). There are two problems with this approach to parameterisation. Firstly, our knowledge of typical parameter values for different vegetation types is imprecise. Published values of radiation use efficiency, for example, vary significantly (Goetz & Prince 1999). Secondly, there is inevitable heterogeneity within each grid square. If modelled processes are strongly non-linear, then the use of a mean parameter value can lead to biased model outputs. Raupach *et al.* (2001) suggest that this problem can be addressed using statistical estimation, which requires not only knowledge of mean parameter values but also their variances and covariances.

### *Validation*

Most of the models covered in this survey have been calibrated or validated at stand scale at a number of points. Validation generally takes the form of comparison of model output with above-ground production at a given site and thus may be

regarded as a test of the full model rather than the GPP component *per se* (e.g. Battaglia & Sands 1997, Gilmanov *et al.* 1997, Clark *et al.* 2000). Some attempts to test modelled GPP separately have been made using eddy flux data (Medlyn *et al.* 1999, Law *et al.* 2000).

At large scale, there are limited ways to validate model predictions. One method is to test model output against a database of physically extensive ground observations (Barrett 2000, Scurlock *et al.* 1999); a second is to aggregate estimates of net ecosystem production, using an atmospheric transport model, for comparison with the international network of measurements of atmospheric CO<sub>2</sub> concentration. Cramer *et al.* (1999) also highlight the potential of model comparison for checking model output.

## Summary

---

Four basic approaches to modelling of radiation conversion are used in Australian NPP models. Although there may be theoretical reasons to prefer one approach over another, in practice each approach appears able to successfully model radiation conversion. The main unresolved scientific problem lies not in our understanding of this process, but in our ability to extend our modelling to large scales.

## References

---

- Barrett DJ (2001) Steady state net primary productivity, carbon stocks and mean residence time of carbon in the Australian terrestrial biosphere. *Global Biogeochem. Cycles* (in press).
- Battaglia M, Sands PJ (1997) Modelling site productivity of *Eucalyptus globulus* in response to climatic and site factors. *Aust. J. Plant Physiol.* 24: 831-850.
- Clark SG, Donnelly JR, Moore AD (2000) The GrassGro decision support tool: its effectiveness in simulating pasture and animal production and value in determining research priorities. *Aust. J. Exp. Agric.* 40: 247-256.
- Coops NC, Waring RH, Landsberg JJ (1998) Assessing forest productivity in Australia and New Zealand using a physiologically-based model driven with averaged monthly weather data and satellite-derived estimates of canopy photosynthetic capacity. *For. Ecol. Manag.* 104: 113-127.
- Cramer W, Kicklighter DW, Bondeau A, Moore B, Churkina C, Nemry B, Ruimy A, Schloss AL (1999) Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biol.* 5 (Suppl. 1): 1-15.
- Demetriades-Shah TH, Fuchs M, Kanemasu ET, Flitcroft I (1992) A note of caution concerning the relationship between cumulated intercepted solar radiation and crop growth. *Agric. For. Meteorol.* 58:193-207
- dePury DGG, Farquhar GD (1997) Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant Cell. Environ.* 20: 537-557.
- Dewar RC (1997) A simple model of light and water use evaluated for *Pinus radiata*. *Tree Physiol.* 17: 259-265.
- Gilmanov TG, Parton WJ, Ojima DS (1997) Testing the CENTURY ecosystem level model on data sets from eight grassland sites in the former USSR representing wide climatic/soil gradient. *Ecol. Model.* 96:191-210.
- Goetz SJ, Prince SD (1999) Modelling terrestrial carbon exchange and storage: evidence and implications of function convergence in light-use efficiency. *Adv. Ecol. Res.* 28: 57-92.
- Kirschbaum MUF (1999). CenW, a forest growth model with linked carbon, energy, nutrient and water cycles. *Ecol. Model.* 181: 17-59.
- Landsberg JJ, Waring RH (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manag.* 95: 209-228.
- Law BE, Waring RH, Anthoni PM, Aber JD (2000) Measurements of gross and net ecosystem productivity and water vapour exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biol.* 6: 155-168.
- Littleboy M & McKeon G (1997) Evaluating the risks of pasture and land degradation in native pastures in Queensland. Appendix 2: Subroutine GRASP: Grass Production Model. Final Report DAQ-124A for the Rural Industries Research and Development Commission.
- Medlyn BE (1998) Physiological basis of the light use efficiency model. *Tree Physiol.* 18:167-176.
- Medlyn BE, Broadmeadow MB, Randle T, Matteucci G, Dufrêne E (1999). Model comparison. *In* ECOCRAFT: Predicted Impacts of Rising Carbon Dioxide and Temperature on Forests in Europe at Stand Scale. *Edited by* P.G. Jarvis. Final Project Report to the European Community, pp 97-135.
- Medlyn BE, McMurtrie RE, Dewar RC, Jeffreys M. (2000) Soil processes dominate long-term response of net primary

- productivity of forests to increased temperature and atmospheric CO<sub>2</sub> concentration. *Can. J. Forest Res.* 30: 873-888.
- Meinke H, Hammer GL, van Keulen H, Rabbinge R (1997) Improving wheat simulation capabilities in Australia from a cropping systems perspective III. The integrated wheat model (I\_WHEAT). *Europ. J. Agron.* 8: 101-116.
- Monteith, JL (1977) Climate and the efficiency of crop production in Britain. *Trans. R. Soc. Lond., Ser. B.* 281:277-294.
- Monteith JL, Huda AKS, Midya D (1989) RESCAP: a resource capture model for sorghum and pearl millet. *In Modelling the Growth and Development of Sorghum and Pearl Millet. Edited by SM Virmani, HLS Tandon and G Alagarswamy. ICRISAT Research Bulletin 12, Patancheru, India, pp 30-34.*
- Moore AD, Donnelly JR, Freer M (1997) GRAZPLAN: Decision support systems for Australian grazing enterprises.3. Pasture growth and soil moisture submodels, and the GrassGro DSS. *Agric. Sys.* 55: 535-582.
- NREL (2000) CENTURY Soil Organic Matter Model Version 5 User's Guide and Reference.  
<http://www.nrel.colostate.edu/projects/century5/reference/index.htm>
- Parton WJ, Scurlock JMO, Ojima DS, *et al.* (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochem. Cycles* 7: 785-809.
- Pastor J, Post WM (1986) Influence of climate, soil moisture and succession on forest carbon and nitrogen cycles. *Biogeochem.* 2: 3-27.
- Raupach MR, Barrett DJ, Briggs PR, Kirby MJ (2001) Terrestrial biosphere models and forest-atmosphere interactions. In: *Forests and Water* (eds. R. Vertessy and H. Elsenbeer). IUFRO. In press.
- Reynolds JF, Chen J, Harley PC, Hilbert DW, Dougherty RL, Tenhunen JD (1992) Modeling the effects of elevated CO<sub>2</sub> on plants: extrapolating leaf response to a canopy. *Agric. For. Meteorol.* 61: 69-94.
- Sands PJ (1995) Modelling canopy production II. From single-leaf photosynthetic parameters to daily canopy photosynthesis. *Aust. J. Plant Physiol.* 22: 603-614.
- Sands PJ, Battaglia M, Mummery D (2000) Application of process-based models to forest management: experience with PROMOD, a simple plantation productivity model. *Tree Physiol.* 20: 383-392.
- Scurlock JMO, Cramer W, Olson RJ, Parton WJ, Prince SD (1999) Terrestrial NPP: Toward a consistent data set for global model evaluation. *Ecol. Applic.* 9: 913-919.
- Wang Y P, Leuning R (1998) A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy I. Model description and comparison with a multi-layered model. *Agric. For. Meteorol.* 91: 89-111.

# Plant Respiration

---

Roger Gifford  
CRC for Greenhouse Accounting  
CSIRO Plant Industry

## Introduction

---

This paper concerns calculation of plant autotrophic respiration rate, which may emit about half of the CO<sub>2</sub> fixed by photosynthesis (Ryle 1984). At the same time it generates chemical energy and reducing power as well as metabolites that are used as the building blocks for synthesis of organic molecules. It does this through multi-step biochemical pathways - glycolysis, the TCA cycle and pentose phosphate pathway and a mitochondrial electron transport chain. Even though about half the gross photosynthate produced is dissipated by respiration our capacity to model it falls well short of our capacity to model photosynthesis.

Mechanistic carbon cycle models are concerned with calculating the CO<sub>2</sub> emitted by whole plant respiration to subtract from photosynthetic fixation by the leaves. To do this, understanding of the "logic" of its regulation should be helpful. The dynamic regulation of respiration is complex. The over-arching logic behind the regulation of the rate of respiration at the cellular level is determined by the relative requirements for chemical energy and reducing power, and C-skeletons for biosynthesis of complex molecules. At the level of electron transport in the production of ATP it is the local supply of ADP and AMP that may be in control.

Respiration may sometimes, however, be controlled by the supply of its substrate - translocated sucrose. Thus respiration can be controlled by the photosynthetic source, the utilization sink, or by a combination of both. A complexity is that, within the electron transport chain, there is also the potential for an alternative oxidase to be engaged that has the effect of allowing respiratory CO<sub>2</sub> release without concurrent generation of ATP. The function of this apparently CO<sub>2</sub>-wasting respiration is unclear and its regulation is not understood (Affourtit *et al.* 2001)

Considered mechanistically from the bottom up, control of respiratory CO<sub>2</sub> release seems hopelessly complicated to capture in productivity models. Accordingly, simplifying notions about the high level logic of respiration have had to be devised. Several approaches have been adopted.

## Respiration-modelling approaches in productivity models

---

### *Non-explicit treatment of respiration*

The simplest way to represent respiration is to embed it implicitly in parameters of empirical growth functions that don't explicitly recognise photosynthesis. Many vegetation production models calculate net primary productivity (i.e. new tissue growth rate) by functions that are calibrated to relate primary production directly to the environmental drivers and modulators of plant growth like radiation, water supply, temperature, nutrition and stress factors. A popular approach to such models is to calculate NPP as the amount of solar radiation intercepted or absorbed by green leaves multiplied by an efficiency of conversion of solar energy into plant dry matter. The efficiency term may be taken to be constant or to be a function of some variables such as temperature. Such models do not need to represent respiration as they enter the biological hierarchy at a higher level than that of process physiology, respiration being built into the empirical parameterisation of the growth functions.

### *Specific respiration*

Models that do attempt to include representation of physiological and biochemical mechanisms of CO<sub>2</sub> exchange need to calculate respiration separately for subtraction from photosynthesis to determine growth. Thus:

$$R = R_s(T) \cdot W \quad (1)$$

where R is respiration rate per plant, W is the dry weight per plant and R<sub>s</sub> is the specific respiration rate that varies with temperature, T. However, it was found that specific plant respiration is far from a constant at any given temperature.

### *Growth and maintenance*

Specific respiration rate is high in young fast growing tissues and small in non-growing tissues and can respond quickly to change in environmental factors. This fact led to recognition that there could be a background or basal rate of specific respiration combined with a respiration rate that was linked to the rate at which the tissue or plant was photosynthesising or growing. This idea was formulated at the whole plant level by

McCree (1970) and by Thornley (1970). McCree suggested that the dynamic component be related to the rate of plant photosynthesis

$$R = mW + pP \quad (2)$$

where R is the respiration rate per plant or per unit ground area, P is the photosynthesis rate per plant or per unit ground area, m is a respiratory maintenance coefficient and p is a coefficient for respiration related to photosynthesis rate.

Thornley (1970) showed that the dynamic part could equivalently be related to new growth (i.e. to photosynthesis minus respiration)

$$R = mW + gG = R_m + R_g \quad (3)$$

Where G is the growth rate per plant or per unit ground area calculated as (P-R), and g is the growth coefficient.

At the same time it was also recognised that respiration linked to the rate of growth was mainly that required to energise synthesis of the new complex molecules (proteins, membranes, cell walls etc) that constitute growth (Beevers 1970).

It has also been recognised that a substantial part of the energy requirement for maintenance may be for protein turnover. Thus another way to express the concept is as:

$$R = m_n W_n + gG \quad (4)$$

where  $W_n$  is the N content of the plant and  $m_n$  is the maintenance expressed on a nitrogen basis. While it was conceived that a major energy demand for plant tissue maintenance would be protein turnover it has also been recognised that maintenance of membrane integrity and solute gradients must contribute (Penning de Vries *et al.* 1983).

A problem with growth and maintenance formulations is that they are purely notional constructs. Growth and maintenance are not biochemically distinct. The concept does not withstand close scrutiny. They are defined only operationally by the measurement approach adopted and the assumptions involved in such measurements. There are several approaches to measuring growth and maintenance components; each involves different assumptions and therefore measures different properties of respiration.

Growth and maintenance coefficients measured even by the same method are not necessarily constant (Amthor 2000) for several reasons. One is that their values depend on the composition of the plant being grown and maintained. Maintenance of wood that is mostly lignocellulosic cell wall

requires much less energy than maintenance of leaves containing a high fraction of functional enzyme-proteins and membranes, for example. And the energy for wood growth is very different from the energy requirement for growing oily or proteinaceous tissues. Penning de Vries *et al.* (1983) addressed the compositional question in determining the growth coefficient by substituting organic synthesis respiration for growth respiration assuming that these processes occur at maximum efficiency and are uninfluenced in their energy requirement by temperature and stress. They calculated theoretical energy requirements to synthesise the variety of compounds found in plants to estimate the synthesis respiration for a diversity of species.

A second reason why growth and maintenance coefficients are not constant is that there are carbon (energy) utilizing plant processes that are not readily classified as either growth or maintenance. Under the growth and maintenance concept such respiration-requiring processes are forced into one or other of the coefficients by whatever means is adopted to determine them. For example, where environmental conditions trigger operation of the alternative oxidase, which may act as a C wasting valve, the  $CO_2$  emitted does not logically fall under either growth or maintenance; its classification under a technique that breaks down respiration into just those two components is not obvious. Phloem loading for long distance transport of photoassimilate is energy demanding but services the carbohydrate requirements of both growth and maintenance. Similarly, nutrient uptake by the root system consumes energy; how it should be classified under the growth and maintenance concept is unclear. Accordingly, van Veen (1980) suggested that ion uptake requires separate consideration. However, there are also other energy requiring processes occurring in plants such as N-fixation in some species, and nitrate reduction which can occur in roots or leaves the proportion varying with species (Thornley and Cannell 2000).

Although for a period it became conventional to relate maintenance respiration closely with protein turnover, the case is not, however, strong for modelling maintenance respiration based on the assumption that it is best related to plant N content.

### *An alternative way to treat components of respiration – the “process-residual” approach*

To deal with the unavoidable fuzzy boundaries between maintenance and growth, Cannell and Thornley (2000)

proposed a different approach in which each respiration-demanding process is regarded as an independently acting process which can be assessed individually. In this approach, the model would first calculate the respiration of each individual process that can be quantified. For example, there might be data that would allow calculation of the energy demand of new synthesis of N-fixation, of N-uptake, of nitrate reduction, of other ion uptake, and of phloem loading. Then any other processes not explicitly calculated would be lumped into the residual respiration. The approach is called the "process-residual" approach. It is adopted in Thornley's Hurley Pasture Model (HPM) and the Edinburgh Forest Model (EFM) (Thornley and Cannell 2000). The HPM and EFM were run with the process-residual approach for a full year or full forest rotation, respectively. It was found that the energy requirements of mineral nutrition are minute compared with those of new materials synthesis, phloem loading and the residual components that cover protein turnover, C-wasting respiration and maintenance of ion and other gradients in cells and tissues.

### *Respiration:photosynthesis ratio*

It has been found in practice that for whole plants and ecosystems the ratio of respiration to gross photosynthesis is conservative over a wide range of plant sizes and growth rates, CO<sub>2</sub> concentrations and temperatures. This is equivalent to conservatism in carbon use efficiency, CUE (NPP/GPP) and in respiration to GPP ratio. In practice measurements have shown that at the whole plant level R:P ratio is typically within the range 0.35-0.6. Utilization of this approach in models has experienced a resurgence over the last few years (Gifford, 1994; 1995, Waring *et al* 1998).

## Survey of specific model treatments of respiration

---

Models that have plant productivity as output must deal with autotrophic respiration in some way, be it implicitly in some cases. Examples of models for which respiration is embedded implicitly in the parameters that relate growth to environmental variables include: the crop models of the APSIM farm-system suite of models, the rangeland production/management model GRASP, the ecosystem level forest model LINKAGES, the agricultural soil C model SOCRATES, the continental C-cycle model VAST and the forest productivity model G'Day when simulating water limiting conditions.

Models which assign values of specific respiration include the carbon cycle model CENTURY, and G'Day when water is not growth limiting during the growing season. In each case, specific respiration is expressed as a function of N-concentration and temperature. Models that utilise the growth and maintenance approach are the forest productivity model CenW (as one option) and the forest growth and yield model Promod. Use of constant values of either R:GPP ratio or NPP:GPP ratio as inputs are allowed as options in CenW and G'Day. They are the sole option in the simple terrestrial C-cycle models CQUEST and CQUESTN, and in the forest growth model 3PG. The forest carbon cycle model FullCAM uses 3PG as a sub-model and hence relies on the NPP/GPP ratio to express respiration.

## Some unresolved issues in autotrophic respiration

---

There is a significant problem in whole-plant respiration studies of not being able routinely to measure autotrophic respiration of leaves by day when photosynthetic CO<sub>2</sub> uptake is occurring. Commonly it is assumed in whole plant studies and models that respiration continues by day at the rate it does at night, possibly responding to short term diurnal variation in leaf temperature. However, there is evidence both for and against a reduction of leaf autotrophic respiration in the light (Lambers 1997).

There are many papers reporting that plant respiration is partially suppressed by elevated atmospheric CO<sub>2</sub> concentration. Both short term reversible effects and long term irreversible effects have been described (Drake *et al.* 1999). While there are significant doubts about the validity of that conclusion under doubled CO<sub>2</sub> concentration, the reality or not of the phenomenon has not yet been resolved (Bunce 2001).

Most C-cycle and productivity modelling approaches adopt a high sensitivity of specific respiration to temperature with a Q<sub>10</sub> > 2 (Ryan 1991). However, in the long term, plant respiration seems to acclimate to a temperature change over several days to a week (Gifford 1995). The acclimated Q<sub>10</sub> may be much less than 2. For example, whole plant specific respiration of sorghum plants (Gifford 1992) grown and measured at a range of constant temperatures was only 1.3 whereas the short-term sensitivity (hours) of whole plant specific respiration to temperature was much greater (Figure 1a). When expressed as a ratio of 24 hour respiration to 24hr photosynthesis per plant, the sorghum plants showed a low response to growth temperature (Figure 1b).

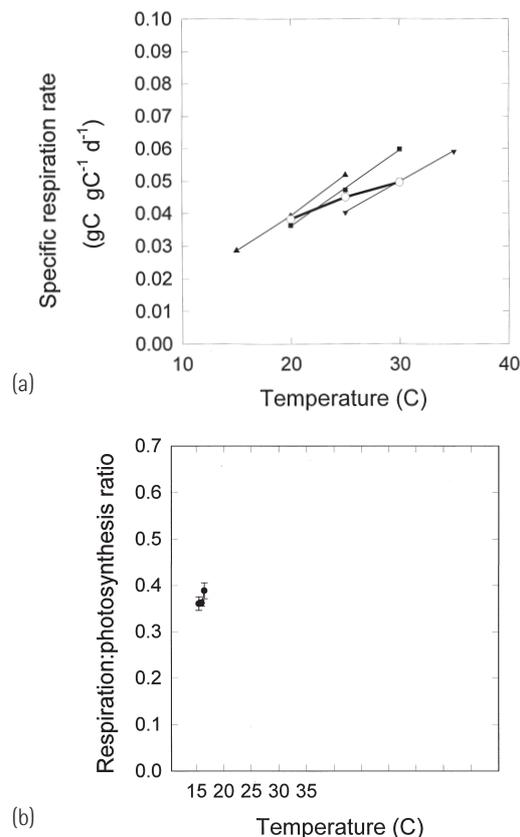


Figure 1. Respiration of *Sorghum bicolor* plants.

a) Specific respiration rates of whole plants (including roots in inert potting medium) grown and measured at the plotted temperatures (open symbols at 20, 25 and 30C), or grown at those three temperatures but measured at temperatures 5C above and below those growth temperatures as well as at the growth temperatures (solid symbols). The  $Q_{10}$  that best fits the temperature-acclimated response (open symbols) is 1.3 (Gifford 1992). Each point is a mean of 4 replicate plants.

b) The 24 hr whole plant respiration to photosynthesis ratio of sorghum plants (including roots in inert potting medium) grown and measured at the plotted temperatures. Each point is a mean of 4 replicate plants. The error bars are  $\pm$  the standard errors of the mean.

Whether "wasteful respiration" occurs in plants is a moot point. The alternative oxidase (cyanide insensitive) pathway of respiration is only sometimes engaged and can vary in its degree of engagement. When it is engaged, it functions to generate much less ATP per unit CO<sub>2</sub> evolved than does normal cytochrome oxidase pathway. Yet it is a reasonable hypothesis that it becomes engaged to optimise overall plant performance in some way (Lambers 1997). Either way, since the underlying

logic of regulation of the alternative pathway is not understood, expressing its functioning explicitly in productivity models is problematic.

### Acknowledgements.

I thank Miko Kirschbaum for inviting the paper as a presentation to a Net Ecosystem Exchange Workshop of the Cooperative Research Centre for Greenhouse Accounting, and for his critical comments on a draft manuscript. John Carter, Miko Kirschbaum, Greg McKeon, David Pepper, Peter Sands, Peter Grace, Rod Keenan, Michael Robertson, Andrew Moore and Richard Simpson kindly provided information as to how the productivity models they work with deal with respiration.

### References

- Affourtit C; Krabb K; Moore AL. (2001) Control of plant mitochondrial respiration. *Biochimica et Biophysica Acta /Bioenergetics*, **1504**:58-69.
- Amthor JS (2000) The McCree-de Wit-Penning de Vries-Thornley respiration paradigms: 30 years later. *Annals of Botany* **86**: 1-20.
- Bunce JA. (2001) Effects of prolonged darkness on the sensitivity of leaf respiration to carbon dioxide concentration in C<sub>3</sub> and C<sub>4</sub> species. *Annals of Botany* **87**: 463-468.
- Beevers H (1970) Respiration in plants and its regulation. pp209-214 in *Prediction and measurement of photosynthetic productivity : proceedings of the IBP/PP Technical Meeting, Trebon, 14-21 September 1969*. International Biological Programme (ed). Wageningen, Centre for Agricultural Publishing and Documentation. 632p.
- Cannell MGR and Thornley JHM (2000) Modelling the components of plant respiration: Some guiding principles. *Annals of Botany* **85**: 45-54.
- Drake BG, Azcon-Bieto J, Berry J, Bunce J, Dijkstra P, Farrar J, Gifford RM, Gonzalez-Meler MA, Koch G, Lambers H, Siedow J, Wullschlegel S (1999) Does elevated atmospheric CO<sub>2</sub> concentration inhibit mitochondrial respiration in green plants? *Plant Cell Environment* **22**: 649-657.
- Gifford RM (1992) Impact of greenhouse effect temperature increase on the carbon balance of vegetation. *Energy Research and Development Corporation (Australia) Project Report No. 1402* (ISBN No. 06 421 71491).

- Gifford RM (1994) The global carbon cycle: a viewpoint on the missing sink. *Australian Journal Plant Physiology* **21**: 1-15.
- Gifford RM (1995) Whole plant respiration and photosynthesis of wheat under increased CO<sub>2</sub> concentration and temperature: long-term vs. short-term distinctions for modelling. *Global Change Biology* **1**: 385-396.
- Lambers H (1997) Oxidation of mitochondrial NADH and synthesis of ATP. pp200-219 in *Plant Metabolism*. DT Dennis, DH Turpin, DD Lefebvre and DB Layzell eds. 2nd Edition. Addison Wesley Longman, Harlow, UK. 529p.
- McCree KJ (1970) An equation for the rate of respiration of white clover plants grown under controlled conditions. pp221-229 in *Prediction and measurement of photosynthetic productivity: proceedings of the IBP/PP Technical Meeting, Trebon, 14-21 September 1969*. International Biological Programme (ed). Wageningen, Centre for Agricultural Publishing and Documentation. 632p.
- Penning de Vries FWT, van Laar HH and Chardon MCM (1983) Bioenergetics of growth of seeds, fruits, and storage organs. pp 37-59 in *Potential productivity of field crops under different environments*. International Rice Research Institute, Los Banos, Phillipines.
- Ryan MG (1991) Effects of climate change on plant respiration. *Ecological Applications* **1**: 157-167.
- Ryle GJA (1984) Respiration and plant growth. In Palmer JM (ed) *Physiology and Biochemistry of Plant Respiration*, Cambridge University Press, Cambridge, UK.
- Thornley JHM (1970) Respiration, growth and maintenance in plants. *Nature* **227**: 304-305.
- Thornley JHM and Cannell MGR (2000) Modelling the components of plant respiration: Representation and realism. *Annals of Botany* **85**: 55-67.
- van Veen BW (1980) Energy costs of ion transport. pp187-195 in *Genetic engineering of osmoregulation. Impact on plant production for food, chemicals and energy*. (DW Rains, RC Valentine, A Hollaender, eds). New York, Plenum Press.
- Waring RH, Landsberg JJ and Williams M (1998). Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology* **18**: 129-134.

# The Role of Allocation in Modelling NEE

---

*Craig Barton*

*CRC for Greenhouse Accounting*

*State Forests of NSW*

*With contributions from Roddy Dewar, Rod Keenan, Keryn Paul, Miko Kirschbaum, Joe Landsberg, Dave Pepper and Peter Sands.*

## Allocation and its relevance to Net Ecosystem Exchange

---

Carbon is converted from CO<sub>2</sub> to carbohydrate in leaves. This assimilate is then translocated throughout the plant where it is either used as fuel for metabolic activity, stored for later use or built into new structure, resulting in growth and reproduction. The term allocation is ambiguously used to refer to i) the proportions of carbon translocated to various plant parts, ii) the relative growth rates of different plant parts and iii) the translocation process itself. The reason for this is that in some models the allocation of carbon (or nitrogen) between plant parts is largely empirical, based on plant component mass at harvests (Comins and McMurtrie 1993), while in others it is a consequence of the transport process (Thornley 1991).

The importance of allocation for modelling net ecosystem carbon exchange (NEE) is that allocation combined with mortality and decomposition determines the amount of carbon sequestered in long term storage pools, such as woody biomass and soil carbon. Carbon allocated to lignified tissue such as wood will have a longer residence time in the ecosystem than that allocated to leaves or fine roots. The relevance of allocation to NEE depends on the time scale of interest. In annual plants, that germinate, grow, reproduce and die within one year, decomposition processes will be more important to NEE than allocation patterns on time scales of greater than one year. However, in long-lived species that produce long-lived structures such as the stems of trees allocation patterns become increasingly important to NEE at this time scale. Since the primary interest of this paper is in the impact of allocation on the long-term (decades) carbon storage by vegetation its focus will be on allocation in woody perennials.

Despite advances in many areas of plant physiology, the underlying mechanisms that control the allocation of carbon within plants are still not understood, and this lack of

knowledge is becoming the limiting factor in the advancement of mechanistic models of plant growth and function. Allocation within functional-structural tree models is critical since in the short term, partitioning of assimilates among the different sink organs and/or functions determines the relative growth rates of the various plant components. Assimilate allocation is also involved in a number of feedback processes which influence plant development in the long term. For example, developing leaves are reliant on carbon allocation from functional leaves however, these leaves will later become carbon sources, thus affecting future carbon inputs. The complex dynamic and feedback aspects to allocation have implications for the long term stability and predictive ability of mechanistic models.

## The current state of knowledge

---

There have been a number of reviews of allocation over the last few years (see Cannell and Dewar 1994; Lacomte 2000) along with many papers promoting new or revamped hypotheses. The review by Cannell and Dewar (1994) is difficult to improve upon and so I shall borrow from them and include some new work that has been published in the interim.

In order to understand the underlying controls of allocation it is helpful to outline the possible drivers of allocation. For a plant to survive resources must be allocated between various plant parts and processes:

### *Allocation for structure:*

- Need leaves to absorb radiation.
- Need stems to position leaves in space and to raise the canopy above competition.
- Need roots to absorb nutrients and water, and to anchor plants.
- Need stems to transport water, nutrients and assimilates.

### *Allocation for metabolic activity:*

- Protein turnover.
- Ion gradient maintenance.
- Nutrient uptake.

### *Allocation to storage:*

- Used to allow plant to cope with fluctuating environment.

### *Allocation to reproduction:*

- Storage in propagules for reproduction.

Our lack of knowledge about the physiological mechanisms that control allocation of carbon between plant parts is one of the main conclusions drawn by a number of authors (Cannell and Dewar 1994; Farrar and Jones 2000). In the absence of knowledge about the physiological mechanisms that control allocation in plants, modelers have proposed hypotheses and devised schemes of allocation which are either empirically, based on observations of relative growth rates of various plant parts, or are teleological e.g. the plant allocates carbon to maximise growth or optimise water use.

The simplest way to model allocation of new growth between plant component parts is to use fixed allocation coefficients chosen to ensure that the allometric relations between plant parts match those observed in the field. However, such a rigid framework does not allow the model to adjust to changes in environmental conditions known to influence allocation. An improvement is to modify an allocation coefficient in response to environmental conditions, e.g. adjust allocation to roots as a function of nutrient or soil water availability, and then adjust the remaining allocation coefficients to maintain the correct proportionality.

More complex models of allocation arise from consideration of the functional relationships between plant parts. I have borrowed the framework presented by Cannell and Dewar (1994) as an aid to discussing the controls and constraints on allocation in trees (Figure 1).

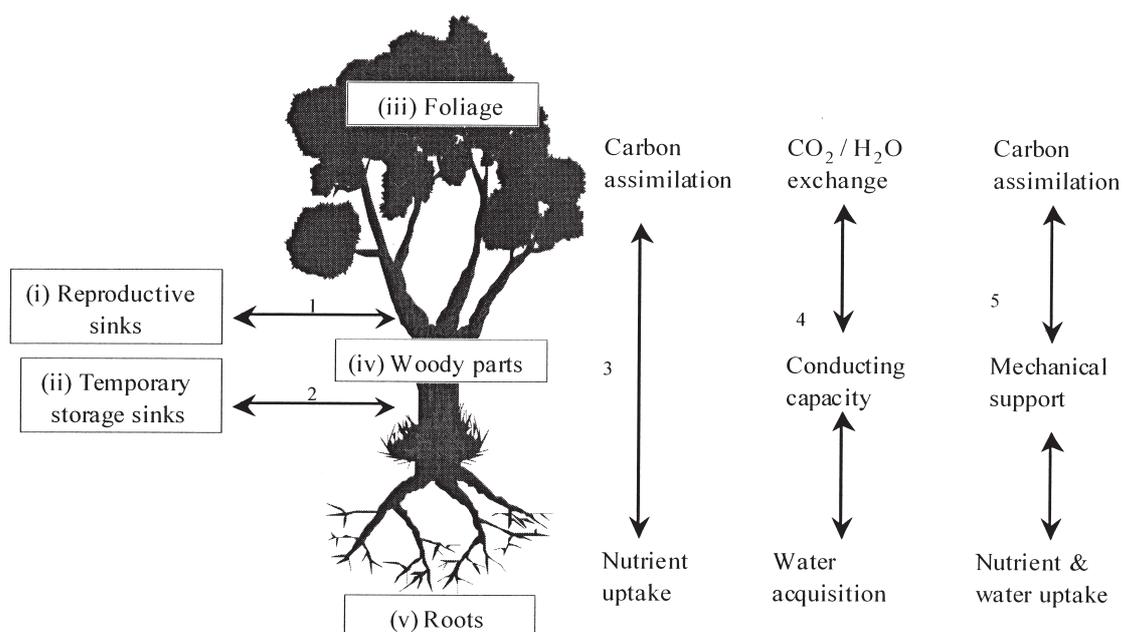


Figure 1 Five relationships [1-5] between five tree parts [(i)-(v)] which provide a basis for considering the constraints and controls on the allocation of assimilates (modified from Cannell and Dewar 1994).

## 1. ALLOCATION TO REPRODUCTIVE SINKS.

In evolutionary terms, a successful plant must leave at least one descendant. Seeds must contain sufficient reserves of carbohydrate and mineral nutrients to give the embryos a good chance of survival. Thus once a plant reaches sexual maturity reproductive sinks will become very important and compete with other sinks such as roots, shoots and cambium for resources. Cremer (1992) reported that on average 5.7 % of above-ground growth was allocated to reproduction in *Pinus radiata* but annual variation was from 1.2 to 12.8 %.

Most forest models ignore allocation to reproductive structures while others use a fixed allocation once the tree reaches sexual maturity (e.g. Kirschbaum, 1999).

## 2. ALLOCATION TO STORAGE.

Storage of assimilate and nutrients is very important if plants, especially long-lived perennial plants, are to survive seasonal environmental conditions and periods of stress. Short term storage enables the plant to buffer differences between supply and demand for assimilates at times when either photosynthesis or growth is limited by environmental conditions. For example, growth is more sensitive to temperature and water potential than is photosynthesis so the ability to store the excess production rather than downregulation of photosynthesis enables the plant to maximise growth as soon as conditions are favourable.

Furthermore, conifers growing in temperate zones start photosynthesis in Spring before the new growth flush and assimilate production is stored in preparation for the heavy demand once growth commences. Storage also enables a tree to recover from biotic and abiotic events such as pest attack and fire. This ability is especially important in long-lived species that must survive at least until reproductive age.

Some models include a storage term but often this is only a passive reserve pool used to store assimilates that are fixed in excess to current demand. These reserves are then drawn down as soon as demand by growth exceeds current supply from photosynthesis. However, there is some evidence to suggest that storage sinks should have an equal or higher priority to utilization sinks (shoots, roots and cambial meristem) e.g. where storage sinks are refilled at the same time as the growth of utilization sinks (Weinstein et al., 1991).

### 3. CARBON V NITROGEN ACQUISITION

Cannell and Dewar (1994) stated: "If we take an average over a period of time when there is no net change in storage reserves, then the assimilation of carbon by foliage, and the acquisition of mineral nutrients by fine roots, must be in balance with the utilization of carbon and mineral nutrients in plant growth. There should thus be a functional balance between the size and activity of the carbon fixation system (shoots) and the size and activity of the nutrient acquisition system (roots)". The Transport-Resistance model (Thornley, 1972a, 1998) attempts to model the allocation of carbon and nitrogen in a mechanistic way. Shoot and root are split into structural and substrate pools (Figure 2). Newly fixed assimilate and nitrogen uptake are placed in their respective substrate pools. Translocation between substrate pools depends on the concentration gradient and a resistance to flow while the growth of roots or shoots is a function of component size and the product of local C and N concentrations. The resistances to transport ensure that nitrogen concentration in the root is higher than that in the shoot and that carbon concentration is higher in the shoot than the root. It is this concentration difference, combined with the dependence of growth on the product of local concentrations, that allows the growth of shoot relative to that of root to respond correctly to changes in photosynthesis or nitrogen uptake.

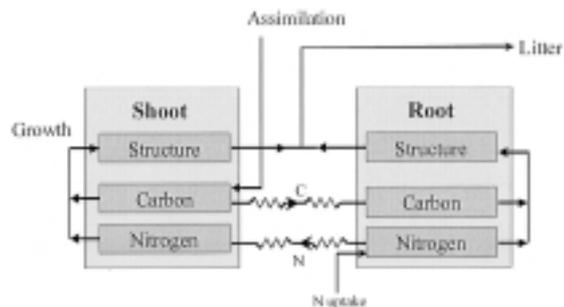


Figure 2 Scheme of the Transport-resistance model (Thornley 1972, 1998)

Dewar (1993) modified the transport-resistance model to be more consistent with the observation that much of the nitrogen used by roots for growth arrives in the phloem via the leaves (Figure 3). He showed that it could still operate even though a fraction (even all) of the nitrogen may be passed to the roots from the leaves.

The essential feature of the transport resistance model - that gradients of C and N substrate concentration exist in opposite directions - can still hold without separate resistances for C and N. Nitrogen is carried by mass flow (Münch flow hypothesis) from the shoot to the root driven by the concentration gradient of C. The concentration of N in the roots can thus be higher than that in the shoots.

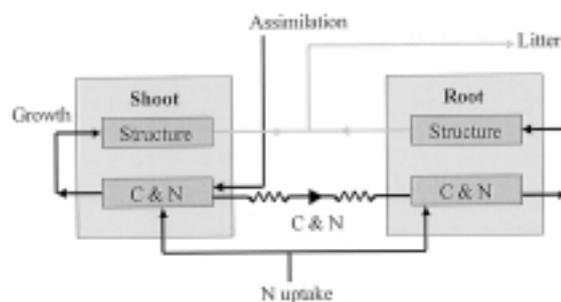


Figure 3 The Münch flow model of combined C and N transport (Dewar, 1993)

### 4. STRUCTURAL COST OF WATER TRANSPORT.

Shinozaki (1964) proposed that each new unit of leaf area requires a unit area of pipeline to transport water from roots to leaves. Mäkelä (1986) developed this idea and showed that the pipe model constraint (constant cross-section of sapwood to foliage area) implies that allocation to sapwood area will increase as the tree becomes taller (longer pipe length) thus leading to a slowdown in growth. The pipe model thus imposes

a constraint between allocation to leaf and allocation to sapwood.

Whitehead *et al* (1984) combined equations describing the driving forces for water movement with equations describing the properties of the flow pathway to give:

$$\frac{A_f}{A_s} \propto \frac{K}{Hg_c D_m} \quad (1)$$

showing that the ratio of foliage area ( $A_f$ ) to sapwood area ( $A_s$ ) is proportional to sapwood conductivity ( $K$ ), and inversely proportional to tree height ( $H$ ), canopy conductance ( $g_c$ ) and saturation deficit of the air ( $D_m$ ).

More recent research on tree hydraulics (Magnani *et al.* 2000) has focused on the fact that many trees appear to maintain leaf water potentials above a certain minimum threshold, thought to be the threshold for xylem cavitation. Control in the short term is through stomatal regulation but in the longer term through changes to allocation. Constant minimum leaf water potential implies that  $A_g/A_f$  increases with tree height (in contrast to pipe model). The implications are qualitatively the same as for the pipe model except that cavitation theory gives a stronger decline in tree growth with height. Data exist to support both models.

There are a number of difficulties in applying these approaches to allocation. i)  $K$  varies with species, age and throughout the tree, ii)  $K$  is not functionally related to specific gravity of sapwood and so the carbon cost per unit conductance requires a further empirical relationship and iii) Old sapwood must cease to function in proportion to loss of foliage.

### 5 Cost of mechanical support.

There is a carbon cost of providing mechanical support against gravitational and wind forces thus there should be a constraint between allocation to foliage and wood. Structural engineering theory can be applied to trees to determine optimal assimilate allocation within the woody structure of trees. One hypothesis is that a tree will allocate growth within its stem to equalise stress within the stem; otherwise there would be a weak point liable to failure. Studies on the shapes of trees and responses to being held still by guys or artificially swayed, all support the view that cambial growth occurs preferentially in areas of greatest stress.

Dean and Long (1986, 1992) used this constraint to develop a model for the allocation of assimilates along the stem giving,

$$D = c(AH)^{0.33} \quad (2)$$

Where  $D$  is stem diameter,  $A$  is leaf area per tree,  $H$  is height to the centre of leaf area and  $c$  is an empirical constant (ca. 3.75). The exponent 0.33 occurs with elastic self similarity and implies that the stem is designed with minimal mass to maintain its shape under load.

This approach has been extended to roots (Mattheck *et al.* 1997) using the assumption that optimum root design guarantees an even distribution of shear loading along the roots. However, they concluded that mechanical constraints may be less important than others in root growth.

## Allocation in models used within the CRC

The main models of interest with respect to the influence of allocation on NEE on a multi-year time scale are forest models. Allocation within crop models is not as important since the turnover of biomass is annual. I will briefly outline the approaches used to allocate carbon and nitrogen in the forest models used within the CRC GA.

### G'DAY:

The original G'Day (Generic Decomposition and Yield, Comins and McMurtrie 1993) had a very simple allocation routine: carbon acquired through photosynthesis is allocated to foliage, fine roots and woody tissue in fixed proportions.  $G$  depends on a number of environmental factors but importantly for allocation on the N:C of foliage.

So the rate of change of a plant carbon pool  $C_x$  is

$$\frac{dC_x}{dt} = \eta_x \cdot G - \gamma_x \cdot C_x \quad (3)$$

Where the subscript  $x$  refers to plant components; foliage, root or wood.  $\eta_x$  are the allocation coefficients (fixed),  $G$  is the gross carbon uptake from photosynthesis and  $\gamma_x$  are the senescence rates.

Nitrogen allocation is also simple. G'Day assumes N is limiting and so the plant takes up all available mineralised soil nitrogen irrespective of root size. This N is allocated to wood first such that the wood N:C remains constant. The remaining nitrogen is divided between the foliage and root such that the ratio of root N:C and foliage N:C remains constant. Consequently the N:C of foliage and root can change with soil N availability and since  $G$  is dependent on foliage N:C a feedback is established between available soil N and  $G$ .

Later versions of G'Day offer more complex allocation options similar to those in CenW described below.

### 3PG:

3PG is a conservation of mass model, so all the carbon fixed (net primary productivity, NPP) must be allocated to one of the three biomass pools; stems, foliage or roots. The version of 3PG described here is 3PGjs version 2 (Sands 2001). Allocation to roots is a function of environment and stand age, while allocation between stem and foliage of the remaining NPP depends on observed allometric relationships between foliage and stem biomass and stem diameter.

Once monthly NPP has been estimated, allocation to roots  $\eta_R$  is calculated as

$$\eta_R = \frac{\eta_{Rmax} \cdot \eta_{Rmin}}{\eta_{Rmin} + (\eta_{Rmax} - \eta_{Rmin}) \cdot F_R \cdot \Phi} \quad (4)$$

where  $\eta_{Rmax}$  and  $\eta_{Rmin}$  are the maximum and minimum possible values of  $\eta_R$ ,  $F_R$  is the soil fertility index (0-1), so allocation to roots will always be more in low-fertility soils than in high-fertility soils under the same growing conditions and  $\Phi$  is a modifier that depends on environment and stand age.

$$\Phi = f_{age} \min(f_{VPD}, f_{SW}) \quad (5)$$

$f_{age}$  declines non-linearly with age to empirically model the decline seen in forest productivity with age.  $f_{VPD}$  (0-1) declines exponentially with increasing VPD and  $f_{SW}$  declines sigmoidally with relative soil water availability at a rate that depends on soil texture parameters.

The ratio of allocation between foliage and stemwood is a function of stem diameter (D) such that as the tree gets bigger more is allocated to stem and less to foliage.

$$\eta_s = \frac{1 - \eta_f}{aD^n + 1} \quad (6)$$

where  $a$  and  $n$  are empirical parameters. Once root and stemwood allocation coefficients are known foliage takes the remainder. Age and size thus act independently on allocation.

### CENW:

CenW has 8 plant carbon and nitrogen pools (reproductive structures, foliage, branch, stem, bark, coarse root, fine root and soluble carbon). New growth is allocated to the different biomass pools based on a number of different considerations. Allocation of carbon is dealt with first. A constant fraction is allocated to reproductive organs once trees have reached the age of sexual maturity.

$$\eta_{repro} = r_1$$

There is a constant proportionality between allocation to stem wood and bark, branch and coarse root so

$$\eta_{bark} = r_2 \eta_{stem}$$

$$\eta_{branch} = r_3 \eta_{stem}$$

$$\eta_{croot} = r_4 \eta_{stem}$$

Allocation to foliage is related to allocation to branches but varies with tree height (H)

$$\eta_{foliage} = r_5 \eta_{stem} \left( \frac{10r_5}{H} \right) \quad (8)$$

thus as the tree gets taller less carbon is allocated to foliage relative to stem, bark, branch and coarse root.

Allocation to fine roots is related to allocation to foliage but varies with foliar nitrogen concentration ( $N_{lim}$ ):

$$\eta_{fineroot} = r_5 \eta_{stem} \left( \frac{10r_5}{H} \right) \{ r_{max} - [N_{lim} (r_{max} - r_{min})] \} \quad (9)$$

where  $N_{lim}$  ranges linearly from  $r_{min}$  when foliar N is high to  $r_{max}$  when foliar N is low. So when foliar N is low more carbon is allocated to fine roots relative to foliage.

The allocation coefficients must sum to one,  $\eta_{stem} + \eta_{repro} + \eta_{bark} + \eta_{branch} + \eta_{croot} + \eta_{foliage} + \eta_{fineroot} = 1$ , so given the fixed parameters  $r_1$  to  $r_5$ , the tree height and the foliar N concentration one can solve the set of equations.

Nitrogen allocation coefficients for each plant component ( $a_i$ ) are then calculated as

$$a_i = \frac{b_i \eta_i}{\sum b_i \eta_i} \quad (10)$$

where  $b_i$  is an empirical nitrogen concentration ratio for plant component  $i$  relative to that in foliage. This means that the nitrogen concentration of all biomass components dynamically adjust with changes in foliar nitrogen concentration as is observed experimentally.

### PROMOD:

Promod (Battaglia and Sands, 1997) does not allocate carbon dynamically. It predicts a static picture of the stand following canopy closure to predict productivity and a site index. This site index can be used with a traditional empirical growth model to predict stand development.

LAI is predicted as a species specific maximum times the minimum of functions of

- i) mean annual temperature,
- ii) mean winter temperature,
- iii) mean annual crop factor (a measure of water stress)
- iv) soil nutrient status

Annual net production ( $G_a$ ) is then calculated as the sum of daily net biomass production based on this fixed leaf area and environmental factors. Leaf area and fine root biomass are assumed to be constant so that allocation to them depends on the senescence rates. Allocation to the stem ( $\eta_{\text{stem}}$ ) is based on an empirical relationship between  $\eta_{\text{stem}}$  and  $G_a$ . Allocation to coarse root and branches are proportional to allocation to stem.

#### LINKAGES:

Linkages is a ecosystem level forest model. It can simulate growth and development of mixed age, mixed species stands and the main aim is to explore interactions between species composition and forest floor nutrient mineralisation and availability as determined by climate and species litter quality.

Individual trees of different species increment in diameter according to species specific growth functions that are modified in response to available light water and nutrients. It deals with allocation through simple allometric functions based on diameter.

#### FULLCAM:

The integrated suite of models that comprise FullCAM are the physiological growth model for forests, 3PG (Landsberg and Waring 1997); CAMFor (Richards and Evans 2000); the Australian Greenhouse Office carbon accounting model for forests based on CO2Fix model of Mohren and Goldewik (1980), GENDEC (Moorhead and Reynolds 1991; Moorhead *et al.* 1999) and the Rothamsted Soil Carbon Model, RothC (Jenkinson *et al.* 1991). Each of these models have been independently developed and are suited to run on a monthly time-step.

The linkage between 3PG and CAMFor is achieved by inputting total biomass increment from 3PG output to the CAMFor biomass table. Allocation of this material to various tree components (above and below ground) will be as per the CAMFor mass distribution table. This table can be filled manually or by using formula embedded within 3PG.

In terms of allocation of NPP to the various tree components, FullCAM does not use the allocation calculations in 3-PG. Instead, the user has to enter the allocation coefficients for each year of the rotation. For each year, allocation coefficients need to be known for stem, branches, bark, leaves and twigs, coarse roots and fine roots. Needing to know these allocation coefficients is one of the main limitations of FullCAM and is an area that requires further work.

## Summary

Allocation plays an important role in NEE as it determines the rate at which carbon is stored in long-term storage pools such as wood and lignified litter.

Cannell and Dewar (1994) summarized it as: "Allocation is the outcome of many processes rather than a process in its own right. For short-lived annual species, it may be adequate and possible to ascribe empirical values to carbon allocation at each stage of plant development. However, this is not satisfactory or possible for perennial species, because important changes will occur in carbon allocation each year and during the lifetime of the stand. The problem is daunting because carbon allocation ultimately involves all the internal, environmental and genetic processes that regulate plant growth".

Without better understanding of the true physiological mechanisms that control allocation within plants we are forced to use allocation routines based on empirical relationships or constrained by known functional relationships between plant parts. This is not necessarily a major drawback as we often use simplified models to represent complex processes with acceptable results e.g. light use efficiency model.

Models currently used within the CRC use fairly simple allocation routines based either on fixed allocation coefficients or fixed proportionality between certain coefficients while others are modified by environmental factors.

How well these models can predict the effects of climate change is yet to be tested.

## References

- Battaglia, M. and Sands, P.J. 1997 Modelling site productivity of *Eucalyptus globulus* in response to climatic and site factors. *Australian Journal of Plant Physiology* **24**, 831-850.
- Cannell, M. G. R. & Dewar, R. C. 1994 Carbon Allocation in Trees - a Review of Concepts For Modeling. In *Advances in Ecological Research*, Vol 25, vol. 25, pp. 59-104.
- Comins, H. N. & McMurtrie, R. E. 1993 Long-Term Response of Nutrient-Limited Forests to CO<sub>2</sub> Enrichment - Equilibrium Behavior of Plant-Soil Models. *Ecological Applications* **3**, 666-681.
- Cremer, K.W. 1992. Relations between reproductive growth and vegetative growth of *Pinus radiata*. *Forest Ecology and Management* **52**, 179-199.

- Dean, T.J. and Long, J.N. 1986 Validity of constant-stress and elastic-instability principles of stem formation in *Pinus contorta* and *Trifolium pratense*. *Annals of Botany* **58**, 833-840.
- Dean, T.J. and Long, J.N. 1992 Influence of leaf area and canopy structure on size-density relations in even-aged lodgepole pine stands. *Forest Ecology and Management* **49**, 109-117.
- Dewar, R. C. 1993 A root-shoot partitioning model-based on carbon-nitrogen water interactions and Munch phloem flow. *Functional Ecology* **7**, 356-368.
- Farrar, J. F. & Jones, D. L. 2000 The control of carbon acquisition by roots. *New Phytologist* **147**, 43-53.
- Jenkinson, D. S., Adams, D. E. and Wild, A. 1991 Model estimates of CO<sub>2</sub> emissions from soil in response to global warming. *Nature* **351**, 304-306.
- Kirschbaum, M.U.F. 1999. CenW, a forest growth model with linked carbon, energy, nutrient and water cycles. *Ecological Modelling* **118**, 17-59.
- Lacointe, A. 2000 Carbon allocation among tree organs: A review of basic processes and representation in functional-structural tree models. *Annals of Forest Science* **57**, 521-533.
- Landsberg, J. J. and Waring, R. H. 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.
- Magnani, F., Mencuccini, M. & Grace, J. 2000 Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. *Plant Cell and Environment* **23**, 251-263.
- Mäkelä, A.A. 1986. Implications of the pipe model theory on dry matter partitioning and height growth in trees. *Journal of Theoretical Biology* **123** 103-120.
- Mattheck, C., Teschner, M. and Schafer, J. 1997 Mechanical control of root growth: A computer simulation. *Journal of Theoretical Biology* **184**, 261-269.
- Moorhead, D. L. and Reynolds, J. F. 1991 A general-model of litter decomposition in the Northern Chihuahuan desert. *Ecological Modelling* **56**, 197-219.
- Moorhead, D.L., Currie, W.S., Rastetter, E.B., Parton, W.J., Harmon, M.E. 1999 Climate and litter quality controls on decomposition an analysis of modelling approaches. *Global Biogeochemical Cycles*, **113**, 575-589.
- Richards G.P., Evans, D.W. 2000 CAMFor User Manual v 3.35 National Carbon Accounting System Technical Report No. 26 (pp 47), Australian Greenhouse Office.
- Sands, P. 2001 3PGps a user friendly interface to 3PG, the Landsberg and Waring model of forest productivity. CSIRO Technical report No. 29, Edition 2.
- Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T. 1964 A quantitative analysis of plant form-the pipe model theory *Japanese Journal of Ecology* **14**, 97-105.
- Thornley, J. H. M. 1972a A balanced quantitative model for root:shoot ratios in vegetative plants. *Annals Of Botany* **36**, 431-441.
- Thornley, J. H. M. 1972b A model to describe the partitioning of photosynthate during vegetative plant growth. *Annals Of Botany* **36**, 419-430.
- Thornley, J. H. M. 1991 A transport-resistance model of forest growth and partitioning. *Annals Of Botany* **68**, 211-226.
- Thornley, J. H. M. 1998 Modelling shoot:root relations: the only way forward? *Annals Of Botany* **81**, 165-171.
- Thornley, J.H.M. and Johnson, I.R. (1990) *Plant and Crop Modelling*. Oxford Science Publications, Oxford.
- Weinstein, D. A., Beloin, R. M. & Yanai, R. D. 1991 Modeling changes in Red Spruce carbon balance and allocation in response to interacting ozone and nutrient stresses. *Tree Physiology* **9**, 127-146.
- Whitehead, D., Jarvis, P.G. and Waring, R.H. 1984 Stomatal conductance, transpiration and resistance to water uptake in a *Pinus sylvestris* spacing experiment. *Canadian Journal of Forest Research* **14**, 692-700

# Stand Age Effects on Productivity in Forests: Representation in Models and Influence on Net Ecosystem Exchange

Michael Battaglia

The CRC for Sustainable Production Forestry and CSIRO Forestry and Forest Products

## Introduction

*Death, like generation, is a secret of Nature. Marcus Aurelius Meditations. iv. 5*

"Birth, death and taxes", the three certainties of life – well apparently not if you are a tree growth modeller. Certainly, most dynamic growth models start with small trees and I suppose we might call that birth, and most models deal to some extent with the 'carbon tax' of respiration but often stand age effects on productivity and the death of trees is dealt with, at best, in a summary manner. There is some irony in this omission since the decline in current annual increment in wood (CAI,  $m^3ha^{-1}yr^{-1}$ ) as stands age is one of the most universally observed patterns of forest growth (Figure 1). The reason for this apparent tension between ubiquity and representation is that despite the prevalence of the patterns of growth, decline and death, the actual mechanisms are poorly understood. Decline and death probably result from the interaction of many factors with the commonly observed relationships 'emerging' from the net effect of many individual stand and tree growth processes.

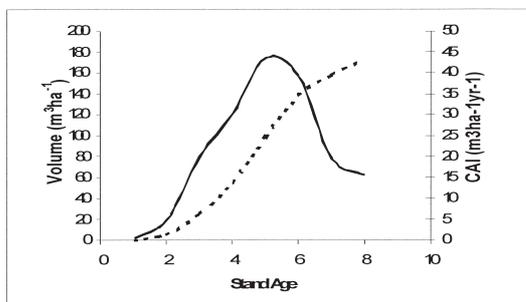


Figure 1. The relationship between stand age and standing volume (dotted) and current annual increment in wood volume (solid) for a young stand in southern Tasmania (after Beadle et al. 1995).

A decline in stand productivity (for the moment we will talk of productivity as stem wood volume increment) almost always

occurs but the timing of the onset of decline in productivity and the extent of this decline vary markedly between sites (Ryan et al. 1997). This variation in timing and degree of decline results in markedly different growth curves for different tree stands (Figure 2). Despite this variation, it is almost always the case that productivity decline starts early in stand life, usually within the first 10 to 20 years, or earlier. The stands themselves may continue to survive for longer than 100 years. Stand level decline in production precedes the decline in the productivity in individual trees (such as photosynthetic productivity per unit leaf area) by decades (Smith and Long 2001). For example, while plantations of eucalypts display growth decline between ages 2 and 10 years (Figure 2) it is widely recognised that forests of eucalypts will continue to live for between 300 and 500 years (Gilbert 1959).

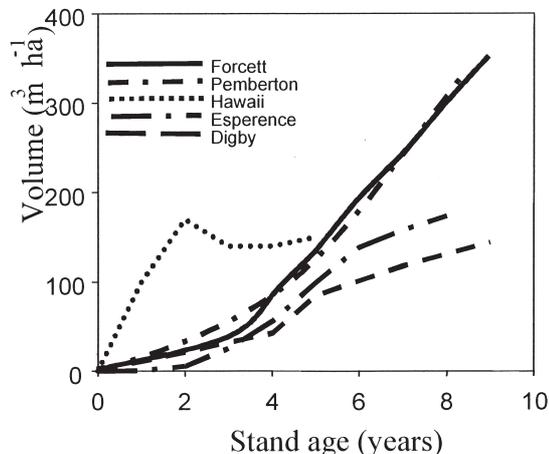


Figure 2. The rate at which growth decline develops affects the shape of the stand growth curve as seen in these examples from a range of eucalypt plantations in Australia and Hawaii.

It is also apparent that the early decline in productivity is much more a stand level phenomenon rather than a tree level phenomenon. Within stands the productivity of dominant trees continues on largely unabated while it is the marked decline in the productivity of the suppressed trees that is driving down stand level production (shown to some extent in Fig. 3)

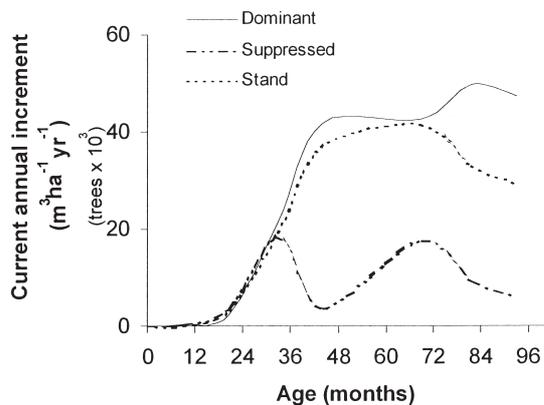


Figure 3. Stand level productivity and the productivity of an individual dominant and an individual suppressed tree at a fertiliser trial at Westfield Tasmania (Data from Smethurst and Baillie CSIRO FFP pers. comm.).

As stands get considerably older there is no doubt that processes that act within the individual tree (such as decrease in photosynthetic rate e.g., Yoder *et al.* 1994) play a role in further decreasing stand level production. However, it may be the failure to separate those processes that act early in stand development from those that act towards the end of stand life that has resulted in the failure to identifying the factors critical to the onset of age related decline in stand productivity.

A number of theories for age related decline have been proposed. These are covered briefly below (for further information seek recent reviews of Murty *et al.* 1996, Gower *et al.* 1996, Ryan *et al.* 1997, Smith and Long 2001). As we work through these it is important to differentiate between those that affect stand stem wood production, those that affect net primary production and those that influence stand gross primary production: the influence of each of carbon sequestration and stand carbon accumulation are different. It is also important to distinguish between processes that operate early in stand development, and contribute to the initial decline in CAI in wood production and reduce net primary production, perhaps ultimately contributing to stand death.

## Respiration

*"Extreme old age has wasted thee away" To the Memory of the Same Dog, William Wordsworth 1770-1850*

For a long time the classical explanation of later-aged decline of growth was that the increasing mass of sapwood in forest stands was responsible for increased stand respiration and hence a lower ratio of net to gross primary productivity. If stand

sapwood cross-sectional area and leaf area are functionally linked (e.g. Medhurst *et al.* 1999), then as trees grow taller stand sapwood mass must increase (since the volume is increasing with height) unless leaf area declines. If the maintenance respiration cost of this wood per unit mass or volume remains constant then total stand respiration will increase per unit of foliage sustained. Hence, stand growth efficiency (amount of stemwood production per unit leaf area *sensu* Ryan and Waring 1992) will decline.

Early in stand development maintenance respiration costs seem to scale approximately to sapwood volume (Lavigne *et al.* 1996). However, woody respiration rates per unit sapwood decline in older trees: apparently maintenance and growth respiration are not independent as assumed in the conventional maintenance/growth respiration paradigm (Lavigne and Ryan 1997, Gifford 2001 {this volume}). It seems that maintenance respiration is higher when growth rate is higher (Lavigne and Ryan 1997). Because of the declining respiration per unit sapwood mass, maintenance respiration in older stands only ends up to have a slight influence on carbon balance (5% difference between 40 & 245 yrs with a 40% decline in production – Ryan 1991, Ryan and Waring 1992).

It seems that despite total stand maintenance respiration rate increasing early in stand development (after the evidence of Lavigne *et al.* 1996) this contributes little to the marked declines in stand productivity observed early in stand development. If it did it would be the dominant trees, which are taller, that would slow down most markedly, whereas observation suggests that their growth pattern is largely unaffected (Smith and Long 2001, also Figure 4). The matching of decreases in maintenance respiration rate per unit sapwood volume with growth rate decreases also acts to reduce the effect of respiration in older stands. It is, therefore, unlikely that changes in maintenance respiration are influential in either the initial growth rate decline or the decline in growth rate late in stand development.

## Resource Capture

A decrease in the capacity of a forest to capture or utilise resources has also been suggested as reason for a decline in stand productivity. The two most persistent and well researched theories in this regard have been age or size related changes in hydraulic conductivity and nutrient immobilisation.

## HYDRAULIC CONDUCTIVITY

*"I would fain die a dry death." William Shakespeare, The Tempest Act i. Sc.1*

It has been observed that as trees grow taller (Yoder *et al.* 1994) or branches get longer (Waring and Silvester 1994, Walcroft *et al.* 1996, Warren and Adams 2000) hydraulic conductance declines leading to decreased water potential in leaves. This may then reduce stomatal conductance and subsequently decrease photosynthesis (Ryan and Yoder 1997). Along the way, and as a consequence (to prevent xylem cavitation according to the functional homeostasis of water transport hypothesis), the tree may change its patterns of allocation, for example by increasing the sapwood cross-sectional area to offset decreased hydraulic conductivity or by a change in the ratio of foliage to fine root mass to bring into balance the supply of, and demand for water (Magnani *et al.* 2000).

Although in favour through the 1990's as an explanation for later-aged forest productivity decline (see Ryan *et al.* 1997) sentiment has now changed and it is felt that while hydraulic conductivity may be a significant factor causing growth reduction in very old forests (>100 years) when compared with young forests (<20 years) it may not be a major component of the initial, and often marked decline in CAI in wood and net primary production (Barbara Bond, *pers. comm.*).

A comparison of the photosynthetic rate of foliage from *Eucalyptus nitens* trees suggests that if changes in hydraulic conductivity are occurring with height and branch length, they are expressed in crown photosynthetic activity of young trees. Trees of 4-year old *E. globulus* when grown at wide spacing under what were largely non-limiting water and nutrient conditions have branches with an average length of 4 m compared with 2.4 m in block plantings. Nevertheless the unit leaf area maximum rate of photosynthesis (under ambient CO<sub>2</sub> and saturating light) was higher for the trees with the open grown branches, 20 μmol m<sup>-2</sup>sec<sup>-1</sup> compared with 18 μmol m<sup>-2</sup>sec<sup>-1</sup> for leaves on branches from close-spaced trees (Henskens *et al.* 2001). Similarly Pinkard *et al.* (1998) show that the photosynthetic rate of young *E. nitens* trees remain constant over a 2 year period between the ages 4 to 6 years as trees doubled in height from approximately 9.5 to 18 m (Pinkard and Beadle 1998a) and that this rate of photosynthesis was equivalent to seedlings of the same species grown in pots that were between 1 to 3 m in height (Pinkard and Beadle 1998b).

However, in line with the hypothesis of functional homeostasis in water transport developed by Magnani *et al.* (2000), the

maintenance of these photosynthetic rates in developing stands of *E. nitens* may be at the cost of a decrease in the ratio of leaf area to sapwood cross-sectional area. Re-analysis of the data from 110 *E. nitens* trees across a range of sites of Medhurst *et al.* 1999 shows that, similar to the data of Magnani *et al.* 2000, this ratio increases with tree height ( $SA=4.24L^{0.6}H^{0.38}$ ,  $r^2=0.94$  where SA is the stem cross-sectional area of sapwood in cm<sup>2</sup>, L is the tree leaf area in cm<sup>2</sup>, and H is height in m). The implications of this change could be two-fold. Firstly, total sapwood respiration might increase if respiration scales proportionally to mass (as per Lavigne *et al.* 1996) and although the changes in allocation may mean that gross primary production remains unaltered, net primary production may decline. But a second, and consequent change arising from the first, might be that leaf area index (LAI) declines. Following the reasoning of Battaglia *et al.* (1997), stand LAI will be determined, in part, by the crown depth at which the photosynthetic light compensation point occurs. Besides being determined by the unit area photosynthetic rate this is also determined by the respiratory cost of foliage that at the branch level includes branch sapwood respiration. Applying the pipe model (Shinozaki *et al.* 1964), increasing stem sapwood cross-sectional area should result in increased total branch cross-sectional area and hence an increased respiratory cost per unit foliage area or mass.

## NUTRIENT IMMOBILISATION

*"Cruel as death, and hungry as the grave." James Thomson (1700–1748) The Seasons. Winter. Line 393*

Woody litter has a low nitrogen to carbon ratio, and a high lignin to nitrogen ratio (Grier 1978). As it accumulates in the litter layer as stands age, through woody matter litterfall and stand self thinning, it is thought that large amounts of nitrogen may be immobilised from throughfall, N-fixation and soil reserve sources (e.g. Chapin *et al.* 1986, Zimmerman *et al.* 1995). The accumulation of woody litter reduces the overall quality of litter (i.e., lignin:nitrogen ratio, C:N ratio) and consequently the decay rate of woody litter declines with stand age (e.g. Polglase and Attiwill 1992) and an increasing proportion of the stand nutrient budget becomes locked up in stand biomass and woody debris.

There are many documented cases of nutrient availability changing as stands develop (see Murty *et al.* (1996) for review) but the results from field observations are variable. For example, it has been shown that young and old lodgepole forests have higher N than intermediate aged forests (Ryan and Waring 1992).

The functional importance of these changes, particularly in younger forests is also unclear. Declining productivity of young forests can be partially halted by fertiliser application (e.g. Binkley *et al.* 1995) and, similarly, large crowns can be maintained on young stands and CAI increased by later-aged application of fertiliser (Smethurst *pers. comm.*, with 5–6 year old *E. nitens* forests). However, even where fertilisation has been maintained at optimal limits, CAI in wood declines in young stands; it seems that fertilisation may increase growth but not change the overall pattern of growth with stand age (Figure 4; Herbert 1984).

While the effects of nutrition do not seem to be strong determinants of changing productivity in young forests, modelling analysis shows that nutrient immobilisation may be an issue in older forests (e.g. Pastor *et al.* 1987 with LINKAGES, Murty *et al.* 1996 GDAY, Sanford *et al.* 1991 with CENTURY).

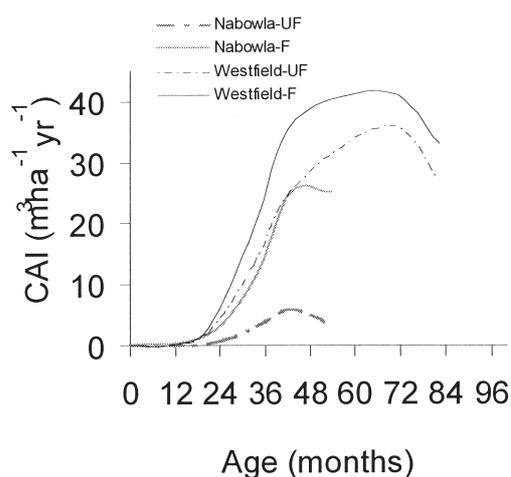


Figure 4. Comparison of pattern of current annual increment in wood volume (CAI) between optimally fertilised (F) and unfertilised stands (UF) of *Eucalyptus nitens* at two sites in Tasmania. Volume growth is changed but the timing and pattern of decline in CAI remains unchanged. Data from P. Smethurst and C. Baillie, CRC Sustainable Production Forestry, *pers. comm.*

## Changed allocation

One reason for changes in CAI in wood volume might be that allocation to stem wood (or foliage) declines because allocation of net primary production to some other pool increases or because turnover of some stand biomass pool increases. This hypothesis of changing stand production does not necessarily imply a change in net primary production. To some extent,

changes in allocation could be the result of other, already discussed, hypotheses rather than a cause of declining productivity in its own right and the change in CAI may be driven by a decrease in net primary production.

### INCREASED BELOWGROUND ALLOCATION

*"The crucial task of old age is balance: keeping just well enough, just brave enough, just gay and interested and starkly honest enough to remain .."* Florida Scott-Maxwell, *The Measure of My Days Knopf 68*

We have seen earlier that a decline in hydraulic conductivity and decreasing soil nutrient supply could both occur as stands age. Magnani *et al.* (2000) show how in the case of declining hydraulic conductivity this can lead to an increase in the ratio of fine roots to foliage. It is also known that belowground allocation of net primary production increases with declining nitrogen availability (e.g., Haynes and Gower 1995, Ryan *et al.* 1996).

Fine root mass in forests is variable with time but studies generally have shown that it increases with stand age. Gholz *et al.* (1986), for example, showed that both fine root mass and fine root production were greater in 9- compared with 27-year-old stands of *Pinus elliottii*. However, the changes may be more complex to interpret in some cases. For example, in *Pinus silvestris*, fine root mass was greater in pole than sapling or mature stands but the sum of fine root necromass and fine root production was greatest in old stands (Makkonen and Helmsaari 2001).

But changes in fine root production are not well correlated with stand productivity (Grier *et al.* 1981 cf. Gholz *et al.* 1986) and annual belowground carbon allocation only changes late in stand development well after CAI and LAI are in decline. It is also difficult to reconcile mass changes with the scale of impact: while with age there is an increasing proportion of net primary production allocated below ground, this mass change is slight compared with the decline in CAI in wood (Smith and Resh 1999).

### INCREASED REPRODUCTIVE ALLOCATION

*"Death rides on every passing breeze, He lurks in every flower."* Reginald Heber (1783–1826) *At a Funeral (i)*

It is possible that an ontogenetic shift in allocation toward reproduction may play a role in the onset of the decline in CAI. The high carbon cost (up to 10–15% of above-ground carbon, Linder and Troeng 1981) and the high nutrient content of seeds

suggests that it may play a role in decline of growth (evidenced by decreased wood increment in mast years Eis *et al.* 1965) and perhaps in the decline in leaf area if nutrients are in low supply. However, while allocation to reproduction increases with age, reproductive output generally is sporadic while growth decline is not suggesting that its role in the process may be slight (Ryan *et al.* 1997 after Eis *et al.* 1965).

## OTHER ALLOCATION CHANGES

*"My way of life is fallen into the sea, the yellow leaf"*  
William Shakespeare (1564–1616). *The Tragedy of Macbeth*.

Could it be that trees have some phenological driven aging process, as is commonly evidenced in many annual or shorter-lived plants? There is evidence of phenological aging in tree meristematic tissues (e.g. grafting of old on to young tissue leads to mature trait expression, Wiltshire *et al.* 1992) but evidence on growth rate relationship is poor and some 'clones' of woody plants have been shown essentially to be eternal (e.g. Potts and Reid 1995)

## Individual tree hypothesis, stand structure and stand-level resource use efficiency

*"Death's truer name is "Onward,""* Tennyson, *Life of Tennyson*. Vol. i. 1

If the early aged decline in stand productivity cannot be explained totally using leaf and tree level ecophysiological processes, can it be explained using stand-level processes and observing changes in stand structure with age?

Some recent work suggests that as stands age (in the first years and coincident with the onset of a decline in CAI in wood) the efficiency of growing wood per unit of resource used declines as a result of the stand differentiating into dominant and suppressed trees (Binkley *et al.* 2001). Total stand resource use remains unchanged; that is suppressed trees continue to use the same quantity of resources, they just do less with these resources. As was observed in Figure 3 for the Tasmanian plantation situation, Binkley *et al.* (2001) observed in their study plantation that growth efficiency remains high for dominant trees (0.54 kg [stemwood]/m<sup>2</sup>[leaf area]) but declines for non-dominant trees (0.3 kg [stemwood]/m<sup>2</sup>[leaf area]). The larger trees in a stand measured by Binkley *et al.* (2001) produced 25% more wood per unit of light, water and nitrogen than the remaining trees. These data find support from earlier

work by O'Hara (1988) who found that stem volume growth per unit of sapwood area was higher for trees with more sapwood area. Given that the relationship between sapwood area and leaf area is usually linear or has an exponent greater than unity (Medhurst *et al.* 1999) this suggests increased leaf area productivity for dominant trees in the study of O'Hara (1988).

These results are perhaps counter-intuitive and until the processes that underlie the changes in growth efficiency of suppressed trees are identified then the question must be considered unresolved. Theoretical studies of Scott *et al.* (1993) and estimates of Kaufmann and Ryan (1986) suggest that one would expect higher average crown leaf area productivity from trees with relatively low leaf area (since then most leaves are operating at close to optimal illumination) or among suppressed trees. The continued maintenance of resource use by suppressed trees while CAI is declining is itself problematic. Does this reflect a change in the efficiency of gross primary production or a change in the allocation pattern (into increased turnover, other organs or increased respiration)? While some of these changes sound like a recasting of the earlier hypotheses, the mixed response between elements of the stand at a young age may have masked their detection.

Along similar lines it has been hypothesised that as stands mature, changes in crown structure mean that the unit area carrying capacity of foliage increases because branches are longer (Smith and Long 2001). As stands get older stem density (stems ha<sup>-1</sup>) declines as a result of stand self-thinning. Consequently, average branch length (and presumably coarse root length) increases. It is likely under these conditions that total stand branch sapwood mass will increase (or LAI and/or light interception will fall). The result of this will be similar to that in the discussion of changes in stem sapwood cross-sectional area above.

## Representation in models and implications for net ecosystem exchange modelling

*"These are the arcs, the trophies I erect, That fortify thy name against old age; And these thy sacred virtues must protect"* Samuel Daniel (1562–1619), *Beauty, Time, and Love Sonnet*

While the actual processes (or combination thereof) that determine the decline of productivity in forest stands remain unclear the studies carried out to date indicate a number of key

system level responses that models should, and should not, reproduce. These are listed below.

- 1 Declining productivity with age is a common, perhaps universal, forest growth phenomena and should be represented in growth models. Failing to do so may result in a substantial over-estimate of carbon sequestration. The extent to which carbon sequestration is over-estimated depends on what are the predominant causes of age related decline (changes in GPP cf. allocation for example) and the extent to which the understorey and later-stage successional species maintain overall rates of forest carbon exchange.
- 2 It seems that the initial decline in stand productivity is not related to a decline in stand resource use (after Binkley *et al.* 2001). Models should show an early age decline in CAI of wood, but this should not be accompanied by decreased net ecosystem exchange. That is, stand water use and nutrient uptake should remain unchanged.
- 3 It is probable that leaf level photosynthetic activity (when averaged across the trees in the stand) declines in older stands but remains unchanged in young stands at the time at which CAI in wood and LAI begin to decline. Models that attempt to simulate age-related decline in productivity with a single process may be unable to capture the full gamut of physiological and growth pattern changes.
- 4 The initial decline in stand productivity should coincide with a decline in LAI. This decline should occur early in stand development (between 10-20% of expect stand longevity).
- 5 Models should probably show a proportional increase of annual net primary production to belowground sinks as stands age. However, these changes need not result in an increase in the absolute allocation belowground.
- 6 It is likely that respiration rate per unit sapwood mass is not constant. Models that assume this will probably over-estimate the role of respiration in the onset of later-aged forest decline.
- 7 In part, it may be stand-level (rather than leaf-level or tree-level) processes that cause the decline in productivity in young stands. Simulation of these effects will require incorporation of stand structure and consideration of between-tree-within-stand variability. This may not be possible with stand level models (all models in Table 1!). Rather than invoke the full complexity of an individual tree array model a suitable compromise may be to allocate stand level production among a notional array of individual trees (e.g., Korol *et al.* 1995).

No existing model is consistent with all the observations listed above on age-related productivity decline. Table 1 shows what process (if any) cause an age related decline in the productivity predictions of a sample of process-based models.

Age related process	3PG/ FullCam	ProMod	CENW	Linkages	G'Day	Century
<b>Explicit decline</b>	👉	👉	👉	👉	👉	👉
age-dependent leaf level processes	👉	👉	👉	👉	👉	N/A
<b>Implicit decline</b>	👉	👉	👉	👉	👉	👉
respiration increases with sapwood mass	👉	👉	👉👉	👉	👉👉	👉
soil nitrogen supply change with time	👉	👉	👉	👉	👉	👉
biomass allocation variable with time	👉	👉	👉	👉	👉	👉
model considers structure and within stand competition	👉	👉	👉	👉	👉	N/A

Table 1. The representation of various age-related phenomena in models of forest growth or forest soil processes.

## Acknowledgements

Without discussions with Dan Binkley, Mike Ryan and Barbara Bond this review would not have been possible: any discrepancies in the manuscript are mine and can not in anyway be attributed to their useful and incisive contributions. I would also like to thank Phil Smethurst and Craig Baillie for providing me with access to data. Thanks also go to Sigrid Resh for initial direction and useful criticism and Maria Cherry and Miko Kirschbaum for proof reading and editorial comment.

## References

- Battaglia, M., M. L. Cherry, C. L. Beadle, P. J. Sands, and A. Hingston. 1997. Leaf area index prediction in eucalypt plantations: effects of water stress and temperature. *Tree Physiology* **18**:521-528.
- Beadle, C. L., J. L. Honeysett, C. R. A. Turnbull, and D. A. White. 1995. Site limits to achieving genetic potential. *in* B. M. Potts, N. M. G. Borralho, J. B. Reid, W. N. Tibbits, and C. A. Raymond, editors. *Eucalypt Plantations: Improving Fibre*

- Yield and Quality Proc. CRCTHF - IUFRO Conf. CRC for Temperate Hardwood Forestry: Hobart, Hobart, 19-24 Feb 1995.
- Binkley, D., M. G. Ryan, J. L. Stape, and H. Barnard. 2001. Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. *Ecosystems* **submitted**.
- Chapin, F. S. I., P. M. Vitousek, and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. *American Naturalist* **127**:48-58.
- Eis, S., J. Garman, and L. F. Ebell. 1965. Relation between cone production and diameter increment of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.) and Western white pine (*Pinus monticola* (Dougl.)). *Canadian Journal of Botany* **43**:1553-1559.
- Gholz, H. L., L. Hendry, and W. P. Cropper. 1986. Organic matter production and distribution in fine roots in plantations of slash pine. *Canadian Journal of Forest Research* **16**:529-538.
- Gilbert, J. M. 1959. Forest succession in the Florentine Valley, Tasmania. *Proc. Roy. Soc. Tas.* **93**:129-151.
- Gower, S. T., R. E. McMurtrie, and D. Murty. 1996. Above-ground net primary production decline with stand age: potential causes. *Trends in Ecology and Evolution* **11**:378-382.
- Grier, G. C. 1978. A *Tsuga heterophylla*-*Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. *Canadian Journal of Forest Research* **8**:198-206.
- Grier, G. C., K. A. Vogt, M. R. Keyes, and R. L. Edmonds. 1981. Biomass distribution and above-and belowground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Canadian Journal of Forest Research* **11**:155-167.
- Haynes, B. E., and S. T. Gower. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. *Tree Physiology* **15**:317-325.
- Henskens, F., M. Battaglia, M. Cherry, and C. L. Beadle. 2001. Physiological basis of spacing effects on tree growth and form in *Eucalyptus globulus*. *Trees Structure and Function* (in press).
- Herbert, M. A. 1984. Variation in the growth of and response to fertilizing black wattle with nitrogen, phosphorus, potassium and lime over three rotations. Pages 907-920 in D. G. Grey, A. P. G. Schonau, C. J. Schutz, and A. van Laar, editors. *Symposium on Site and Productivity of Fast Growing Plantations*. South African Forest Research Institute, Pretoria.
- Kaufmann, M. R., and M. G. Ryan. 1986. Environmental, physiographic, and stand effects on individual tree growth in subalpine forests. *Tree Physiology* **2**:47-59.
- Korol, R.L., Running, S.W. and Milner, K.S. 1995. Incorporating intertree competition into an ecosystem model. *Canadian Journal of Forest Research* **25**: 413-424.
- Lavigne, M. B., and M. G. Ryan. 1997. Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. *Tree Physiology* **17**:543-551.
- Lavigne, M. B., S. E. Franklin, and J. Hunt, E.R. 1996. Estimating stem maintenance respiration rates of dissimilar balsam fir stands. *Tree Physiology* **16**:687-695.
- Linder, S., and E. Troeng. 1981. The seasonal course of respiration and photosynthesis in strobili of Scots pine. *Forest Science* **2**:267-276.
- Magnani, F., Mencuccini, and J. C. Grace. 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. *Plant, Cell and Environment* **23**:251-263.
- Makkonen, K., and H. Helmisarri. 2001. Fine root biomass and production in Scots pine stands in relation to stand age. *Tree Physiology* **21**:193-198.
- Medhurst, J. L., M. Battaglia, M. L. Cherry, M. A. Hunt, D. A. White, and C. L. Beadle. 1999. Allometric relationships for *Eucalyptus nitens* (Deame {is that 'Deane'} and Maiden) Maiden plantations. *Trees, Structure and Function* **14**:91-101.
- Murty, D., R. E. McMurtrie, and M. G. Ryan. 1996. Declining forest productivity in aging forest stands: a modeling analysis of alternative hypotheses. *Tree Physiology* **16**:187-200.
- O.Hara, K. L. 1988. Stand structure and growing space efficiency following thinning in an even-age Douglas-fir stand. *Canadian Journal of Forest Research* **18**:859-866.
- Pastor, J., R. H. Gardner, V. H. Dale, and W. M. Post. 1987. Successional changes in nitrogen availability as a potential factor contributing to spruce decline in boreal North America. *Canadian Journal of Forest Research* **17**:1394-1400.
- Pinkard, E. A., and C. L. Beadle. 1998a. Patterns of above-ground carbon allocation of *Eucalyptus nitens* (Deane and

- Maiden) Maiden following green pruning. Canadian Journal of Forest Research **28**:1419-1428.
- Pinkard, E. A., and C. L. Beadle. 1998b. Regulation of photosynthesis in *Eucalyptus nitens* (Deane and Maiden) Maiden following green pruning. Trees **12**:366-376.
- Pinkard, E. A., C. L. Beadle, N. J. Davidson, and M. Battaglia. 1998. Photosynthetic responses of *Eucalyptus nitens* (Deane and Maiden) Maiden to green pruning. Trees: Structure and Function **12**:119-129.
- Polglase, P. J., and P. M. Attiwill. 1992. Nitrogen and phosphorus cycling in relation to stand age of *Eucalyptus regnans* F. Muell.: I. return from plant to soil. Plant Soil **142**:156-166.
- Potts, B. M., and J. B. Reid. 1985. Analysis of a hybrid swarm between *Eucalyptus risdonii* Hook. f. and *E. amygdalina* Labill. Aust. J. Bot. **33**:543-562.
- Ryan, M. 1991. A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. Tree Physiology **9**:255-266.
- Ryan, M. G., and B. J. Yoder. 1997. Hydraulic limits to tree height and tree growth. Bioscience **47**:235-242.
- Ryan, M. G., and R. H. Waring. 1992. Maintenance respiration and stand development in a subalpine lodgepole pine forest. Ecology **73**:2100-2108.
- Ryan, M. G., D. Binkley, and J. H. Fownes. 1997. Age-related decline in forest productivity: pattern and process. Advances in Ecological Research **27**:214-262.
- Ryan, M. G., R. M. Hubbard, S. Pongracic, R. J. Raison, and R. E. McMurtrie. 1996. Foliage, fine-root, woody tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. Tree Physiology **16**:333-343.
- Scott, R. D., J. N. Long, and F. W. Smith. 1993. Canopy stratification and leaf area efficiency: a conceptualization. Forest Ecology and Management **60**:143-156.
- Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira. 1964. A quantitative analysis of plant form - the pipe model theory. I. Basic analyses. Jap. J. Ecol. **14**:97-105.
- Smith, F. W., and J. N. Long. 2001. Age-related decline in forest growth: an emergent property. Forest Ecology and Management **144**:175-181.
- Smith, F. W., and S. C. Resh. 1999. Age-related changes in production and belowground carbon allocation in *Pinus contorta* forests. Forest Science **45**:333-341.
- Walcroft, A. S., W. B. Silvester, J. C. Grace, S. D. Carson, and R. H. Waring. 1996. Effects of branch length on carbon isotope discrimination in *Pinus*. Tree Physiology **16**:281-286.
- Waring, R. H., and W. B. Silvester. 1994. Variation in foliar <sup>13</sup>C values, within the crowns of *Pinus* trees. Tree Physiology **14**:1203-1213.
- Warren, C. R., and M. A. Adams. 2000. Water availability and branch length determine  $\delta^{13}\text{C}$  in foliage of *Pinus pinaster*. Tree Physiology **20**:637-643.
- Wiltshire, R. J. E., B. M. Potts, and J. B. Reid. 1992. A paedomorphocline in *Eucalyptus*: II. Variation in Seedling Morphology in the *E. risdonii/tenuiramis* complex. Aust. J. Bot. **40**:789-805.
- Yoder, B. J., M. G. Ryan, R. H. Waring, A. W. Schoettle, and M. R. Kaufmann. 1994. Evidence of reduced photosynthetic rates in old trees. Forest Science **40**:513-527.
- Zimmerman, J. K., W. M. Pulliam, D. J. Lodge, V. Quinones-Orfila, N. Fetcher, S. Guzman-Grajales, J. A. Parrotta, C. E. Asbury, L. R. Walker, and R. B. Waide. 1995. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. Oikos **72**:314-322.

# Phenology and Reproduction

Chris Beadle

*The CRC for Sustainable Production Forestry and CSIRO Forestry and Forest Products*

Phenology is the study of periodicity phenomena in plants. As such it includes the impact of external variables on reproductive processes. In this section, three areas that can be broadly lumped under this heading will be considered. No attempt is made at this stage to explore their likely significance to net ecosystem exchange. For example with foliage type, its impact would depend on the proportion of trees in the 'juvenile phase' and this may be very low. No attempt has been made to explicitly include foliage type in models to date. In this preliminary review, trees and forests are the major focus. The inclusion in models of the major variables considered in the text is summarised in Table 1.

## Juvenile and mature foliage

Many species have contrasting foliage types. These are generally distinguished as juvenile and mature (or adult). In eucalypts, foliage type may be characterised by differences in leaf size and shape. In some acacias e.g. *Acacia melanoxylon*, bipinnate leaves precede the development of phyllodes. The latter are formed as a result of expansion of the petiole and consequently have different anatomy than the leaves. Does this characteristic of heteroblasty have functional significance? The following variables are used to explore this possibility.

### Specific leaf area

Specific leaf area (SLA) measures leaf area per unit dry mass. It can be shown that SLA of a range of eucalypt species decreases with stand age from about 35 m<sup>2</sup> kg<sup>-1</sup> at age less than three months to about 5 - 10 m<sup>2</sup> kg<sup>-1</sup> at age one to two years (Linder 1985, Kirschbaum *et al.* 1992, Cromer *et al.* 1993). Part of this observation is contained in SLA being smaller in mature than in juvenile foliage although SLA also decreases with leaf age independent of foliage type. One must conclude that, for at least the first part of its life cycle, leaf area can be developed for a relatively lower investment in biomass. In the two major commercial species that are planted, *Eucalyptus globulus* and *E. nitens*, juvenile foliage is produced and retained for periods of up to three to four years. Specific leaf area also increases with canopy depth and can be affected by species and treatment e.g. well-watered versus water-stressed trees: these

differences can be significant (White 1996). Changes with canopy depth are a direct result of the effect of incident quantum flux density on SLA during leaf development.

SLA is included explicitly as a constant in some models but not in others (Table 1) and can include the effects of leaf age.

	SLA	k	Albedo	Seasonality	Leaf longevity
APSIM				✓	
CENTURY				✓	✓
CenW	✓	✓	✓	✓	✓
G'DAY	✓	✓		✓	
GRASP				✓	
PROMOD		✓		✓	
3-PG	✓	✓		✓	✓

Table 1. Inclusion in models of major variables considered here.

### Interception, absorption and reflection of light

Leaf angle varies in eucalypt species and this has led to reports that the light extinction coefficient (*k*) can vary between 0.17 and 0.75 for a range of species and ages of eucalypts (Anderson 1981). In *E. globulus* and *E. nitens*, the juvenile leaves are opposite, sessile and oblong, the mature leaves, alternate petiolate and narrowly lanceolate. In two provenances of *E. nitens* showing marked differences in retention of juvenile foliage, it was observed that annual stem volume increment increased in proportion to the amount of juvenile foliage retained (Beadle *et al.* 1989). However, there was no difference in the ratio of foliage mass to basal area between provenances suggesting that faster growth is more related to canopy size than foliage type. This finding suggests that selecting a single value of *k* for juvenile and mature foliage may be satisfactory. Where *k* has been included in models (Table 1), it has been as a constant.

Foliage type is quite often associated with differences in surface properties and albedo. For example, juvenile foliage is often glaucous in appearance and this may lead to differences in the reflection, absorption and transmission of light. Increasing densities of wax deposited on the leaf surfaces of *Eucalyptus urnigera* may reduce absorption of incident energy by up to 30% (Thomas 1965).

## Interception loss

*Rainfall interception, canopy storage of water and interception loss are, amongst other variables, a function of leaf shape, size, surface characteristics and orientation (Jackson 1975). Foliage type may therefore impinge on rainfall interception.*

## Resistance to stress

The impact of foliage type on resistance to stress is unclear. One study suggests that glaucous water-repellent leaves, which are characteristic of some juvenile foliage, are associated with increased freezing tolerance (Thomas and Barber 1974).

## Gas exchange

Brodribb (1992) demonstrated that, while photosynthetic rates per unit leaf area were similar between leaves and phyllodes of *A. melanoxylon*, leaves had greater rates of photosynthesis per unit dry mass. Thus, leaves are more efficient than phyllodes at producing photosynthate per unit of carbon invested in foliage production. Similar conclusions are likely to pertain to gas exchange of juvenile and mature foliage of eucalypts that have distinctive differences in SLA.

## Pest and disease risk

The glaucous coating of juvenile leaves may provide a physical barrier to browsing by adult *Paropsis charybdis* beetles (Edwards 1982) and, through its hydrophobicity, resistance to the deposition and germination of spores of *Phaeoceptorium eucalypti* (Heather 1967). These early studies raised an awareness of the importance of foliage type in pest and disease attack. However it is not always the juvenile foliage that is the less susceptible. The female moths of *Mnesampela privata*, currently the most prevalent pest problem of eucalypt plantations in southern Australia, have a greater preference for juvenile foliage for egg laying (Steinbauer and Floyd 2001). In the same plantations *Mycosphaerella*, one of the most significant of fungal pathogens causing defoliation, is also prevalent on juvenile foliage (C. Mohammed, pers. comm.).

Pests and diseases are not modelled although some models (e.g. 3-PG), can cope with defoliation. GRASP describes animal intake and live weight gain.

## Persistence of juvenile foliage

In many species, juvenile foliage is retained for short periods only. However the *Maidenaria* section of the *Symphomyrtus* subgenus that includes *E. globulus* and *E. nitens* are characterised by species that retain their juvenile foliage for

long periods (Noble 1989). Phase change may also be under genetic control (Jordan *et al.* 1999) and this raises the possibility that genotype may be of significance when dealing with foliage type in models.

## Leaf production/litterfall

Australian forests, including all significant planted forests, are evergreen. However each is subject to periods of leaf expansion and leaf shedding. Canopy size is therefore a dynamic property of forests. Leaf area index ( $L^*$ ) is the key measure of canopy size and the key variable in light interception models describing tree and stand growth. The magnitude of any seasonal change in  $L^*$  will have implications for net ecosystem exchange and, for example, any conclusions that are reached using remote sensing techniques and NVDI.

## Seasonality

There are few time series studies that describe how  $L^*$  changes seasonally. In temperate climates in Australia, periods of leaf development and expansion will, in the absence of water stress, be largely a function of temperature. Seasonal patterns of litterfall in temperate eucalypt forest are closely related to maximum temperature (Turnbull *et al.* 1983). In tropical and subtropical climates, rainfall patterns will probably be the major determinant. Net increases in  $L^*$  will occur during periods of leaf expansion, net decreases during periods of litterfall. Seasonal variation will be higher if periods of maximum leaf production are out of phase with periods of maximum foliage loss. For example, increases of foliage mass equivalent to net changes in  $L^*$  of between 1.1 and 3.0 between an end of winter minimum and end of summer maximum were recorded in a range of treatments in *Pinus radiata* (Raison *et al.* 1992).

Several models (CENTURY, CenW, G'DAY, GRASP, 3-PG) include seasonality in the sense that pools and fluxes change with time in response to changes in inputs that are driven by changing environment e.g. temperature and light. The level of detail included however varies from model to model and some variables e.g.  $L^*$  in PROMOD are averages for the annual cycle. None of the models include seasonality in a strict phenological sense.

## Number of cohorts and leaf longevity

Leaf longevity is the period that a leaf remains functional between initiation and fall and to some extent is an inherent property of a species. Thus slower growing species, like conifers, tend to have longer leaf longevity than faster growing species,

like eucalypts (Beadle 1997) but the activity of leaves is lower in the former than the latter. Factors like light environment will affect longevity. Thus leaves on isolated trees and in developing stands will tend to have greater leaf longevity because they remain above the light compensation point for longer periods than leaves in closed forests.

Cohorts refer to the numbers of age classes of leaves that contribute to the canopy. Not unexpectedly, the number of cohorts tends to be greater the slower growing the species. The activity of each cohort tends to decrease with age. More cohorts mean greater variation in photosynthetic activity both vertically and horizontally through the canopy.

Leaf longevity is modelled in some instances (CENTURY, CenW, 3-PG) but cohorts are not included.

### *Growth habit*

Some species have a continuous growth habit. This is driven by a naked bud system that allows growth as long as critical values of the factors that allow growth, available water and nutrients, high and low temperature limits, have not been exceeded. Eucalypts are the prime example of this habit and there may be several periods of growth in any annual cycle. In contrast, *P. radiata* produces a dormant bud and there is usually a period when no growth occurs, though in Australia, there may be more than one phase of growth in any annual cycle. Growth habit is an inherent property of a species. In exotic environments, this may determine where a species will grow.

Growth habit is modelled in the sense that growth will occur when the conditions are suitable for carbon gain. Phenological switches are not included in forest models though are in APSIM and CENTURY so that grain/seed yield can be predicted.

### *Pests and diseases*

The impacts of pests and diseases on leaf area development are complex. Leaf spot diseases like *Mycosphaerella* effectively reduce the amount of leaf area for light interception (Lundquist and Parnell 1987) and eventual leaf death increases litterfall. Diseases, like *Phytophthora cinnamomi*, that affect the conducting tissues and cause water stress (Dawson and Weste 1984), may reduce light-use efficiency and photosynthesis. Defoliating insects reduce leaf area though this may be offset by an increase in the photosynthetic capacity of the remaining foliage as well as an increase in the rate of development and increased photosynthetic capacity of new foliage, similar to that observed following green pruning (Caldwell *et al.* 1981, Senock *et al.* 1991, Pinkard *et al.* 1998).

The effects of pests and diseases are not modelled in any of the forest models though grasses and crops can be grazed (e.g. in GRASP).

## Reproduction

---

### *Partitioning of carbon to reproductive structures*

Estimates of standing biomass and its partitioning rarely include reproductive structures. In a study in *Eucalyptus teretecornis* plantations, the partitioning of dry mass to reproductive parts varied between 0.56 and 0.79% of total biomass in five- to eight-year-old plantations (Bargali *et al.* 1991). These numbers are arguably low. In a study of a range of species in the Brookhaven National Forest in New York, partitioning of above-ground dry mass to fruits, peduncles and flowers varied between 0.28 and 8.7% (Whittaker and Woodwell 1968). Thus values can be significant. It is likely that a proportion of reproductive effort will be affected by environmental controls and environmental stress. Partitioning to reproductive structures is modelled in CenW.

### *Impact on carbon stored*

Some reproductive structures, like pollen and seed production, have a rapid turnover. Thus reproduction may be a drain on carbon resources that is not measured. Its magnitude may be significant, with maybe up to 5-10% of total carbon gain going to reproduction and therefore not being stored. It is even more important for nutrients because of their higher concentration in reproductive compared to other tissues (M. Kirschbaum, CSIRO Forestry and Forest Products, 2001, pers. comm.).

The following also need to be considered.

- seasonality of reproductive effort
- triggers for flowering (photoperiod, vernalisation)
- degree days
- succession (global change context)

Reproductive effort is particularly relevant to crop models (Merv Probert, CSIRO Tropical Agriculture, 2001, pers. comm.) where partitioning into the reproductive structures is the measure of harvestable yield. The growth of agricultural crops is also driven by heat units and modified by photoperiod, vernalisation and environmental stress. Some of these issues are considered by APSIM and CENTURY.

## References

- Anderson, M.C. (1981). The geometry of leaf distribution in some south-eastern Australian forests. *Agric. Meteorol.* 25, 195-205.
- Bargali, S.S., Singh, S.P. and Singh, R.P. (1991). Structure and function of an age series of eucalypt plantations in Central Himalaya. I. Dry matter dynamics. *Ann. Bot.* 69, 405-411.
- Beadle, C.L., McLeod, D.E., Turnbull, C.R.A., Ratkowsky, D.A. and McLeod, R. (1989). Juvenile/total foliage ratios in *Eucalyptus nitens* and the growth of stands and individual trees. *Trees* 3, 117-124.
- Beadle, C.L. (1997). Dynamics of leaf and canopy development. In: *Management of soil, water and nutrients in tropical plantation forests* (E.K.S. Nambiar and A.G. Brown, eds). Australian Centre for International Agricultural Research. pp 169-212.
- Brodribb, T. (1992). A physiological comparison of leaves and phylloidesin *Acacia melanoxylon*. Hons thesis, University of Tasmania. 50 pp.
- Caldwell, M.M., Richards, J.H., Johnson, D.A., Nowak, R.S. and Dzurec, R.S. (1981). Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunch grasses. *Oecologia* 50, 14-24.
- Cromer, R.N., Cameron, D.M., Rance, S. J, Ryan, P.J. and Brown, M. (1993). Response to nutrients in *Eucalyptus grandis*. I. Biomass accumulation. *For. Ecol. Manage.* 62, 211-230.
- Dawson, P. and Weste, G. (1984). Impact of root infection by *Phytophthora cinnamomi* on the water relations of two *Eucalyptus* species that differ in susceptibility. *Phytopathology* 74, 486-490.
- Edwards, P.B. (1982). Do waxes on juvenile *Eucalyptus* leaves provide protection from grazing insects? *Aust. J. Ecol.* 7, 347-352.
- Heather, W.A. (1967). Leaf characteristics of *Eucalyptus bicostata* Maiden *et al.* seedlings affecting the deposition and germination of spores of *Phaeoseptoria eucalypti* (Hansf.) Walker. *Aust. J. Biol. Sci.* 20, 1155-1160.
- Jackson, I.J. (1975). Relationships between rainfall parameters and interception by tropical forest. *J. Hydrol.* 24,215-238.
- Jordan, G., Potts, B.M., and Wiltshire, R. (1999). Strong, independent quantitative genetic control of vegetative phase change and first flowering in *Eucalyptus globulus* ssp. *globulus*. *Heredity* 83, 179-187.
- Kirschbaum, M.U.F. , Bellingham, D.W. and Cromer, R.N. (1992). Growth analysis of the effects of phosphorus nutrition in *Eucalyptus grandis* seedlings. *Aust. J. Plant Physiol.* 19, 55-66.
- Linder, S. (1985). Potential and actual production in Australian forest stands. In: *Research for forest management* (J.J. Landberg & W. Parsons, eds). CSIRO, Melbourne. pp 11-35.
- Lundquist, J.E. and Parnell, R.C. (1987). Effects of *Mycosphaerella* leaf spot on growth of *Eucalyptus nitens*. *S. Afr. For. J.* 140, 51-59.
- Noble, I.R. (1989). Ecological traits of the *Eucalyptus* L'Herit subgenera Monocalyptus and Symphyomyrtus. *Aust. J. Bot.* 37, 207-224.
- Pinkard, E.A., Beadle, C.L., Davidson, N.J. and Battaglia, M. (1998). Photosynthetic responses of *Eucalyptus nitens* (Deane and Maiden)Maiden to green pruning. *Trees* 12, 119-129.
- Raison, R.J., Khanna, P.K., Benson, M.L., Myers, B.J., McMurtrie, R.E. and Lang, A.R.G. (1992). Dynamics of *Pinus radiata* foliage in relation to water and nitrogen stress: II Needle loss and temporal changes in foliage mass. *For. Ecol. Manage.* 52, 159-178.
- Senock, R.S., Sisson, W.B. and Donart, G.B. (1991). Compensatory photosynthesis of *Sporobolus flexuosus* (Thurb.)Rydb. Following simulated herbivory in the Chihuahuan desert. *Bot. Gaz.* 152, 275-281.
- Steinbauer, M.J. and Floyd, R.B. (2001). Risk assessment for Autumn Gum Moth. *CRC Sustainable Production Forestry Technical Report* 55, 19-22.
- Thomas, D.A. (1965). Physiological aspects in natural selection in the cline of *Eucalyptus urnigera*. PhD Thesis, University of Tasmania. 377 pp.
- Thomas, D.A. and Barber, H.N. (1974). Studies on leaf characteristics of a cline of *Eucalyptus urnigera* from Mount Wellington, Tasmania. I. Water repellency and the freezing of leaves. *Aust. J. Bot.* 22, 501-512.
- Turnbull, C.R.A. and Madden, J.L. (1983). Relationship of litterfall to basal area and climatic variables in cool temperate forests of southern Tasmania. *Aust. J. Ecol.* 8, 425-431.
- White, D.A. (1996). Physiological responses to drought of *Eucalyptus globulus* and *Eucalyptus nitens* plantations. PhD Thesis, University of Tasmania. 166 pp.
- Whittaker, R.H. and Woodwell, G.M. (1968). Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. *J. Ecol.* 56, 1-25.

# How Does Ecosystem Water Balance Influence Net Primary Productivity? - A Discussion

Derek Eamus  
University of Technology, Sydney

## Abstract

Net primary productivity is determined by the rate of photosynthesis and the rate of autotrophic respiration. Photosynthetic carbon gain of a canopy is determined by leaf-scale photosynthesis, by interception of light by a canopy, the amount of canopy and the efficiency of utilisation of light energy.

It is axiomatic that the water balance of an ecosystem influences the NPP of an ecosystem, but what are the mechanisms by which water balance influences NPP? The aims of this paper are to look at some of these mechanisms, to highlight some of those processes that do not feature sufficiently prominently in some models of NPP and to assess the extent to which Australian ecosystems are water limited.

Water balance of an ecosystem is determined by input, loss and storage. Inputs include direct inputs to the ecosystem as rainfall, mist, fog and snow melt. Few models account for the last three. Indirect inputs include surface flow (flooding), river flow and groundwater flow of water that arrived in other ecosystems. Few models account for these processes. Outputs include evapotranspiration, surface and lateral soil flows out of the ecosystem and deep percolation to depths 2 m below the maximum rooting depth of the vegetation. There is patchy accommodation of all 3 processes in most models of NPP in Australia. A significant relationship between rainfall and above-ground biomass or NPP is observed for most of the Australian continent.

## Introduction

### *The purpose of this review*

The first aim of this brief review is to address the question:

*What mechanisms link ecosystem water balance to NPP?*

A second aim is to highlight which of these processes are infrequently incorporated into models through a comparison of

several models of productivity used in Australia. Finally, a brief discussion of the relationship between rainfall and biomass or NPP is given for Australia.

### *Net primary productivity*

Net primary productivity is an important quantitative characteristic of an ecosystem (Churkina *et al.* 1999), and much effort has been expended to determine NPP of different ecosystems around the world (Kicklighter *et al.* 1999). Seasonal changes in NPP, resulting from seasonal changes in net ecosystem exchange, and the temporal displacement between carbon gain through photosynthesis and carbon loss through respiration, are principal causes of seasonal changes in atmospheric CO<sub>2</sub> (Keeling *et al.* 1996). NPP can be used in estimating crop yield and forest production. Because measurements of NPP of all ecosystems, at all times, are impractical, terrestrial models are used to estimate NPP.

### *Ecosystem water balance – a priori considerations*

Ecosystem water balance is here defined as the water status (water potential) of vegetation, the water content of the depth of soil that interacts with vegetation (and therefore inclusive of groundwater and an associated capillary fringe) and the water content of the atmosphere interacting with vegetation.

The water balance of an ecosystem is determined by the difference in rates of input and loss of water. Storage of water within the system acts as a buffer, which can moderate the response of vegetation to changes in input and loss. Three storage sites exist – soil, plant and atmosphere. Plant storage capacity is small and quickly depleted in vegetation. Recharge of plant water occurs daily and probably seasonally. However, water stored in plants may influence daily patterns of vegetation water use and should not be ignored. Rates of water use, of course, correlate well with NPP; reduced rates of water use resulting from reduced water availability, occur with concomitant reductions in rates of photosynthesis.

Stored soil water content can be very large (or small), depending on soil type, rooting depth, rainfall and the availability of groundwater. The contribution of soil stores can be very substantial, for example in north Australian savannas

(Cook *et al.* 1998). Changes in soil water content are a major cause of changes in NPP. There is an increasing realisation that changes in groundwater availability and groundwater quality (especially salt content) are having an influence on NPP.

The water vapour pressure of the lower atmosphere is subject to large daily and seasonal fluctuations, and can cause significant changes in rates of photosynthesis and hence NPP through stomatal responses.

Input of water to an individual ecosystem can be in the form of rain, mist, fog and snow, directly into an ecosystem. In addition, water input can be the result of lateral flow of soil water and groundwater, floodwater, or river water, all of which may arrive from an adjacent ecosystem. Few models accommodate these latter sources, despite their importance in some systems. The importance of river water and groundwater has been established for *Eucalyptus camaldulensis* and other species in numerous sites (Thorburn and Walker 1993; George *et al.* 1999).

The loss of water from an ecosystem is the result of several processes. These include:

- transpiration from vegetation;
- evaporation from soil, surface water and wet canopies;
- surface flow out of the ecosystem;
- lateral flow through the soil to streams/rivers/lakes; and
- percolation to depths 1–2 m below the rooting zone of vegetation (where it is unavailable to vegetation and therefore considered 'out' of the ecosystem) and subsequent groundwater recharge.

Transpiration is the most frequently modelled process, despite the importance of other loss processes.

### *Short-term change compared to long-term differences, in ecosystem water balance*

NPP can be compared at one site, through time, and therefore the issue is – how do changes in water balance within an ecosystem influence NPP of that system? Alternatively, NPP of ecosystems that differ in annual water balance can be compared, and therefore the issue is – how do differences in water balance of different ecosystem contribute to observed differences in NPP? Most of what is written below can be applied to both questions.

## Linkages between ecosystem water balance, ecosystem processes and NPP

### ABOVE-GROUND PROCESSES

#### *Stomatal conductance*

Stomatal aperture is the end-point resolution of a large number of input variables. Of particular interest are the impacts of soil water content, atmospheric water content and plant water status on stomatal conductance ( $g_s$ ). Declining soil water content results in a decline in aperture and hence  $g_s$ . This decline is rarely linear. Similarly, increases in leaf-to-air vapour pressure difference cause non-linear declines in  $g_s$ . These responses are common knowledge, and we have an increasing understanding of the cellular mechanisms underlying these responses, based upon chemical (abscisic acid and xylem sap pH) and hydraulic signals. However, infrequently acknowledged are, first, the interaction of soil water and atmospheric water content as a determinant of  $g_s$ ; second, the difference in stomatal responses to these factors among different species and different plant functional types (for example, different phenological guilds or  $C_3$  versus  $C_4$  plants); and third, the influence of leaf age and leaf developmental history on stomatal responses.

Leaf water potential is a useful measure of plant water status but it is a poor instantaneous predictor of  $g_s$  during a day as there is an inverse relationship between  $g_s$  and leaf water potential during a day such that as leaf water potential declines in the morning,  $g_s$  increases. However, maximum  $g_s$  over a period of many days does decline as leaf water potential declines during the development of soil water deficit (Davies *et al.* 1994).

Leaf turgor potential correlates well with  $g_s$  but is not incorporated in any models as field data are not available. However, pre-dawn leaf water potential does correlate with  $g_s$  and such data are more readily available (Prior *et al.* 1997). Pre-dawn water potential is an intuitively useful parameter since it integrates soil water availability over the root zone.

Plants regulate the difference in water potential ( $\Psi_w$ ) between root and leaf (Eamus and Prior 2001). As soil  $\Psi_w$  declines, leaf  $\Psi_w$  declines to maintain a gradient of  $\Psi_w$  for water uptake from soil to leaf. However, if plants regulate the difference to remain within set-limits,  $g_s$  must vary to regulate water loss, thereby regulating leaf  $\Psi_w$ . Consequently a threshold leaf  $\Psi_w$

can be defined below which  $g_s$  declines with continued decline in leaf  $\Psi_w$ . However, little is known about what determines the value, daily and seasonally, of this threshold  $\Psi_w$  and the extent to which an ecosystem mean value can be ascertained.

Many of the following mechanisms linking changes in ecosystem water balance to NPP have, as their final response in a chain of events, a change in stomatal conductance. However, it is important to understand the proximal events linking changes in ecosystem water balance with changes in NPP.

### *Hydraulic architecture of trees*

The hydraulic architecture of plants directly influences tree water use. Hydraulic architecture is likely to set the upper limit to tree height (Ryan and Yoder 1997) and canopy area per tree. Therefore, an understanding of hydraulic architecture is likely to be an important factor for modellers of NPP. Xylem specific and leaf specific hydraulic conductivities tend to be higher in mesic sites than more xeric sites (Willigen and Pammenter 1998).

Leaf ( $k_l$ ) or sapwood ( $k_s$ ) specific conductivity ( $E/(\delta P/\delta x)$  where  $E$  is transpiration rate;  $\delta P$  is the pressure gradient between the ends of the branch or stem of length  $x$ ) and growth efficiency ( $m^3 \text{ wood}/m^2 \text{ leaf area}$ ) were correlated in a study of several clones of *Eucalyptus* growing on mesic or xeric sites (Willigen and Pammenter 1998). This is a result of the maintenance of a high stomatal conductance and hence assimilation rate. Reductions in  $k_l$  or  $k_s$  reduce stomatal conductance and transpiration without reducing leaf water potential (Sperry *et al.* 1993; Sperry and Pockman 1993).

Low soil water content, and high evaporative demand, singly or in combination, increase the prevalence of xylem embolism and decrease hydraulic conductance. This reduces the supply of water to canopies, which must adjust  $g_s$  in order to maintain leaf water potential within acceptable limits, thereby reducing canopy photosynthesis. Stomata behave in a manner that limits the difference in water potential between root and leaf so as to avoid the development of 'run-away' embolism (Cochard *et al.* 1996).

The ratio of sapwood cross-sectional area to leaf area supported by that sapwood area (the Huber value) provides a measure of the efficiency and sufficiency of the conducting pathway for water supply. Although Huber values are determined by the ratio of soil water availability to evaporative demand in many cases, and systematic differences in Huber value between climate zones and plant functional types appear in the literature (Mencuccini and Grace, 1995; Eamus and Prior 2001), exceptions are noted (Willigen and Pammenter 1998).

Vulnerability of xylem to embolism is determined by the hydraulic architecture of plants. Vulnerability of trees to embolism can vary seasonally and is influenced by site factors such as rainfall, soil water availability and evaporative demand (Willigen and Pammenter 1998). Different functional plant groups differ in systematic ways with respect to sensitivity to embolism (Eamus and Prior 2001). As previously observed, the prevention of excessive embolism through regulation of  $g_s$  is a common trait and therefore the development of embolism vulnerability curves would be a useful development for modelling stomatal responses to ecosystem water balance.

### *Leaf area index*

Increased leaf area index (LAI) with increasing water availability is commonly observed. However, it is clear that in some systems at least, increased water availability does not prevent seasonal declines in leaf area index. Although temperature may be a more important control signal in temperate zones, genetic programming overrides changes in soil water availability in many cases. Thus, artificial extension of the wet season through irrigation into the dry season does not inhibit leaf fall in many drought-deciduous species (Myers *et al.* 1998), a fact poorly reflected in models of NPP. Water stress and temperature are frequently interactive, as are water stress and photo-inhibition, through excess light interception by a canopy. Few models incorporate this interactive term.

Canopy leaf area is considered primarily in terms of light interception and photosynthetic carbon gain. However, canopy development is a major determinant of canopy water interception and interception losses. Since canopy interception loss can account for a significant fraction of rainfall, and is more important in small rainfall events than large, the impact of canopy interception on input of available water to soil requires consideration. The impact of canopy interception loss on soil water input varies significantly with canopy development and is therefore seasonally variable.

### *Vegetation structure*

Vegetation structure is a major determinant of light capture and hence NPP. The fraction of PAR absorbed by canopies (fPAR) is of primary importance in calculating NPP. However, does water balance influence fPAR?

The fraction of PAR absorbed by canopies is determined by leaf attributes (cuticular and epidermal reflectance; thickness; pigment concentration; leaf orientation); canopy attributes (leaf area index; leaf distribution in space and time;) time of day (sun angle) and time of year (phenological patterns of leaf flush

and leaf fall; sun angle). Ecosystem water balance cannot influence time of day or year, but does influence most other attributes, especially reflectance, leaf thickness and pigment content (and hence absorbance), phenological patterns in wet-dry climates and LAI.

Use of satellite Normalised Difference Vegetation Index (NDVI) data generally allows robust estimates of canopy attributes and temporal patterns of changes in canopy structure and behaviour. However, production efficiency models using satellite information frequently do poorly with respect to seasonally dry ecosystems and evergreen biomes where seasonal fluctuation in canopy structure are minimal (Bondeau *et al.* 1999).

Of particular interest in this context would be an assessment of how models adjust fPAR, canopy light use efficiency (cLUE), or quantum yield ( $\theta$ ), as a function of season (temperature and ecosystem water balance being of particular importance).

In a recent comparison of 11 global NPP models, it was found that the relative importance of seasonal change in canopy structure differs between ecosystems and changes with season (Bondeau *et al.* 1999). Boreal evergreen and temperate deciduous ecosystems were most easily modelled, while savannas and tropical evergreen systems were the hardest. It was concluded that rain-green systems (eg savannas) required more studies that collect seasonal patterns of soil moisture and LAI (see below).

### *Temporal patterns of water input*

Two meters of rainfall falling over five consecutive months in a wet season, followed by a rainless dry season, does not support the same LAI as 2m of rainfall falling evenly throughout the year. Therefore the temporal pattern of water input is an important determinant for the development of LAI and hence NPP. Monthly averages for rainfall are likely to underestimate the impact of rainfall at the start and end of wet seasons. In the absence of seasonality of rainfall monthly time-steps can still introduce errors in estimating effective rainfall. Four millimeters of rainfall every day for a month in a hot, cloud-free environment has less impact on soil recharge than two rainfall events of 60 mm each at two week intervals.

## BELOWGROUND PROCESSES

### *Allocation to root biomass, root depth and groundwater availability*

Allocation to roots increases, generally, as soil water availability declines. Increased allocation must, by definition, result in

decreased allocation to above-ground parts and therefore reduce the potential for canopy development and NPP.

Maximum rooting depth of ecosystems varies substantially between biomes and climate zones. Despite much effort, there has been little success in predicting maximum and average rooting depth for different ecosystems. Consequently measurements of actual root distribution are required, rather than assumptions. Most models of ecosystem NPP do not have a realistic approximation of rooting depth and the contribution of either deep stores of soil water or groundwater. Cook *et al.* (1998) have shown that it is the water stored between 1-6 m depth and the *gradual* increase in groundwater depth during the dry season that explains the ability of evergreen savanna trees to transpire and photosynthesise at comparable rates in the wet and dry season.

### *Soil-root hydraulic effects*

As soil water content declines, soils shrink and the volume of soil that is occupied by water declines. Consequently hydraulic contact between soil water and root declines with concomitant declines in hydraulic conductance of the soil-root pathway. Recent modelling by Williams *et al.* (1998) has concluded that this is a major reason for stomatal conductance declining in a Brazilian cerrado (savanna) and concomitant declines in canopy CO<sub>2</sub> uptake. These authors concluded that daily changes in soil-root hydraulic conductance were best able to explain divergence in modelled and observed CO<sub>2</sub> fluxes, especially in the dry season. This approach seems highly promising.

A mechanism employed by plants to overcome soil drying, however, is to increase root growth. Of particular relevance is the interaction between the rate of soil drying and the rate of root growth. The rate of soil drying will depend upon soil characteristics and the amount of evapotranspiration. The rate of root growth is determined by soil characteristics, rates of carbohydrate supply from the shoot and genetic limitations. Increased root growth will reduce the availability of carbon for supporting leaf growth, but the increase in water uptake resulting from this presumably offsets this reduction. Thus a cost-benefit analysis of different allocation patterns may reveal the rules of optimality employed by plants.

Re-distribution of water by roots within the soil profile (for example "hydraulic lift", a process whereby roots in moist soil at depth extract water from this soil and release it into the upper soil profile, at night) has the potential to significantly influence the water balance of an ecosystem. The contribution of such

redistribution to ecosystem water use in Australia is poorly quantified, but undoubtedly occurs (Burgess *et al.* 1998).

## Respiration

Soils represent a major terrestrial carbon store and soil respiration, a mixture of autotrophic and heterotrophic respiration, represents a significant component of ecosystem C flux, especially at night. The large sensitivity of soil CO<sub>2</sub> efflux to short-term changes in temperature is well-documented (Raich and Potter 1995), although recent studies highlight the absence of a temperature dependence (Janssens *et al.* 1998). However, the dependence of soil respiration (that is CO<sub>2</sub> efflux resulting from autotrophic and heterotrophic respiration) on soil water content is perhaps less fully acknowledged. Furthermore, the relative importance of temperature and soil water in determining soil respiration appears to be determined by the degree of seasonality of the two (that is, the amplitude of seasonal variation in either; Chen *et al.* 2001).

Changes in plant water status presumably influence respiration, but to a relatively minor extent over the range of daily and seasonal change in water status. Interestingly, although it is known that light partially inhibits respiration, there is little recognition that deciduous and evergreen species may differ in how respiration varies between day and night (Villar *et al.* 1995). Since evergreen and deciduous trees differ in many ways in their response to declines in ecosystem water balance, it is possible that the response of respiration rate to changes in water balance may also differ.

## Comparing several models of NPP

Table 1 presents a summary of the presence/absence of some of the key processes linking ecosystem water balance to NPP in several models reviewed here. Transpiration, soil water balance and deep drainage of water are calculated in most models and an adequate depth for tree roots is allowed in most models. Calculating vegetation water use as a function of rainfall, LAI and climate are commonly undertaken with high levels of success. However, the input of groundwater to transpiration, groundwater quality (principally salinity) and disturbance (especially fire) are rarely present in models. It is likely, therefore, that such models will not adequately predict Australian savanna productivity, for example, where disturbance is central to understanding the functioning of these systems, or salt affected sites, which account for a significant area in Australia. Finally,

the importance of xylem embolism and changes in soil-root hydraulic conductance as determinants of canopy conductance and hence productivity, are infrequently acknowledged in models. Few models are able to realistically calculate canopy conductance as a function of an interaction of soil and atmospheric water contents.

## Sensitivity analyses

In a major comparison of 15 global NPP models, significant differences in the spatial and seasonal distribution of simulated NPP were observed (Schloss *et al.* 1999). To determine causes of these differences between models, sensitivity analyses to different aspects of climate were undertaken. For ecosystems where NPP was not limited by precipitation, annual estimates of NPP were similar. However, in ecosystems that were limited by precipitation, large differences in sensitivities occurred, with the largest differences occurring where both rainfall and temperature limited NPP. Interestingly, latitudinal distribution of NPP estimated by these 15 models was most highly correlated with precipitation, but for seasonal estimates of NPP, the correlation among NPP, precipitation, solar radiation and temperature declined significantly. It is clear that such a comparison of sensitivity for annual, seasonal and latitudinal distribution of NPP should be undertaken for the Australian models. In particular, use of the Australian savannas is recommended because previous comparisons indicate that such systems are the hardest to model (Kicklighter *et al.* 1999).

## Relationship between rainfall and biomass/NPP in Australia

Using data supplied by Dr M Battaglia (CRC for Hardwood Forestry, Hobart) and Dr D Barrett (CSIRO, Canberra), Figs. 1a, b (Barrett) and 1c (Battaglia) were generated. It is apparent that fine tissue productivity (Fig 1a; assumed to be directly proportional to total NPP) and total above-ground biomass (Fig. 1b) increase asymptotically with rainfall. Data cover a range of sites across the Australian continent and a wide range of vegetation types, from ecosystems dominated by tall trees to low shrub-dominated systems. It is clear that the response of above-ground biomass or fine tissue productivity reaches a plateau as rainfall increases much above 2000 mm per year. Similarly, for *Eucalyptus globulus*, growing in Western Australia, Tasmania, South Australia and Victoria, mean annual volume increment, (taken to be proportional to NPP), increases as the ratio of (rainfall + irrigation)/(Potential Evaporation) increases (Fig 1c) asymptotically. This ratio is used, rather than

rainfall alone, as it represents a better measure of regional water balance than rainfall alone.

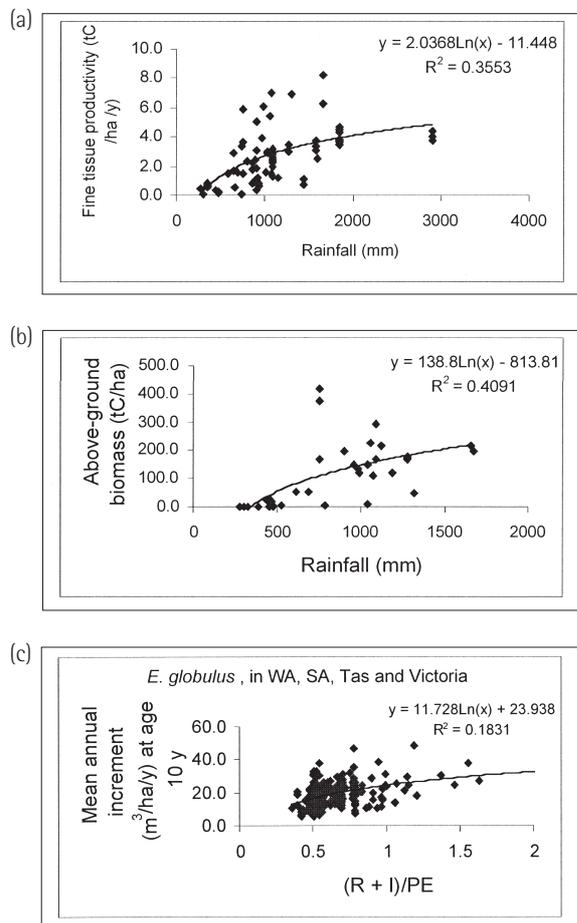


Figure 1. Using data supplied by Drs D Barrett (Figs 1a,b) and M Battaglia (Fig 1c) it is clear that fine tissue productivity, total above-ground biomass and mean annual increment increase with an increasing supply of water. Figs 1a, b include data from sites scattered across Australia and include woody and non-woody sites; Fig. 1c relates only to *Eucalyptus globulus* plantations growing in WA, SA, Tasmania and Victoria.  $R$  = rainfall;  $I$  = irrigation input;  $PE$  = potential evaporation.

There are several reasons why there is much scatter of points around the line. First, rainfall (or rainfall plus irrigation) is not the sole determinant of ecosystem water balance. Evaporative demand, soil depth and soil texture are additional determinants of ecosystem water balance. Second, the timing of rainfall is important to the influence of rainfall on productivity, as discussed previously. Figure 2 shows a relationship between biomass increment and rainfall for a number of sites throughout Australia. The regression was fitted without the addition of the data point represented by the square on the far

lower right of the figure, which is a north Australia savanna site where the large annual rainfall does not support the productivity predicted from the regression. This is because of the highly seasonal input of rainfall in north Australian savannas and the high level of disturbance (principally fire) that is present.

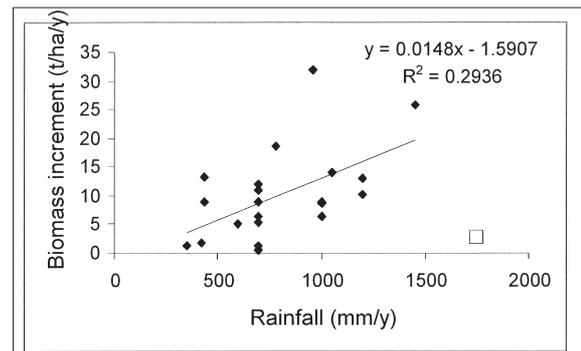


Figure 2. Above-ground biomass increment for a range of sites in eastern, southern and northern Australia; data from published literature (◆). The open square represents a site in a savanna close to Darwin, NT.

A third reason for the scatter of points around regression lines is the confounding influence of additional site factors, especially temperature and site fertility. Figure 3 (re-drawn from Specht and Specht 1999) shows that above-ground biomass increment increases with increasing evaporative coefficient (the slope of a plot of  $(E_a/E_p)$  against available moisture, where  $E_a$  and  $E_p$  are actual and potential rates of evapotranspiration respectively) and temperature.

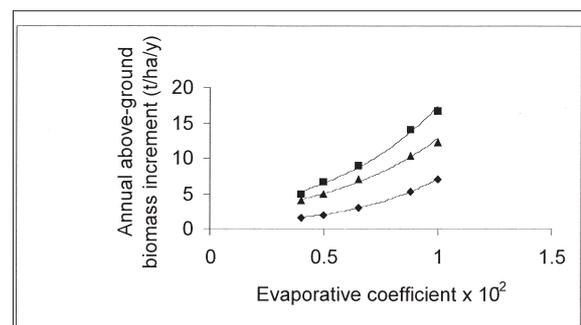


Figure 3. As evaporative coefficient (the slope of a plot of  $(E_a/E_p)$  against available moisture, where  $E_a$  and  $E_p$  are actual and potential rates of evaporation respectively) and temperature increase, above-ground biomass increment increases. Squares represent tropical ecosystems; triangles represent sub-tropical ecosystems; and diamonds represent temperate ecosystems (Re-drawn from Specht and Specht (1999)).

## Conclusions

Large numbers of interacting processes link differences in ecosystem water balance, or changes in water balance with time within an ecosystem, to NPP. This preliminary eclectic discussion mentioned some. Two significant activities for the development of models of Australian NPP would be, first, application and comparison of current models to tropical savannas, using a common set of climate and vegetation parameters, because of the challenges that this poses to current

models; and second, a comparison of different model sensitivities to changes in processes linking water balance and NPP.

What are **the key processes currently missing** from models that require consideration for continental-scale modelling of NPP? From a consideration of the above it is likely that there are four major improvements (in relation to water balance only) that could be made. In order of priority, these are:

- disturbance, especially fire, requires consideration;

Table 1. A comparison of some of the attributes of some of the models of NPP used within Australia.

	3PG	APSIM	CenW	CENTURY	FULLCAM	G'DAY	GRASP	GRAZPLAN	LINKAGES	PROMOD
Timestep	Monthly	Daily	Daily	Monthly	See 3PG	Daily	Daily	Daily	Monthly	Daily
Stomatal responses included	Yes	No	Yes	No	" "	Yes	No	No	N/a	No
Rainfall intensity varied	No	Yes	No	No	No	No	Yes	No	No	No
Transpiration calculated	Yes	Yes	Yes	Yes	" "	Yes	Yes	Yes	Yes	Yes
Soil water balance modelled	Yes	Yes	Yes	Yes	" "	Yes	Yes	Yes	Yes	Yes
Soil depth adequate	Yes	Yes	Any depth	1.2 m	" "	Yes	Yes	Yes	N/a	Yes
Rainfall/Ep	No	Yes	No	Yes	N/a	Yes	Yes?	No	N/a	Yes
Xylem embolism included	No	No	No	No	" "	No	No	No	N/a	No
Soil-root hydraulic effects	Partially	Yes	No	No	" "	No	No	Partially	N/a	No
Interception losses included		Yes	Yes	No	" "	Yes	Yes	Yes	N/a	No
Lateral soil flow	Yes	No	No	No	" "	No	Not currently	Yes	N/a	Implied
Runoff	Yes	Yes	No	Yes	" "	Yes	Yes	Yes	N/a	Implied
Deep drainage	Yes	Yes	Yes	Yes	" "	Yes	Yes	Yes	N/a	Implied
Seasonality of LAI/canopy	Yes	Yes	$\alpha$ p.s.s	Yes	" "	Yes	Yes	Yes	N/a	Yes
Biomass allocation variable	Yes	Yes	Not linked to water balance	Yes	" "	No	Yes		Species specific	No
Canopy conductance linked to soil water content/VPD	Yes	No	Yes		" "	Yes	$E_p = E_{pan}$ or $(VPD + P_{AR})$	No	No	$E_a/E_{pan} = (\theta)$
Groundwater or lateral flow input allowed	No	No	No	No	No	No	No	No	No	No
Groundwater quality as an input	No	No	No	No	No	No	No	No	No	No
Disturbance	No	No	No	Yes	No	No	No	No	No	No

SOCRATES is a soil model hence not included in table.

- empirical data are required for Australian ecosystems on the relationships among biomass allocation, site aridity (for example monthly rainfall/potential evaporation) and site fertility so that these can be incorporated into models;
- ecosystem-scale canopy conductance response characteristics relative to monthly aridity index;
- finally, allowance for a contribution to transpired water other than rainfall (groundwater and associated capillary fringe; and lateral flow).

## References

- Bondeau, A., Kicklighter, D.W. and Kaduk, J. 1999. Comparing global models of terrestrial net primary productivity: importance of vegetation structure on seasonal NPP estimates. *Global Change Biology* 5 (suppl) 35-45.
- Burgess, S.S.O., Adams, M.A., Turner, N.C., and Ong, C.K. 1998. The redistribution of soil water by tree root systems. *Oecologia* 115, 306-311.
- Chen, X., Eamus, D., and Hutley, L.B., 2001. Seasonal patterns of soil carbon dioxide efflux from a wet-dry tropical savanna of northern Australia. Submitted, *Australian Journal of Botany*.
- Churkina, G., Running, S.W. and Schloss, A.L. 1999. Comparing global models of terrestrial net primary productivity: the importance of water availability. *Global Change Biology* 5 (suppl) 46-55.
- Cochar, H., Breda, N. and Granier, A. 1996. Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought—evidence for stomatal control of embolism. *Annales des Sciences Forestieres* 53, 197-206.
- Cook, P.G., Hatton, T.H., Pidsley, D., Herczeg, A.L., O'Grady, A. and Eamus, D. 1998. Water balance of a tropical woodland ecosystem, northern Australia: a combination of micro-meteorological, soil physical and groundwater chemical approaches. *Journal of Hydrology* 210, 161-177.
- Davies, W.J., Mansfield, T.A. and Hetherington, A.M. 1994. How do chemical signals work in plants that grow in drying soil? *Plant Physiology* 104, 309-314.
- Eamus, D. and Prior, L. 2001. Ecophysiology of trees of seasonally dry tropics, with particular reference to phenological comparisons. *Advances in Ecological Research* 32, 113-197.
- George, R.J., Nulsen, R.A., Ferdowsian, R., and Raper, G.P. 1999. Interactions between trees and groundwaters in recharge and discharge areas – A survey of Western Australian sites. *Agricultural Water Management* 39, 91-113.
- Keeling, C.D., Chin, J.F.S. and Whorf, T.P. 1996. Increased activity of northern vegetation inferred from atmospheric CO<sub>2</sub> measurements. *Nature* 382, 146-149.
- Kicklighter, D.W., Bondeau, A., Schloss, A.L., Kaduk, J. and McGuire, A.D. 1999. Comparing global models of terrestrial NPP: global patterns and differentiation by major biomes. *Global Change Biology* 5 (Suppl), 16-24.
- Mencuccini, M. and Grace, J. 1995. Climate influences the leaf-area/sapwood area ratio in Scots pine. *Tree Physiology* 15, 1-10.
- Myers, B.A., Williams, R.J., Fordyce, I., Duff, G.A. and Eamus, D. 1998. Does irrigation affect leaf phenology in deciduous and evergreen trees of the savanna of northern Australia? *Australian Journal of Ecology* 23, 329-339.
- Prior, L.D., Eamus, D. and Duff, G.A. 1997. Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in *E. tetradonta* saplings in a wet-dry savanna in northern Australia. *Australian Journal of Botany* 45, 241-258.
- Raich, J.W. and Potter, C.S. 1995. Global patterns of CO<sub>2</sub> emission from soils. *Global Biogeochemical Cycles* 9, 23-36.
- Ryan, M.G. and Yoder, B.J. 1997. Hydraulic limits to tree height and tree growth. *BioScience* 47, 235-242.
- Schloss, A.L., Kicklighter, D.W., Kaduk, J. and Wittenberg, U. 1999. Comparing global models of terrestrial NPP: comparison of NPP to climate and NDVI. *Global Change Biology* 5 (Suppl.) 25 -34.
- Specht, R.L., and Specht A. 1999. Australian plant communities: Dynamics of structure, growth and biodiversity. Oxford University Press.
- Sperry, J.S., Alder, N.N. and Eastlack, S.E., 1993. The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation. *Journal of Experimental Botany* 44, 1075-1082.
- Sperry, J.S. and Pockman, W.T. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. *Plant, Cell and Environment* 11, 35-40.
- Thorburn, P.J. and Walker, G.R. 1993. The source of water transpired by *E. camaldulensis*: Soil, groundwater or streams. In 'Stable isotopes and plant carbon/water relations'. J R Ehleringer, A E Hall and G D Farquhar (Eds). San Diego Academic Press. Pp 511-527.

- Villar, R., Held, A. and Merino, J. 1995. Dark leaf respiration in light and darkness of an evergreen and deciduous plant species. *Plant Physiology* 107, 421-427.
- Williams, M., Malhi, Y., Nobre, A.D., Rastetter, E.B., Grace, J. and Pereira, M.G. 1998. Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: a modelling analysis. *Plant, Cell and Environment* 21, 953-968.
- Willigen, C.V. and Pammenter, N.W. 1998. Relationship between growth and xylem hydraulic characteristics of clones of *Eucalyptus* at contrasting sites. *Tree Physiology* 18, 595-600.

# Other Soil Constraints on Net Primary Production

---

*Robert Edis*  
*The University of Melbourne*

## Introduction

---

The modelling of net ecosystem exchange of C requires the incorporation of all factors that influence the sequestering of C as biomass (primary production) or the release of C as CO<sub>2</sub> through respiration by plants or soil micro-organisms. Which factors are included, and how they are included will depend upon their importance to the objectives of the exercise. Implicit treatment of some important factors may be adequate, whilst explicit incorporation in modelling may be required for others. In this paper, consideration is given to select soil constraints that may warrant explicit inclusion in modelling continental (Australia) net ecosystem exchange. Various aspects of net primary production are dealt with elsewhere in these proceedings, in particular water and nutrients. In this paper the soil constraints considered are salinity, waterlogging, impedance (excessive soil strength), and soil acidity. These constraints need to be considered in terms of their impacts upon biomass production and turnover of organic matter; distribution of significant effects across the continent; if and how to model, and; what measurements are possibly required.

## The Issues

---

### *Salinity*

High concentrations of salt in soil decrease plant performance through increased osmotic potential which decreases the free energy of soil water, and through phytotoxic effects of the component ions. The sensitivity of plants to salts (in Australia, principally NaCl) varies markedly between species, varieties and individuals. In general there is a level of salinity, as indicated by the electrical conductivity (saturated extract) (EC<sub>se</sub>), below which there is little or no effect and above which there is a near linear decrease in productivity with increasing EC<sub>se</sub> (Peverill *et al.* 1999). In Australia, salinisation of the rootzone is generally the result of rising watertables of saline groundwaters. As a result, salinisation is often coincident with waterlogging of part of the rootzone. Tree species vary greatly in their tolerance to

salinity and waterlogging (Lambert and Turner, 2000). At very high levels of salinity the productivity of the land is insignificant, and biomass accumulation of even the most tolerant species is negligible.

About 2 Mha of Australia is estimated to be affected by human-induced salinity to some extent, but estimates vary between 0.8 (Schofield, 1992) and 3.8 Mha (Poulter and Chaffer, 1991). Much of it occurring in SW Western Australia and within the wheat belt of South Australia, Victoria, New South Wales and Queensland. Approximately 5.7 Mha are within regions mapped to be at risk or affected by dryland salinity. It has been estimated that in 50 years' time the area of regions with a high risk may increase to 17 Mha (three times as much as now) (National Land and Water Audit 2000). Only about 0.5 Mha are thought to be extremely effected (Lambert and Turner, 2000), and given the greater ease at which extreme impact can be identified, this estimate of area is likely to be reliable.

Given that salinisation in Australia is mostly driven by sometimes complex hydrology at catchment or landscape scales, modelling the build-up of salts in the rootzone in response to plant water use is unlikely to be useful at the continental scale. Also, given the variability of susceptibility of plants to salinity, low-level salinity effects are likely to be countered by selection of more tolerant varieties, making modelling of subtle impacts on NEE impractical. Where high salt concentrations exist in soil that inhibit root growth, the effect maybe accommodated by restricting effective rooting depth or through the use of root hospitality factors (Probert and Keating, 2000). This approach requires site property factors, which are yet to be devised but could be incorporated into plant production models. This effectively treats salinisation as a static site factor modifying process rates, rather than as a dynamic process. Possibly such factors could be developed for areas where salinity is a major issue, such as SW Western Australia, but this is probably not warranted Australia wide, except for the purposes of scenario testing. Whilst models such as APSIM (Probert and Keating, 2000) have the capacity to model salt build-up in response to plant water use, this level of complexity is probably not warranted given that salinisation is largely driven by regional hydrologic processes. Possibly the most parsimonious way to deal with salinity effects on NEE would be through estimated areas of extreme salinisation taken out of production for

agriculture and forestry. In such areas biomass production could be assumed to be zero. More marginal effects could be incorporated into scenarios based upon estimates of potential areas salinised (such as those made in Australian Dryland Salinity Assessment 2000, National Land and Water Audit (2000)) to test the sensitivity of continental NEE to potential salinity conditions. This would require estimating the reduction in biomass production associated with the levels of salinity proposed. Salinity is a big problem in Australia, and further work is required to determine how to best incorporate it.

### **Waterlogging**

Waterlogging of soils is a major constraint to plant productivity through restricting oxygen supply to respiring plant roots, and impacts upon NEE by reducing biomass production and reducing organic C mineralisation (at least whilst the soil is waterlogged). Other impacts include redox transformation of nutrients and toxic elements, disease exacerbation and the production other greenhouse gases such as CH<sub>4</sub> and N<sub>2</sub>O. Waterlogging is a major limitation in many years in Australia's potentially most productive area for dryland agriculture and forestry. Waterlogging (or poor aeration) may be caused by a shallow watertable, impeding soil layers leading to a perched watertable, or poor soil structure with few macropores, in areas with poor external drainage and sufficient rain. There is little data available, but in my opinion most soils that occur in the high rainfall zones (>400 mm rainfall), with the exception of Ferrosols, Dermosols and Podosols, are likely to have inadequate aeration for optimum growth for some period in most years. Areas with high rainfall have high potential productivity, however waterlogging and excessive soil strength on drying limit the realisation of that potential. In Victoria alone an estimated 1.8 Mha is estimated to suffer waterlogging, with another 2.3 Mha susceptible (Anon. 1992). Some of the land that supported only low stocking rates of animals has been converted to productive grain-producing land, through management of soil structure and improved external drainage.

As inadequate aeration can be changed by management (improving drainage, adopting structure-sensitive practices, use of raised beds), and is dynamic within and between years, it is probably worth including in estimating NEE of C. Because aeration is dynamic, it cannot be treated using a site factor as was suggested for salinity. In the absence of a watertable, poor aeration could be modelled explicitly, using a modelled soil water status and corresponding air-filled capacity, with a decline in productivity with time that air-filled porosity is less than about 10% of the total soil volume. This would require soil

property data and crop response equations for which parameter values may not be immediately available. Waterlogging of the subsoil effectively limits the rooting depth. In the presence of a near-surface watertable, the rooting depth could be limited to the depth at which aeration is limiting. In this case, aeration could be treated as a site property. (See also Paul, 2001 (this volume)).

### **Impedance (excessive soil strength)**

Excessive soil strength limits the volume of soil that roots can explore to access nutrients and water. This reduction in the effective soil volume makes much of the soil's resources unavailable, and makes the system much more susceptible to drought. The physiological effects of excessive soil strength have been reviewed by Masle (2001), who identify mechanical stress as one of the most important of poor plant growth in the field.

Impedance may be in the form of a hard layer that limits downward penetration of roots, or as strong clods, the interiors of which are effectively inaccessible to plants. Some soil have a short period of favourable conditions between limitations caused by excessive soil strength when dry and inadequate aeration when moist. Limitations to downward exploration may be caused by massive soil horizons or compacted layers, the strengths of which are dependent upon moisture status. As soils dry they become stronger, and will often reach a strength that prohibits root penetration (rule of thumb: penetrometer resistance of 2 MPa). Soils that are likely to develop excessive strength (hardsetting) are very widespread and include, in particular, texture contrast soils such as Sodosols and Chromosols. Sodosols are particularly widespread in Australia (Figure 1), and are also vulnerable to waterlogging. Problems associated with excessive soil strength and waterlogging are likely to occur in soils in which "soil structural decline" has

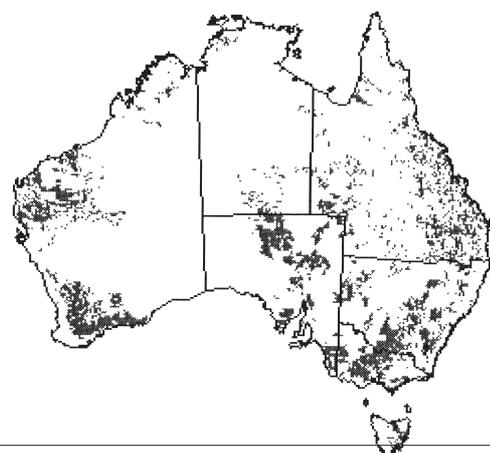


Figure 1. Approximate distribution of Sodosols in Australia (CSIRO, 1998)

occurred. In Victoria, 30% of total land is estimated to be severely degraded in terms of soil structure, and 37% moderately degraded, adding up to about 9.8 Mha in this state alone (Office of the Commissioner for the Environment, 1991). The impact of impedance on organic C turnover is uncertain, with clodiness likely to afford some level of protection of internal organic matter.

Modelling the development of excessive strength with drying is problematic. As soil moisture-dependent strength is a dynamic property, it cannot be treated as a site factor, but needs to be modelled with time. One approach is to consider a reduction in the effective soil volume being explored, and varying this according to moisture status (and therefore strength). Another approach could be to use the non-limiting water range. As poor aeration and excessive soil strength often occur at the same site at different times of the year, it has been proposed that they be considered together using the concept of least or non-limiting water range (Letey 1985, Zou *et al.*, 2000). This is the range of water contents above which aeration is limiting and below which soil strength is limiting. The period of time spent outside the non-limiting range could be used to adjust productivity down, and would need to be species specific.

Downward exploration of roots may also be due to indurated (hardened) material such as laterite, hardpans or rock, the strength of which may be effectively independent of moisture status. The impact of layers with permanent excessive strength could be dealt with in modelling by limiting the rooting depth, although the extent of these layers in the landscape is not comprehensively known.

Whilst impedance has a major impact on productivity, the extent of these impacts, and how they are effected by management, warrants further urgent investigation. Then the best way forward to model NEE may become clearer.

### Soil Acidity

There are estimated to be 33.4 MHa of acid soils (pH < 4.8 calcium chloride extract) Australia wide, with 13.5 MHa in NSW alone (AACM International Pty Ltd, 1995). They occur mainly to the west and north of the Great Dividing Range, in arable and grassland areas with rainfall > 500 mm pa. These areas are also prone to dryland salinization. The estimated production losses are > \$100 M annually.

The effect of low pH on plant growth is mostly through the increased mobility of toxic elements, particularly aluminium and manganese, and through reduction in the availability of some nutrients such as calcium. Low soil pH is in itself not

usually driving lowered productivity. Therefore, the impact of a given low pH will vary from soil to soil. In addition, plants vary in their sensitivity to exchangeable aluminium. Models such as APSIM can be used to estimate proton balances in soil, and thereby model how soil pH is likely to change with time under a production system (Probert and Keating, 2000; Verburg *et al.*, 2001). However, the ability to simulate soil pH does not of itself provide a means of simulating long-term effects of soil acidification in the whole system (Probert and Keating, 2000). The biggest modelling knowledge gap appears to be the estimation of impact of pH, rather than the dynamics of pH change. These impacts could probably be treated as a site property factor. There is therefore, a need to be able to better describe the impact of acidification on different plants on different soils (in particular, with different exchangeable aluminium contents). Then, since soil acidity is sensitive to management (for example, addition of lime), scenarios testing the impact of different management and policy choices on NEE could be made.

## Triage and Conclusions

- 1 Given the large area impacted by impedance and poor aeration, and that the productivity of these areas could be substantially increased if these limitations were alleviated, it seems reasonable to give them the highest priority for attention. This is further supported by the dynamic nature of aeration and strength within and between years. To be useful in a greenhouse accounting context, models would need to be sensitive to the impact of management decisions on NEE, not only of CO<sub>2</sub> but also gases such as methane and nitrous oxide.
- 2 Soil acidification impacts upon net primary productivity, but the confounding influences of variable plant sensitivity, variable effects on soil chemistry (such as on aluminium release), and management make modelling difficult. It may be more useful to include the impact of acidity in local calibration of models, and include acidity as a site factor. Scenarios of future NEE could be run, for example with and without liming, if system responses to acidification were better understood.
- 3 As with acidity, salinity may be best dealt with in the local calibrations of models including salinity as a site factor, with the exceptions of extreme manifestations. Extreme manifestations could be treated as zero or minimal productivity, and the impact of the expansion of severely

affected lands thus estimated. The rate of organic matter decomposition under these conditions requires further investigation.

In conclusion, poor aeration and excessive soil strength have been identified as the most pressing issues that require attention. Further work is required not just for modelling, but also for understanding the impacts and extent of these constraints and the role of management in alleviating or worsening them. There is much activity underway at present in assessing our land systems (for example, the National Land and Water Resources Audit), and the comments made in this preliminary paper will need refinement and change as a result of further, more detailed analyses.

## References

---

- AACM International Pty Ltd (1995). *"Social and Economic Feasibility of Ameliorating Soil Acidification – A National Review"*. The Land and Water Resources Research and Development Corporation, Canberra.
- Anon (1992). Victoria's Decade of Landcare Plan. Landcare Australia, Melbourne.
- CSIRO (1998). The Australian Soil Classification (web version). <http://www.cbr.clw.csiro.au/aclep/asc/soilhome.htm>
- Lambert, M. and Turner, J. (2000). *"Commercial Forest Plantations on Saline Lands"* CSIRO Publishing, Melbourne.
- Letey, J. (1985). Relationship between soil physical properties and crop production. *Advances in Soil Science*. 1:277-294.
- Masle, J. (2001). High soil strength: Mechanical forces at play on root morphogenesis and in root:shoot signalling. In: *"Roots the Hidden Half"* (3<sup>rd</sup> Edition) In press.
- National Land and Water Audit (2000). *Australian Dryland Salinity Assessment 2000*, National Land and Water Resources Audit c/o Land & Water Australia On behalf of the Commonwealth of Australia (see also [http://anra.skm.com.au/ANRA/land/docs/national/Salinity\\_Contentents.html](http://anra.skm.com.au/ANRA/land/docs/national/Salinity_Contentents.html))
- Office of the Commissioner for the Environment (1991). 1991 State of the Environment Report: Agriculture and Victoria's Environment.
- Peverill, K.I., Sparrow, L.A. and Reuter, D.J. (Eds) (1999). *"Soil Analysis: an Interpretation Manual"*, CSIRO Publishing, Melbourne.
- Poulter, D.G. and Chaffer, L.C. (1991). Dryland salinity: some economic issues. *Agriculture and Resources Quality*. 3: 361-370
- Probert, M.E. and Keating, B.A. (2000). What soil constraints should be included in crop and forest models? *Agriculture, Ecosystems and Environment*. 82: 273-281.
- Scofield, N.J. (1992). Tree planting for dryland salinity control in Australia. *Agroforestry Systems*. 20:1-23
- Verburg, K. Braschkat, J., Hochman, Z., Moore, A.D., Helyar, K.R., Probert M.E., Hargreaves, J.N.G. and Simpson, R.J. (2001). Modelling acidification processes in agricultural systems. In: Z. Rengel (Ed) *"Handbook of Soil Acidity"* (Chapter 7). In press.
- Zou, C., Sands, R., Buchan, G. and Hudson, I. (2000). Least limiting water range: a potential indicator of physical quality of forest soils. *Australian Journal of Soil Science*. 38: 947-958.

# Nutrient Uptake and Use in Plant Growth

*John R Evans and Everard Edwards  
CRC for Greenhouse Accounting  
The Australian National University*

## Introduction

In order for plants to grow, they must intercept light to enable photosynthesis to convert CO<sub>2</sub> into the basic molecules for metabolism such as sugars and amino acids. Water and nutrients are usually acquired from the soil and together with photosynthate, are used to create new plant tissues. At least 13 different nutrients are required by plants for normal growth. Of these, six are required in large amounts while only trace amounts of the others are needed.

The availability of nutrients influences plant growth and can determine community structure. It is possible to generalize about the response of plants to limited amounts of most nutrients. However, there are species and community specific responses and adaptations that enable plants to cope with specific nutrient limitations. Australia has soils of low fertility because of their age but the native vegetation has evolved to exploit them. Additional nutrients placed into nutrient limited systems may increase plant growth but may also change the species composition.

Modelling plant growth requires a description of the pools and fluxes of nutrients in different plant parts and soil as well as nutrient inputs and losses. Obtaining a complete description for one or more nutrient in an ecosystem is a formidable challenge and means that few exist. It is therefore generally necessary to combine different aspects from a variety of sources to arrive at a complete description. Because of the wide range of time scales, different models focus on certain processes and can ignore others. For example, the rate at which nitrogen becomes available may be crucial in defining how quickly an annual crop develops, while the factors which determined the size of the total pool of soil nitrogen may reflect processes occurring over centuries. Perennial vegetation can buffer itself against nutrient limitations, accumulating them when available for later use when water or temperature favours growth.

## Essential elements

The average elemental composition of dried plant material is given in Table 1. The actual composition varies between plant organs and depends on species and growth conditions, but the important feature to note is the difference between the 6 macronutrients N, K, Ca, Mg, P and S and the micronutrients. The macronutrients are either involved in the structure of proteins and nucleic acids, or are key cations involved in charge

Element	Amount ( $\mu\text{mol g}^{-1}$ DW)	Role	Australian Fertilizer Use (Mt $\text{y}^{-1}$ )
N	1000	Protein, nucleic acids	0.9
K	250	Major cytoplasmic cation, protein synthesis	
Ca	125	Cell walls and membranes	
Mg	80	Chlorophyll, protein and DNA synthesis	
P	60	Nucleic acids, P-esters	1.6
S	30	Cysteine, Methionine, redox reactions	
Cl	3	Oxygen evolving complex	
B	2	?	
Fe	2	Redox reactions, cytochromes	
Mn	1	Oxygen evolving complex, SOD	
Zn	0.3	ADH, CA, SOD RNA polymerase	
Cu	0.1	Plastocyanin, cytochrome oxidase, SOD	
Mo	0.001	Nitrate reductase, nitrogenase	

*Table 1 Essential elements and their amounts in plant tissue (Marschner, 1986) and the amount applied as fertilizer (McLennan, 1998).*

stabilisation. The micronutrients tend to be in the catalytic sites of specific enzymes or make the prosthetic group of the molecule.

When native vegetation has been replaced by crops and pastures in Australia, phosphorus and nitrogen fertilizers have been applied to improve productivity. The widespread application of superphosphate also added sulphur to the phosphorus deficient soils. With the removal of the superphosphate bounty, there was a reduction in the amount applied which lead to the appearance of sulphur deficiencies and the need to apply sulphur fertilizers. Soil nitrogen pools have been increased by fertilizer application and/or the inclusion of legumes that fix nitrogen symbiotically in crop rotations.

Micronutrient deficiencies have tended to become evident when land is cleared and planted to cereals. Mn, Cu and Zn have been applied at rates around 6kg ha<sup>-1</sup> to correct for specific deficiencies experienced by cereals. To establish effective nitrogen fixation by legumes, Mo has had to be applied, at rates of just 140g ha<sup>-1</sup>. Overall, fertilizer has been applied to about 19 Mha for crops and 30Mha for sown pastures in Australia, representing 6% of the land (McLennan, 1998). Much of the phosphorus applied became bound in the soil and was unavailable to plants in the short term. Bound phosphorus is typical of many Australian soils and has lead to specific adaptations by plants to acquire this element (cluster roots, mycorrhizal associations).

## Nutrient limitation alters allocation and photosynthesis

When individual plants are grown with restricted access to a particular nutrient, growth is reduced and specific deficiency symptoms may develop. A general feature is increased allocation into roots and decreased allocation to leaves and stems (Poorter & Nagel, 2000). Increased allocation to roots enables the plant to explore greater soil volumes to capture nutrients necessary for continued leaf expansion. Over time, the amount of leaf area or mass per unit root mass is reduced compared to a plant of the same total size given free access to nutrients. Restricted nitrogen or phosphorus availability increases root mass per unit plant mass for monocots, dicots, C<sub>4</sub> and woody plants (Cook & Evans, 1983, Cromer & Jarvis, 1990, Kirschbaum, Bellingham & Cromer, 1992, Sage & Percy, 1987). It is likely to be the case for mature trees despite being difficult to measure the proportion of annual carbon gain allocated to

roots. Allocation to roots was found to decrease as foliar nitrogen concentration increased (Beets & Whitehead, 1996).

The responsiveness to nutrient limitation varies between different organs and processes. The greatest effect may be on total plant growth. In the case of wheat, plants grown with lower nitrate concentrations applied to the soil produced fewer tillers and hence dramatically altered the potential total leaf area of the plant (Fig. 1). Demand for nitrogen was further reduced by having smaller leaves. This meant that the nitrogen content per unit leaf area varied by only 40%. Due to the curvilinear relationship between photosynthetic rate and nitrogen content per unit leaf area, CO<sub>2</sub> assimilation rate differed by only 15%. The consequence of this hierarchy is that light interception changes by far more than photosynthetic rate per unit leaf area when nutrients are limiting.

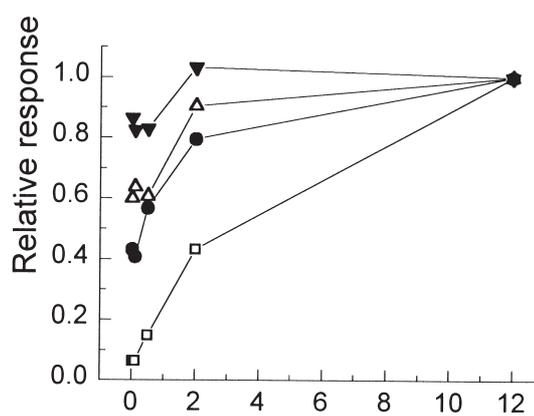


Figure 1 Nitrate concentration applied (mM)

Responsiveness of total area (□), flag leaf area (●), nitrogen content per unit leaf area (Δ) and photosynthetic rate per unit leaf area (▼) of wheat plants grown with varying concentrations of nitrate (Evans, 1983).

For a given species, photosynthetic rate is closely related to the nitrogen content per unit leaf area. Nitrogen content varies over the life of a leaf as it is first expanded and matures and then nitrogen is withdrawn again prior to abscission. Consequently, the photosynthetic rate of a leaf varies through its lifespan. Photosynthetic rate of leaves are strongly related to the specific leaf area (projected leaf surface per unit leaf dry mass) and nitrogen concentration per unit dry mass (Reich, Walters & Ellsworth, 1997). Variation in photosynthetic rate per unit leaf nitrogen between species is largely associated with variation in specific leaf area. Data for *Eucalyptus* (Mooney, Ferrar & Slatyer, 1978) and *Acacia* (Evans *et al.*, 2000) species are consistent with the global relationship derived by Reich *et al.* 1997. Photosynthetic rate per unit leaf nitrogen increases as

specific leaf area increases. However, leaf lifespan tends to decrease as specific leaf area increases, so photosynthesis per unit nitrogen over the lifespan of a leaf would reveal a different relationship.

## Strategies for acquiring nutrients

---

In each environment, nutrient concentrations vary between soil horizons, will depend on the soil chemistry and may vary in time depending on temperature and moisture. Different plant species may exploit different niches within the same environment, gaining access to nutrients that are not available to other species. The soil horizon that is explored by roots varies greatly between species. Perennial vegetation can have long-lived roots that penetrate deeply into the soil, whereas ephemeral and annual species tend to colonise surface soil more extensively. Much of the nutrient capital is present in the surface litter and soil layers and so roots proliferate there. The volume of soil that can be explored by a given root mass varies greatly between species and is related to branching patterns and specific root length. Fine roots have a limited lifespan and may not be present in a given patch of soil when a nutrient becomes available. For some species, roots proliferate when they sense the presence of a nutrient.

Some roots have a specialised structure and physiology to enable them to capture a particular nutrient. For example, most Australian soils have low phosphorus levels and much of the phosphorus is bound to Fe or Al. Proteaceous species, as well as some other genera (e.g. white lupin) form cluster roots (Dinkelaker, Hengeler & Marschner, 1995, Watt & Evans, 1999). These dense arrays of short rootlets look like bottlebrushes and can form extensive mats in the litter layer near the soil surface or can be distributed through the soil. They exude organic acids and phosphatases that solubilize phosphorus bound in the soil or in organic matter, enabling uptake by the plant. Cluster roots have very high rates of exudation compared to other roots, but even species without these specialised root structures can chemically modify the soil to assist in extracting phosphorus by exuding citrate e.g. *Danthonia* (Barrett & Gifford, 1999) or phosphatases e.g. wheat (Barrett, Richardson & Gifford, 1998).

Having a dimorphic root structure may enable plants to extract nutrients from soil that would otherwise be too dry for roots to function normally. In the deep sands in WA, deep sinker roots can extract water from depth and rehydrate surface soil layers,

thereby enabling the finer surface roots to continue to function into early summer (Pate & Dawson, 1999).

Other roots have developed symbiotic associations with nitrogen fixing bacteria or mycorrhizae to enable them to capture a scarce nutrient. Legumes can fix nitrogen from the air in their nodules in exchange for carbon compounds supplied by the host. Over time, this can lead to a significant buildup of organic nitrogen that cycles through the litter and can become available to non-leguminous co-occurring species. Plants that fix nitrogen symbiotically seem to have greater requirements for phosphorus, which is why phosphatic fertilizers are generally applied to improved pastures containing legumes. The trace element molybdenum has also had to be applied in much of Australia to overcome deficiencies as this element is required by the nitrogenase enzyme. Roots of many species form associations with mycorrhizae that improve phosphorus and/or nitrogen nutrition of the host plant. The very fine fungal threads can explore much larger soil volumes for a given amount of biomass than plant roots which enables access to poorly mobile elements like phosphorus. They are also able to chemically extract nutrients bound either to soil particles or in organic matter, which may not be present in the soil solution. Quantification of the amount of nutrient acquired through symbiotic associations is difficult. It has been estimated that symbiotic nitrogen fixation contributes 1900 kt y<sup>-1</sup> to Australian soils, compared to fertilizer applications of 380 kt y<sup>-1</sup>, while atmospheric nitrogen deposition of 1150 kt y<sup>-1</sup> is roughly balanced by that released back to the atmosphere by fire 1200 kt y<sup>-1</sup> (McLaughlin, Fillery & Till, 1992). Since that estimate, nitrogenous fertilizer use has increased to 900 kt y<sup>-1</sup> (McLennan, 1998), but it is applied to only a small proportion of Australia's land surface.

## Net Primary Productivity and foliar nitrogen content

---

Because photosynthesis is driven by light and is associated with transpiration, it is not surprising that there are good correlations between plant growth and either intercepted radiation or cumulative transpiration. In many instances, it may be easier to predict growth calculated from intercepted radiation or transpiration than to measure growth directly. Generally these approaches have conversion coefficients that are reduced by stresses and require calibration. Altering nutrient availability in a given environment can change the productivity of the vegetation. Improved nutrition may enable greater leaf area production that results in greater interception of light and

greater transpiration at times of the year when vapour pressure difference is low, thereby increasing seasonal dry matter productivity for a given amount of water.

An alternative approach is to examine the relationship between NPP and nitrogen present in leaves per unit ground area (Fig. 2). Three different data sets for *Pinus radiata* are shown. The Biology of Forest Growth site at Pierce's creek near Canberra includes three irrigation treatments, two of which also received fertilizer. For the two New Zealand studies, one was planted onto pasture that had received cobaltised superphosphate to stimulate nitrogen fixation by clover, the other compared control with fertilizer or lupin treatments. Additional nitrogen from fertilizer or symbiotic fixation resulted in greater nitrogen contents in the leaf canopy and was associated with increased annual above ground biomass production. The overall response appears to be curvilinear, beginning to saturate at canopy leaf nitrogen contents above 150 kg ha<sup>-1</sup>. Also shown are data collected from three *Eucalyptus* plantations where addition of fertilizer increased both leaf nitrogen per unit ground area and above ground production. Annual productivity for *Eucalyptus* was similar to that observed for *Pinus* for a given amount of leaf nitrogen. The third example of woody vegetation is that of a natural *Banksia* woodland adjacent to land that has been cleared for pasture and cropping. Additional water and nutrients are available to the natural vegetation along the boundary, enabling a comparison of productivity along a transect. Leaching of nitrogen fixed symbiotically by subterranean clover and lupin, together with aerial drift of fertiliser laden soil has resulted in dramatically enhanced growth over 25 years. Annual productivity adjacent to the boundary is six times greater than in the undisturbed community. Again, productivity is related to leaf nitrogen content per unit ground area, but dry matter produced per unit leaf nitrogen was only half that of the plantations.

Four examples of productivity by herbaceous plants in relation to the nitrogen present in their leaves are also shown in Fig. 2. *Danthonia* microcosms were grown for four years in controlled environments with three rates of nitrogen addition. Wheat crops grown near Cambridge in the UK and *Lolium perenne* grown near Zurich, Switzerland, each with two fertilizer treatments, also fall along a similar curve. Pasture growth at a FACE experiment at Bulls in New Zealand are also shown. Biomass produced per unit of leaf nitrogen was equivalent to that seen for the *Pinus* and *Eucalyptus* studies. This suggests that growth form does not play an important role in this relationship.

In order for productivity to increase linearly with nitrogen in leaves, the nitrogen must be effectively arranged in leaf

canopies. The average nitrogen content per unit leaf area is 100 and 170 mmol N m<sup>-2</sup> for herbaceous and tree species, respectively, so 50 kg N ha<sup>-1</sup> is roughly equivalent to a leaf area index of 3.5 and 2. As leaf area index increases, there needs to be increased allocation of biomass into the stem in order to display the foliage and gradients in leaf nitrogen content per unit area are observed. Despite perennial woody vegetation requiring more tissue for support that must respire than herbaceous plants, it is not apparent from Fig. 2 that this reduces productivity per unit leaf nitrogen.

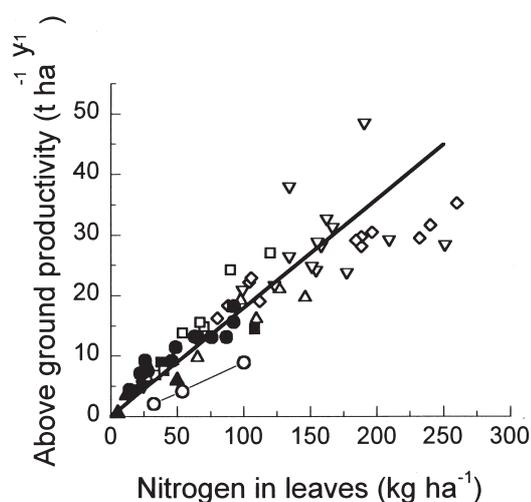


Figure 2

Annual above ground productivity as a function of nitrogen content in leaves for a range of plant communities. (*Pinus radiata*  $\Delta$ ,  $\nabla$ ,  $\diamond$ ; Beets & Madgwick, 1988, Beets & Pollock, 1987a, b, Crane & Banks, 1992); *Eucalyptus grandis*  $\square$  (Cromer *et al.*, 1993, Leuning, Wang & Cromer, 1991, Turner & Lambert, 1983); *Eucalyptus globulus*  $\square$  (Cromer & Williams, 1982); *Banksia prionotes*  $\circ$  Grigg, Pate & Unkovich, 2000); *Danthonia richardsonii*  $\blacktriangle$  (Lutze & Gifford, 1998, 2000); *Triticum aestivum*  $\blacksquare$  (Austin *et al.*, 1980); *Lolium perenne*  $\bullet$  (Daupp *et al.*, 2000)); pasture  $\blacktriangledown$  (Newton, P pers. comm.). The solid line represents 180 g DM (g Np)<sup>-1</sup> y<sup>-1</sup>

Not shown in Fig. 2 are data where water stress reduced productivity. In some cases, water stress may cause the shedding of leaves such that productivity per unit nitrogen in leaves does not decline greatly. However, for plants with long-lived leaves such as pines, leaf area is retained despite water stress, resulting in reduced productivity per unit nitrogen in leaves (Raison & Myers, 1992).

An intriguing feature of Fig. 2 is that the different data sets are collected from sites differing in rainfall, annual radiation, temperature and soil type. Despite this, the data fall along a common line. At the leaf level, photosynthetic rate per unit leaf

nitrogen varied five-fold depending on the specific leaf area. This effect is evident in the growth of seedlings. When growth analysis was carried out across a range of *Acacia* species, productivity per unit foliage nitrogen was indeed positively related to SLA (Atkin *et al.*, 1998). The tendency would be for SLA to be lower for vegetation having greater amounts of nitrogen per unit ground area in Fig. 2, conferring lower rates of photosynthesis per unit nitrogen. However, this effect is clearly cancelled out by other factors in determining annual productivity. Canopy nitrogen content may be a way of integrating site productivity that is rather insensitive to vegetation type, fertility, temperature and radiation. One factor that can reduce annual productivity per unit nitrogen in leaves is water stress, although not in all cases.

## How models deal with nutrient limitations

While most of the models that are being discussed at this workshop acknowledge the fact that nutrients can limit plant growth, they deal with the problem in different ways (Table 2). A site productivity factor is used in PROMOD that scales the LAI of the closed canopy, effectively defining the size of the largest cycling nitrogen pool at a site. As shown in Fig. 1, LAI is probably one of the most sensitive responses to limiting nitrogen. Socrates also simply applies a site factor to scale potential productivity. LINKAGES applies nitrogen response functions with three different types to describe different plant types, which are multiplied against potential productivity. GRASP and APSIM link nitrogen uptake to transpiration, setting a maximum limit for a season. APSIM, 3PG, G'day and CenW link nitrogen limitation to allocation, such that when nitrogen is limiting, there is increased allocation to roots and decreased allocation to foliage, which in turn reduces canopy photosynthesis. Allocation is sensitive to nutrient supply and provides a direct mechanism for linking nutrient limitation to growth. APSIM and G'day link radiation use efficiency while CenW links photosynthesis to leaf nitrogen concentration. The evidence that links changes in radiation use efficiency to leaf nitrogen content is very limited and not very convincing. Certainly the effect is of secondary importance compared to the changes in leaf area. Similarly, while photosynthetic rate is related to nitrogen and phosphorus contents per unit leaf area, it is unusual for nutrient contents per unit leaf area to be low enough to significantly reduce photosynthetic rates in a canopy. GRAZPLAN is the only model that relates nutrient

uptake to root mass and age to describe the soil volume available for uptake. It is coupled to the amount of nutrient present in soil solution and the nutrient demand for growth. If the nutrient concentration of plant tissue falls below a threshold, it can scale down radiation use efficiency if it is the most limiting factor.

Model	LAI	Multiplier	Transpiration	Allocation	Photosynthesis	Root activity
PROMOD	X					
Linkages		X				
Socrates		X				
GRASP			X			
APSIM			X	X	X	
3PG				X		
G'day				X	X	
CenW				X	X	
Grazplan						X

Table 2 Models and how they handle nutrient limitation

## References

- Atkin O.K., Schortemeyer M., McFarlane N. & Evans J.R. (1998) Variation in the components of relative growth rate in ten *Acacia* species from contrasting environments. *Plant, Cell and Environment*, **21**, 1007-1017.
- Austin R.B., Bingham J., Blackwell R.D., Evans L.T., Ford M.A., Morgan C.L. & Taylor M. (1980) Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *Journal of Agricultural science*, **94**, 675-689.
- Barrett D.J. & Gifford R.M. (1999) Increased C-gain by an endemic Australian pasture grass at elevated atmospheric CO<sub>2</sub> concentration when supplied with non-labile inorganic phosphorus. *Australian Journal of Plant Physiology*, **26**, 443-451.
- Barrett D.J., Richardson A.E. & Gifford R.M. (1998) Elevated atmospheric CO<sub>2</sub> concentrations increase wheat root phosphatase activity when growth is limited by phosphorus. *Australian Journal of Plant Physiology*, **25**, 87-93.

- Beets P.N. & Madgwick H.A.I. (1988) Above-ground dry matter and nutrient content of *Pinus radiata* as affected by lupin, fertiliser, thinning, and stand age. *New Zealand Journal of Forestry Science*, **18**, 43-64.
- Beets P.N. & Pollock D.S. (1987a) Accumulation and partitioning of dry matter in *Pinus radiata* as related to stand age and thinning. *New Zealand Journal of Forestry Science*, **17**, 246-271.
- Beets P.N. & Pollock D.S. (1987b) Uptake and accumulation of nitrogen in *Pinus radiata* stands as related to age and thinning. *New Zealand Journal of Forestry Science*, **17**, 353-371.
- Beets P.N. & Whitehead D. (1996) Carbon partitioning in *Pinus radiata* stands in relation to foliage nitrogen status. *Tree Physiology*, **16**, 131-138.
- Cook M.G. & Evans L.T. (1983) Nutrient responses of seedlings of wild and cultivated *Oryza* species. *Field Crops Research*, **6**, 205-218.
- Crane W.J.B. & Banks J.C.G. (1992) Accumulation and retranslocation of foliar nitrogen in fertilized and irrigated *Pinus-radiata*. *Forest Ecology and Management*, **52**, 201-223.
- Cromer R.N., Cameron D.M., Rance S.J., Ryan P.A. & Brown M. (1993) Response to nutrients in *Eucalyptus-grandis*.1. biomass accumulation. *Forest Ecology and Management*, **62**, 211-230.
- Cromer R.N. & Jarvis P.G. (1990) Growth and biomass partitioning in *Eucalyptus-grandis* seedlings in response to nitrogen supply. *Australian Journal of Plant Physiology*, **17**, 503-515.
- Cromer R.N. & Williams E.R. (1982) Biomass and nutrient accumulation in a planted *E. globulus* (Labill.) fertilizer trial. *Australian Journal of Botany*, **30**, 265-278.
- Daupp M., Suter D., Almeida J.P.F., Isopp H., Hartwig U.A., Frehner M., Blum H., Nosberger J. & Luscher A. (2000) Yield response of *Lolium perenne* swards to free air CO<sub>2</sub> enrichment increased over six years in a high N input system on fertile soil. *Global Change Biology*, **6**, 805-816.
- Dinkelaker B., Hengeler C. & Marschner H. (1995) Distribution and function of proteoid roots and other root clusters. *Botanica Acta*, **108**, 183-200.
- Evans J.R. (1983) Nitrogen and photosynthesis in the flag leaf of wheat (*Triticum aestivum* L.). *Plant Physiology*, **72**, 297-302.
- Evans J.R., Schortemeyer M., McFarlane N. & Atkin O.K. (2000) Photosynthetic characteristics of 10 Acacia species grown under ambient and elevated atmospheric CO<sub>2</sub>. *Australian Journal of Plant Physiology*, **27**, 13-25.
- Grigg A.M., Pate J.S. & Unkovich M.J. (2000) Responses of native woody taxa in *Banksia* woodland to incursion of groundwater and nutrients from bordering agricultural land. *Australian Journal of Botany*, **48**, 777-792.
- Kirschbaum M.U.F., Bellingham D.W. & Cromer R.N. (1992) Growth analysis of the effect of phosphorus-nutrition on seedlings of *Eucalyptus-grandis*. *Australian Journal of Plant Physiology*, **19**, 55-66.
- Leuning R., Wang Y.P. & Cromer R.N. (1991) Model simulations of spatial distributions and daily totals of photosynthesis in *Eucalyptus grandis* canopies. *Oecologia*, **88**, 494-503.
- Lutze J.L. & Gifford R.M. (1998) Carbon accumulation, distribution and water use of *Danthonia richardsonii* swards in response to CO<sub>2</sub> and nitrogen supply over four years of growth. *Global Change Biology*, **4**, 851-861.
- Lutze J.L. & Gifford R.M. (2000) Nitrogen accumulation and distribution in *Danthonia richardsonii* swards in response to CO<sub>2</sub> and nitrogen supply over four years of growth. *Global Change Biology*, **6**, 1-12.
- Marschner H. (1986) *Mineral nutrition of higher plants*. Academic, London.
- McLaughlin M.J., Fillery I.R. & Till A.R. (1992) Operation of the phosphorus, sulphur and nitrogen cycles. In: *Australia's renewable Resources: Sustainability and Global Change* (eds R.M. Gifford & M.M. Barson), pp. 67-116.
- McLennan W. (1998) *Year Book Australia*. Australian Bureau of Statistics.
- Mooney H.A., Ferrar P.J. & Slatyer R.O. (1978) Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. *Oecologia*, **36**, 103-111.
- Pate J. & Dawson T. (1999) Novel techniques for assessing the performance of woody plants in uptake and utilization of carbon, water and nutrients: Implications for designing agricultural mimic systems. In: *Agriculture as a Mimic of Natural Ecosystems* (eds E. Lefroy, R. Hobbs, M. O'Connor, JS, & Pate). Kluwer, Dordrech.
- Poorter H. & Nagel O. (2000) The role of biomass allocation in the growth response of plants to different levels of light, CO<sub>2</sub>, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology*, **27**, 595-607.

- Raison R.J. & Myers B.J. (1992) The biology of forest growth experiment - linking water and nitrogen availability to the growth of *pinus-radiata*. *Forest Ecology and Management*, **52**, 279-308.
- Reich P.B., Walters M.B. & Ellsworth D.S. (1997) From tropics to tundra - global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 13730-13734.
- Sage R.F. & Pearcy R.W. (1987) The nitrogen use efficiency of C<sub>3</sub> and C<sub>4</sub> plants 1. Leaf nitrogen, growth, and biomass partitioning in *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.). *Plant Physiology*, **84**, 954-958.
- Turner J. & Lambert M.J. (1983) Nutrient cycling within a 27-year-old *Eucalyptus grandis* plantation in New South Wales. *Forest Ecology and Management*, **6**, 155-168.
- Watt M. & Evans J.R. (1999) Proteoid roots. Physiology and development. *Plant Physiology*, **121**, 317-323.

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

Miko Kirschbaum

CRC for Greenhouse Accounting  
CSIRO Forestry and Forest Products

With contributions from John Carter,  
Peter Grace, Rod Keenan, Joe Landsberg,  
Greg McKeon, Andrew Moore, Keryn Paul,  
David Pepper, Merv Probert, Peter Sands,  
Richard Simpson and Jan Skjemstad.

## 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 CO<sub>2</sub> 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.

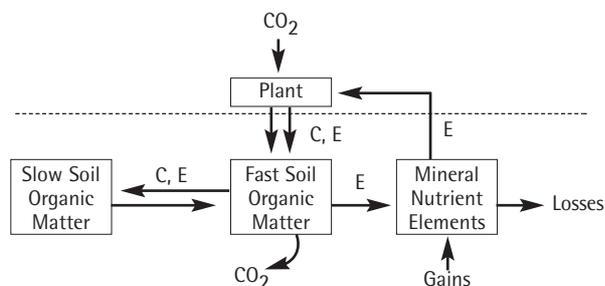


Figure 1: Diagrammatic representation of the inter-relationships between carbon and nutrient cycles. Nutrient cycles are denoted as 'E' and could represent nitrogen, phosphorus or sulphur.

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.

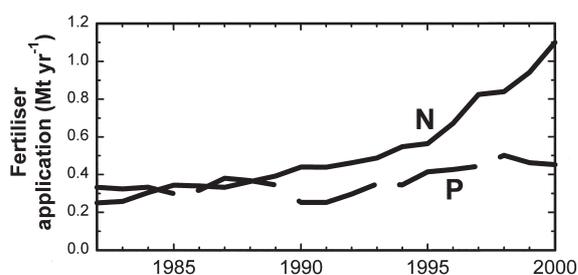


Figure 2: Annual application of nitrogen and phosphorus fertilisers in Australia (after ABARE 2001).

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 <sup>1</sup>	0.33	0.38
Fixed by plants <sup>2</sup>	1.9		
<b>TOTAL</b>	<b>3.4</b>	<b>1.1</b>	<b>0.46</b>
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
<b>TOTAL</b>	<b>2.3</b>	<b>0.35-0.5</b>	<b>0.08-0.11</b>
<b>BALANCE</b>	<b>1.1</b>	<b>0.6-0.75</b>	<b>0.35-0.38</b>

<sup>1</sup> 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.

<sup>2</sup> 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.

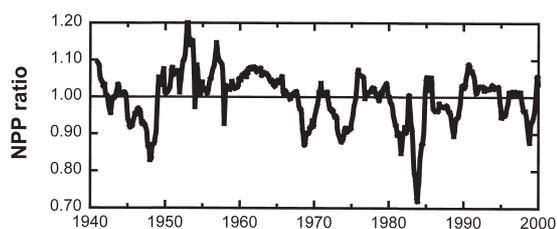


Figure 3: Ratio of two simulations of net primary production: one with and one without inclusion of the linkages between above and low-ground processes. Shown is the ratio of calculated NPP in the two simulations (with and without feed-backs). The simulations were based on the observed Canberra climate. 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  $5\text{tC ha}^{-1}$  (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.

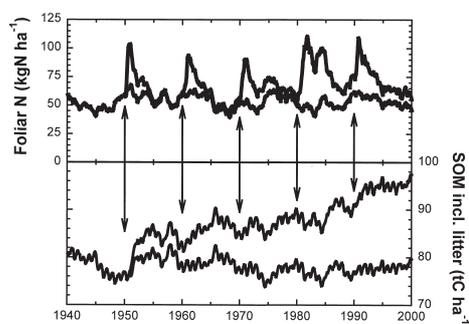


Figure 4: Simulations of the effect of fertiliser addition on foliar nitrogen contents and soil organic carbon storage (including litter). The lower curves in each panel show simulations without fertiliser addition, and the upper curves show simulations with fertiliser additions. Arrows indicate the times when  $100\text{ kgN ha}^{-1}$  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  $500\text{ kgN ha}^{-1}$  leading to enhanced soil carbon storage by more than  $15\text{ tC ha}^{-1}$  (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 <sup>1</sup>	-	Y	-	Y
CENTURY	Y	Y	Y	Y	-	Y
CenW	Y	-	-	Y	-	Y
FullCAM	Y	-	-	Y	-	Y
G'Day	Y	Y <sup>3</sup>	Y <sup>3</sup>	Y	-	Y
Gendec	Y <sup>4</sup>	-	-	-	Y	Y
GRASP	-	-	-	Y	-	-
GRAZPLAN	Y	Y	Y	Y	-	Y
Linkages	Y	-	-	Y	-	Y
Promod	-	-	-	Y	-	-
Roth-C	-	-	-	-	Y	Y
Socrates	-	-	-	Y <sup>5</sup>	Y <sup>5</sup>	Y
3-PG	-	-	-	Y	-	-

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

<sup>2</sup>The dependence on nitrogen is the same as for Gendec.

<sup>3</sup>G'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.

<sup>4</sup>Gendec, 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).

<sup>5</sup>Socrates 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.

<b>GAINS</b>	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

<b>LOSSES</b>	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 FulICAM. 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 CO<sub>2</sub> 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).

## References

- ABARE (2001). Australian Commodity Statistics. Australian Bureau of Agricultural and Resource Economics.
- Baldock, J.A., Oades, J.M., Waters, A.G., Peng, X., Vassallo, A.M. and Wilson, M.A. (1992). Aspects of the chemical structure of soil organic materials as revealed by solid-state <sup>13</sup>C NMR spectroscopy. *Biogeochemistry* **16**: 1-42.
- Battaglia, M. (2001). Stand age effects on productivity in forests: representation in models and influence on net ecosystem exchange. (This volume).
- Comins, H.N. and McMurtrie, R.E. (1993). Long-term biotic response of nutrient-limited forest ecosystems to CO<sub>2</sub>-enrichment; equilibrium behaviour of integrated plant-soil models. *Ecological Applications* **3**: 666-681.

- Jeffreys, M.P. (1999). Dynamics of stemwood nitrogen in *Pinus radiata* with modelled implications for forest productivity under elevated atmospheric carbon dioxide. Ph. D. thesis, Univ. of NSW, Sydney, Australia, 343 pp.
- Kirschbaum, M.U.F. (1993). A modelling study of the effects of changes in atmospheric CO<sub>2</sub> concentration, temperature and atmospheric nitrogen input on soil organic carbon storage. *Tellus* **45B**: 321-334.
- Kirschbaum, M.U.F. (1999a). CenW, a forest growth model with linked carbon, energy, nutrient and water cycles. *Ecological Modelling* **181**: 17-59.
- Kirschbaum, M.U.F. (1999b). Modelling forest growth and carbon storage with increasing CO<sub>2</sub> and temperature. *Tellus* **51B**: 871-888.
- Kirschbaum, M.U.F., Carter, J.O., Grace, P.R., Keating, B.A., Keenan, R.J., Landsberg, J.J., McKeon, G.M., Moore, A.D., Paul, K.I., Pepper, D.A., Probert, M.E., Richards, G.P. Sands, P.J. and Skjemstad, J.O. (2001): Brief description of several models for simulating net ecosystem exchange in Australia. (This volume).
- Kirschbaum, M.U.F., King, D.A., Comins, H.N., McMurtrie, R.E., Medlyn, B.E., Pongracic, S., Murty, D., Keith, H., Raison, R.J., Khanna, P.K. and Sheriff, D.W. (1994). Modelling forest response to increasing CO<sub>2</sub> concentration under nutrient-limited conditions. *Plant, Cell and Environment* **17**: 1081-1099.
- Kirschbaum MUF, Medlyn BE, King DA, Pongracic S, Murty D, Keith H, Khanna PK, Snowdon P and Raison RJ (1998) Modelling forest-growth response to increasing CO<sub>2</sub> concentration in relation to various factors affecting nutrient supply. *Global Change Biology* **4**, 23-41.
- McKane, R.B., Rastetter, E.B., Shaver, G.R., Nadelhoffer, K.J., Giblin, A.E., Laundre, J.A. and Chapin, F.S. III (1997). Reconstruction and analysis of historical changes in carbon storage in arctic tundra. *Ecology* **78**: 1188-1198.
- McLaughlin, M.J., Fillery, I.R. and Till, A.R. (1992). Operation of the phosphorus, sulfur and nitrogen cycles. In: "Australia's Renewable Resources: Sustainability and Global Change." (Eds: Gifford, R.M. and Barson, M.M.), Bureau of Rural Resources, Proceedings No. 14.
- McMurtrie, R.E. and Comins, H.N. (1996). The temporal response of forest ecosystems to doubled atmospheric CO<sub>2</sub> concentration. *Global Change Biology* **2**: 49-57.
- Medlyn, B.E., McMurtrie, R.E., Dewar, R.C. and Jeffreys, M.P. 2000. Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO<sub>2</sub> concentration. *Canadian Journal of Forest Research* **30**: 873-888.
- Post, W.M., Pastor, J., Zinke, P.J. and Stangenberger, A.G. 1985. Global patterns of soil nitrogen storage. *Nature* **317**: 613-616.
- Rastetter, E.B., McKane, R.B., Shaver, G.R. and Melillo, J.M. 1992. Changes in C storage by terrestrial ecosystems: how C-N interactions restrict responses to CO<sub>2</sub> and temperature. *Water Air and Soil Pollution* **64**: 327-344.
- Schlesinger WH (1990) Evidence from chronosequence studies for a low carbon-storage potential of soils. *Nature* **348**: 232-234.
- State of the Environment Advisory Council (1996). Australia - State of the Environment. Commonwealth of Australia, v.p.

# Carbon Dynamics and Nutrient Mineralisation

Peter R. Grace  
Sinclair Knight Merz

## Introduction

Mineralisation refers to the net release of mineral N with the decay of organic matter, and immobilisation refers to the transformation of inorganic compounds to the organic state. Both processes are mediated by soil microorganisms with immobilisation occurring when microorganisms assimilate inorganic N (ammonium and nitrate) in the synthesis of the organic constituents of their cells. A balance exists between these two concurrent processes.

When litter with a high C/N ratio (approximately 30/1 or higher) is added to soil, net immobilisation may occur for a period of time (days to weeks) which is dependent on the prevailing soil moisture and temperature. After a proportion of C from the litter source has been consumed by organisms and respired (significantly reducing the overall C/N ratio of the substrate), net mineralisation may occur. Nitrogen mineralisation from litter and soil organic pools represents the vast majority of N inputs into natural non-leguminous terrestrial ecosystems. In the case of managed crops, forests and grass pastures, an additional source of mineral N may be added in the form of fertilisers which is either taken up directly by plants or may be assimilated by microorganisms during an immobilisation event and possibly mineralised at a later date.

The transformations of organic and mineral N through the mineralisation and immobilisation processes as described is therefore the main driver of C and N change in soils as it involves a wide range of substrates from litter and soil. A model-based description of this process must therefore consider all aspects of the microbiological degradation of litter and soil organic matter. Explicit inclusion of these transformations in model structures is essential if a holistic approach to ecosystem net primary production is required. If the purpose of the model is to solely examine soil C change with time as a function of litter inputs, the mineralisation/immobilisation reaction can be implemented implicitly using differential litter quality as a primary driver.

## Model development

### Litter components

In developing a dynamic soil organic matter/nutrient simulation model, emphasis is heavily on the use of micro-scale data outlining the dynamics of the essential soil chemical constituents (inorganic and inorganic), combined with a representation of the biological components through which these nutrients are transformed. In one of the earliest examples of soil C/N cycling relevant to the simulation of ecosystem productivity, the Phoenix model (McGill *et al.*, 1981) (Figure 1), required a combination of direct microscopy of soil microorganisms and detailed chemical extraction methodologies for isolating conceptualised bio-geochemical organic nutrient pools. The model was primarily calibrated using data from a large grassland ecosystem study carried out at the Pawnee site in North America during the late 1970's and could be considered the first serious attempt to combine soil chemical, biological and ecological processes to explore nutrient feedbacks on plant production.

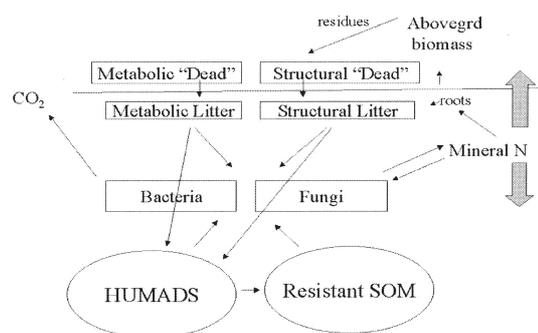


Figure 1. Structure of the Phoenix soil and litter decomposition model and flows of C and N from various above- and belowground compartments.

Phoenix's detailed biological structure also meant that the model required a great deal of parameterisation. Whilst some of the core biochemical components and parameters describing nutrient transfer were based on a compendium of field data, the specific growth rates and maintenance coefficients of micro-organisms in the model were based on laboratory data and values varied considerably. These components may be considered the weakest part of this model (hence being the

reason why this detailed microbial representation has lost favour), in contrast to the rigor in which the bio-geochemical components of the model were assembled.

Consistent with its ecological basis, senesced plant litter and roots were classified according to the distribution of their metabolic and structural material which decomposed independently of each other. The metabolic component (cytoplasmic material) with a rapid decomposition rate; the structural component (sheath, stem wall) more resistant to decomposition. In this case, the split between metabolic and structural material was calculated on the basis of the litter's C/N ratio, with high C/N litter having a proportionally larger structural component. These two conceptual pools provide a common thread in the development of the litter decomposition routines in the Rothamsted, SOCRATES and CENTURY models. The latter may be considered somewhat of a hybrid in that the alternative 3-pool, or biochemical approach to litter characterisation (i.e. carbohydrate, cellulose and lignin) is also partially utilised in developing the structural and metabolic split i.e. through the use of the lignin/N ratio. The 3-pool biochemical classification of litter (Parnas, 1975; Juma and Paul, 1981; Seligman and van Keulen, 1981) is currently being applied in both the ecological (GENDEC), but more so in, the agronomic (APSIM, FarmWise, CERES) spheres of soil C/N modelling.

A third approach is the use of litter cohorts as outlined in the LINKAGES model. Litter is compartmentalised according to its lignin/N ratio and annual weight loss of each of these cohorts is tracked until a critical N concentration is reached and its contents added to the soil humus pool.

### *Soil components*

Two distinct modelling streams in soil organic matter dynamics have evolved since the 1980's and have broadly been distinguished through their respective alignments with the ecological and agricultural (as distinct from agronomic) sciences. In both spheres of interest, specific attention also been given to the concept of physical protection of soil organisms and organic matter in C/N cycling.

The inclusion of a measurable soil microbial biomass entity (Jenkinson and Rayner, 1977) has been a common thread in the ancestral lineage of many of the agricultural-based soil C/N models since the mid-1970's. The models of van Veen *et al.* (1984), Jenkinson (1990), Ladd *et al.* (1995) and Grace and Ladd (1995) have all been developed with this basic structure in mind. These models have tended to be calibrated on data from disturbed agricultural soils with long histories of cropping. In

the latter models, the more stable humus fraction is considered to be a separate measurable entity as well. In the case of the Rothamsted-C model of Jenkinson *et al.* (1987) a pool of inert organic matter is also included which is based on measured <sup>14</sup>C radiocarbon dates of arable soils. Where the main distinction in the agricultural and ecological models has occurred has been in the description of non-living humus fractions or pools.

A comprehensive listing of model structures in use in the international soil C/N modelling community can be found in Paustian (1994). The tendency in ecological models has been to segregate humus into active, recalcitrant and stable organic matter (or terms of similar meaning e.g. active, slow and passive) in structures best represented by the CENTURY model.

Models which have conceptual soil organic matter components (e.g. CENTURY) have historically been developed with resource sustainability in mind and include potential feedbacks of nutrient availability on net primary production and hence litter production. The majority of calibration activities have focused on data from natural, low-input, undisturbed natural systems. Their application has primarily been for long-term simulations, to investigate the impact of ecological perturbations on nutrient cycling and to examine possible successional changes in ecosystems using weekly to monthly timesteps. In contrast, agronomic models have tended to be used for single season simulations, using daily changes in nutrient and water availability to constrain crop growth and development which is primarily driven by light interception.

In general, soil C/N models developed primarily for estimating soil organic matter storage, whether they be from an agricultural or ecological background, tend to have a rudimentary plant production module only. This provides an estimation of organic input and a potential sink for aboveground nutrient uptake. On the other hand, many of the agronomic, or decision support models (e.g. APSIM) have extremely detailed plant production routines with a tendency towards simplistic soil C/N modules and measurable pools similar to those proposed in the SOCRATES and Rothamsted C models.

### *Mineralisation and immobilisation*

One of the first attempts at incorporating this process into functional simulation models is described in Godwin & Vlek (1985) for the agronomic CERES-Maize model. The approach was based on the PAPRAN pasture model of Seligman & van Keulen (1981) and differed to the traditional approach of soil modellers of the time. It comprised a 3-pool chemical

fractionation to characterize the quality crop residues (as opposed to the 2-pool conceptual split) and it did not include an explicit microbial biomass pool through which the mineralisation/immobilisation process was mediated. Microbial biomass was considered (as it is), in intimate association with the fresh organic matter (or crop residue) pool. The simplicity of the structure has survived the test of time in some agronomic models with some modifications proposed by Bowen *et al.* (1993) and Quemada and Cabrera (1995) providing realistic predictions of mineral N availability in single-season simulations.

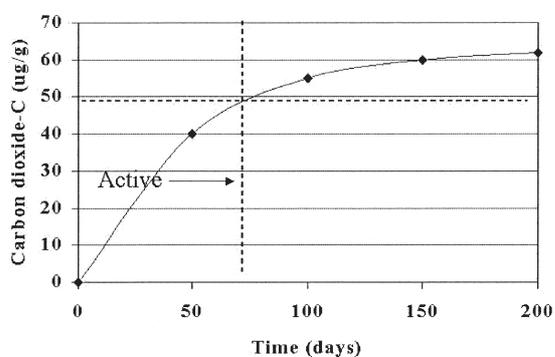


Figure 2. Graphical representation of cumulative carbon dioxide evolution for a hypothetical soil in a long-term aerobic incubation at optimal moisture (water-holding capacity) and temperature (25°C). The active component of soil C (in this case 49 ug/g soil) is estimated by a statistical curve splitting which determines the point where CO<sub>2</sub> evolution is entering a near-static mode after the rapid decomposition of labile material.

Basically the processes of mineralisation and immobilisation explicitly described in model structures can be distinguished on the same ecological and agricultural lines which differentiate the soil components in the models. In the agricultural models, an explicit microbial pool, as routinely measured by chloroform fumigation and incubation (Jenkinson and Powlson, 1976) or extraction methods (Sparling *et al.*, 1988) is preferred in contrast to the conceptual active fraction in ecological models. Many studies have measured microbial biomass in soils and default values do exist thus reducing the need for laboratory analyses.

With respect to the conceptual approaches to mineralisation and immobilisation, the active fraction is considered to be a labile or easily decomposable pool of C and N in soil. The active, slow and passive fractions of the CENTURY model have been determined (E.A. Paul, personal communication) using a combination of long-term soil incubations and acid hydrolysis of mineral soil (eqn.1)

$$\text{Slow C} = \text{Total C (Combustion)} - \text{Active C (incubation)} - \text{Passive C (HCL hydrolysis)} \quad (1)$$

Usually a minimum of 200 days laboratory incubation under optimal moisture and temperature (25°C) is necessary to construct the characteristic cumulative CO<sub>2</sub> evolution and/or N mineralisation curve required (Figure 2) for a curve-splitting analysis in determining the size of the active soil pool. In some cases, the determination of both the active and slow pools can be determined with the incubation technique alone if CO<sub>2</sub> evolution rates are relatively static by the end of the incubation period. This period may be extended if information on the slow pool is also required.

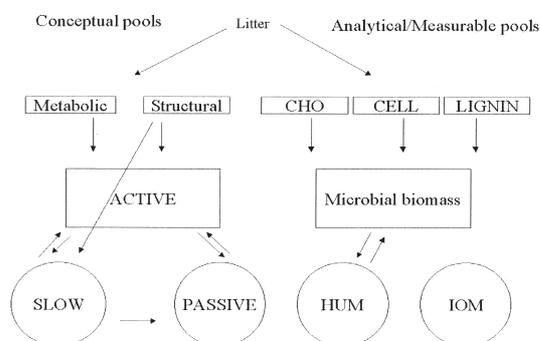


Figure 3. Generic structures of conceptual and measurable soil models and associated C and N flows, currently in use in Australia.

## Model performance

If we consider the models currently used in Australia to simulate soil C and N cycling, we have a mixture of structures which can be essentially characterised by their alignment to either the conceptual or measurable components of litter and soil (Figure 3). In terms of mineralisation and immobilisation, there is also a further division, with models including N cycling in either an explicit quantifiable form, or implicitly, using a qualitative characterisation for litter inputs into the model (Table 1). In the latter, litter decomposability is an implicit function of the C/N ratio and the relative amounts of carbohydrate, cellulose and lignin. In both the SOCRATES and Rothamsted models, it is not necessary to input these specific chemical composition values directly as the relative proportions

of decomposable and resistant plant material in litter have been estimated from a combination of incubation studies. The actual values of the ratio of decomposable-to-resistant plant material used in the models decreases from 0.25 to 0.66, (i.e. for woodlands and legume respectively) with interim values for grasslands and agricultural crops.

An interesting observation is that apart from the LINKAGES model, all models currently in use in Australia have an ancestral linkage, with their structures broadly based on either the CENTURY or Rothamsted approaches. Comparisons of model performances in terms of the ability to mimic soil C changes have been limited, but the CENTURY, Rothamsted and SOCRATES models have all performed similarly well when compared using Australian datasets (Grace *et al.*, submitted; Skjemstad, 1996). A model comparison in Canada (Izaurrealde *et al.*, 1996) where a variety of models of increasing complexity were compared, selected the SOCRATES model ahead of the CENTURY and Rothamsted approaches.

SOCRATES differs from both CENTURY and Rothamsted in that it does not require a detailed fractionation of the soil to be performed prior for initialising the soil carbon pools. This is because SOCRATES does not possess a third soil carbon pool, analogous to the passive or inert fractions in the CENTURY and Rothamsted models respectively. The simplified structure of SOCRATES also utilises default values for initialising the microbial and humus pools based on published literature of their relative proportions in response to previous land use. This same feature of not having to use detailed soil data is also utilised in the CENTURY model if the "equilibrium" method is

used to initialise the three soil C pools. This method can be used when a land-use change has been in evidence and it utilises the model itself to estimate the carbon contents (based on the original vegetation) prior to the change being instigated. This approach implies that in the first place the model structure must be correct and capable of delivering valid outputs.

## Requirements for model applications

The structure of a model is dependent upon the problem being examined and the detail required to accurately produce meaningful information. Simply stated, model selection depends on model objectives. Holistic models of net ecosystem exchange do require an explicit representation of the soil N cycle to ensure that possible constraints on N availability on plant growth and development are included and their impact quantified within a whole ecosystem framework. Explicit inclusion of mineralisation and immobilisation are not required if the model's primary objective is just estimating C storage in soils. The amount of carbon to be input into the soil matrix is a key element of these latter models, but not a requirement in their structure.

In terms of simulating net ecosystem exchange of C, linked soil-plant structures have evolved at all levels of temporal resolution. They range from highly mechanistic approaches such as Ecosys (Grant *et al.*, 1993) which attempts to simulate all pathways of the C cycle (including photosynthesis and respiration) and associated elements at hourly timesteps, to

Model	Litter	Litter	Soil	Mineralisation and Immobilisation <sup>1</sup>
APSIM	Measurable	Measurable	Measurable	Explicit
CERES/DSSAT	Measurable	Measurable	Measurable	Explicit
GENDEC	Measurable	Measurable	Measurable	Explicit
CENTURY	Conceptual	Conceptual	Conceptual	Explicit
CenW	Conceptual	Conceptual	Conceptual	Explicit
G'Day	Conceptual	Conceptual	Conceptual	Explicit
Grazplan	Conceptual	Conceptual	Measurable	Explicit
Roth-C	Conceptual	Conceptual	Measurable	Implicit
SOCRATES	Conceptual	Conceptual	Measurable	Implicit
LINKAGES	Conceptual	Conceptual	Measurable	Implicit
Promod	n.a.	n.a.	n.a.	n.a.
GRASP	n.a.	n.a.	n.a.	n.a.
3PG	n.a.	n.a.	n.a.	n.a.

<sup>1</sup>"Explicit" is a quantitative representation of N dynamics, in contrast to "Implicit", which is a qualitative representation of N only, specifically through its influence on litter decomposability. n.a. not applicable

*Table 1. Classification of soil-plant models currently in use in Australia with respect to their litter and biogeochemical components and their capacity to simulate the mineralisation and immobilisation of nitrogen soils.*

SOCRATES with a monthly timestep, whereby plant biomass inputs are based on simplistic rainfall-derived regression equations. It is recognised that the more parameters that are within a model's structure, the more degrees of freedom there are for errors to propagate and effect the end result. It must also be recognised that without mechanistic models we would be unable to fully elucidate the complex interactions that occur in carbon cycling in ecosystems. Both levels of model development are essential in our quest to accurately describe ecosystem processes and closing our gaps in knowledge. To this end, a convergence in model structures has gradually been occurring over the past decade.

The model comparison carried out by Izaurrealde *et al.* (1996) for the Canadian prairies is a good example of examining the level of complexity required in a model to quantify net regional C fluxes incorporating a mosaic of natural and arable ecosystems. In this comparative study, the model user had experience in simulation methods, but no experience in the use of specific models e.g. CENTURY, SOCRATES, Epic, DNDC and RothC. Experienced users were on hand to develop simulations with the Ecosys model. The RothC and DNDC models were eliminated in a preliminary exercise. RothC, because of its inability to maintain the soil C in its equilibrium state, whilst DNDC required a great deal of detailed information and proved unstable in its performance. SOCRATES was chosen on the basis of its accuracy and simple structure. The latter consideration was deemed essential for simulating a wide range of soil types and management systems and also by the fact that simplistic regression relationships based on published production data itself could be used to estimate crop productivity. This eliminated the increased data demands required for yield prediction in the other models.

Simple model structures such as SOCRATES are also applicable where N feedbacks on the system need to be addressed explicitly. A nitrogen version of the SOCRATES is easily constructed using a complementary N pool structure with fixed C/N ratios. Mineralisation has been validated against the litter incubation study of Mtambanengwe *et al.* (1998). Typical responses of the soil microbial and mineral N pools in response to scenarios where litter of contrasting qualities (N contents) are added to mineral soil are depicted in Figure 4. Some models also tend to use a variable C/N ratio for the composition of microbial biomass pool. A comparison of simulated mineral N production using fixed microbial C/N values of 4 and 9 respectively for a 200 day incubation shows that only an additional 2 kg N/ha is produced during that time (Figure 5). This suggests the sensitivity of the N content of this pool in the

SOCRATES-N does not have a great impact on N mineralisation and the inclusion of this function in simulation models may not be a necessity.

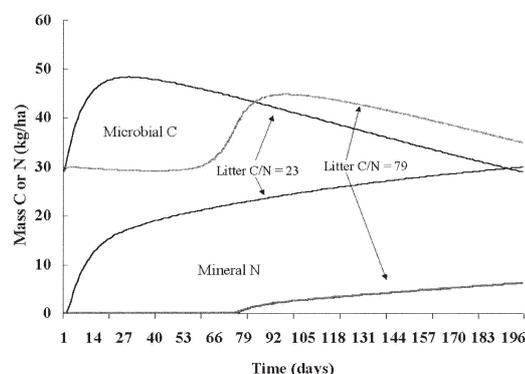


Figure 4. Response of the soil microbial biomass (C/N of 4) and the soil mineral N pool over the first 200 days in the SOCRATES-N model after the addition of litter of contrasting C/N ratios to a sandy-loam soil at 25°C and optimal (60%) water-holding capacity.

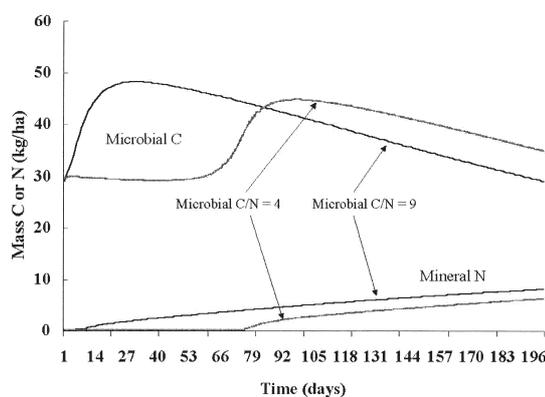


Figure 5. Comparative responses of the soil microbial biomass with C/N ratios of 4 and 9 respectively and the soil mineral N pool in the SOCRATES-N model after addition of litter with a C/N of 79 at 25°C and optimal (60%) water-holding capacity.

## Conclusion

Simulation models of terrestrial carbon cycling have been developed over the past 30 years for both ecological and agronomic applications, but have tended to be represented by similar structures. The explicit inclusion of N and other nutrients in these models is highly dependent on its end-use, but reductionist approaches with minimal data requirements have been proven to be as accurate as their more mechanistic counterparts. There is an obvious role for a suite of models with

increasingly complexity in examining the net ecosystem exchange of carbon. This capacity to look at ecosystems with varying detail will ensure that problem solving in terrestrial biology and ecology remains a converging and not a diverging science. Convergence with creativity will increase the essential element of collaboration and scientific sharing that is required for progress to be made in understanding, mitigating and adapting to the impacts of global climate change.

## References

- Bowen, W.T., Jones, J.W., Carsky, R.J. and Quintana, J.O. (1993) Evaluation of the nitrogen model of CERES-Maize following legume green manure incorporation. *Agron. J.* 85, 153-159.
- Godwin, D.C. and Vlek, P.G. (1985) Simulation of nitrogen dynamics in wheat cropping systems. In Day, W. and Atkin, R.K. (Eds.), *Wheat Growth and Modelling*. Plenum Publishing Corp, New York, 311-332.
- Grace, P.R., Georgis, K., Reeves, T.G. and Alston, A.M. (submitted) Simulating changes in soil organic carbon in cropping systems of the semi-arid Mallee region of Australia. *Ag. Systems*.
- Grace, P.R. and Ladd, J.N. (1995) SOCRATES (Soil Organic Carbon Reserves and Transformations in agro-Eco-Systems). CRC for Soil and Land Management, Adelaide, 17pp.
- Grant, R.F., Juma, N.G. and McGill, W.B. (1993) Simulation of carbon and nitrogen transformations in soil: Mineralisation. *Soil Biol. Biochem.* 25, 1317-1329.
- Izaurrealde, R.C., McGill, W.B., Jans-Hammermeister, D.C., Haugen-Korzyra, K.L. and Hiley, J.C. (1996) Development of a technique to calculate carbon fluxes in agricultural soils at the eco-district level using simulation models and various aggregation methods. Interim Report, Submitted to the Scientific Authority of the Agriculture and Agri-Food Canada Greenhouse Gas Initiative, University of Alberta, Edmonton, 69pp.
- Jenkinson, D.S. (1990) The turnover of organic C and N in soil. *Phil. Trans. Roy. Soc. Lon. B* 329, 361-368.
- Jenkinson, D.S., Hart, P.B.S., Rayner, J.H. and Parry, L.C. (1987) Modelling the turnover of organic matter in long-term experiments at Rothamsted. *INTECOL Bulletin* 15, 1-8.
- Jenkinson, D.S. and Rayner, J.H. (1977) The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Sci.* 123, 298-305.
- Jenkinson, D.S. and Powlson, D.S. (1976) The effect of biocidal treatments on metabolism in soil. V. A method of measuring soil biomass. *Soil Biol. Biochem.* 8, 209-
- Juma, N.G., and Paul, E.A. 1981. Use of tracers and computer simulation techniques to assess mineralization and immobilization of soil nitrogen. In: Frissel, M.J. and van Veen, J.A. (Eds.), *Simulation of Nitrogen Behavior of Soil-Plant Systems*. Pudoc, Wageningen, 145-154.
- Ladd, J.N., Amato, M., Grace, P.R. and van Veen, J.A., 1995. Simulation of  $^{14}\text{C}$  turnover through the microbial biomass in soils incubated with  $^{14}\text{C}$ -labelled plant residues. *Soil Biol. Biochem.* 27, 777-783.
- McGill, W.B., Hunt, H.W., Woodmansee, R.G. and Reuss, J.O. (1981) Phoenix, a model of the dynamics of carbon and nitrogen in grassland soils. In: Clark, F.E., Rosswall, T. (Eds.), *Terrestrial Nitrogen Cycles*. *Ecol. Bull. (Stockholm)*. 33, 49-115.
- Mtambanengwe, F., Chivaura-Mususa, C. and Kirchmann, H. (1998) Assessment of plant-litter quality related to short-term carbon and nitrogen mineralisation in soil. In: Bergstrom, L. and Kirchmann, H. (Eds.), *Carbon and Nitrogen Dynamics in Natural and Agricultural Tropical Ecosystems*, CAB International, Wallingford, 85-102.
- Parnas, H. (1975) Model for decomposition of organic material by microorganisms. *Soil Biol. Biochem.* 7, 161-169.
- Paustian, K. (1994) In: Pankhurst, C.E., Doube, B.M., Gupta, V.V.S.R. and Grace, P.R. (Eds.), *Soil Biota: Management in Sustainable Farming Systems*, CSIRO, Melbourne.
- Quemada, M. and Cabrera, M.L. (1995) CERES-N model predictions of nitrogen mineralised from cover crop residues. *Soil Sci. Soc. Amer. J.* 59, 1059-1065.
- Seligman, N.C. and van Keulen, H. (1981) PAPRAN: A simulation model of annual pasture production limited by rainfall and nitrogen. In: Frissel, M.J. and van Veen, J.A. (Eds.), *Simulation of Nitrogen Behaviour of Soil-Plant Systems*, PUDOC, Wageningen, Netherlands, 191-221.
- Skjemstad, J. (1996) Determining the potential for carbon sequestration in Australian soils. Final Report RIRDC project CSO-5A, 66pp.
- Sparling G.P. and West, A.W. (1988) A direct extraction method to estimate soil microbial C: calibration in situ using microbial respiration and  $^{14}\text{C}$  labelled cells. *Soil Biol. Biochem.* 20, 337-343.
- vanVeen, J.A., Ladd, J.N. and Frissel, M.J. (1984) Modelling C and N turnover through the microbial biomass in soil. *Plant Soil* 76, 257-274

# Temperature and Moisture Effects on Decomposition

Keryn Paul  
CSIRO Forestry and Forest Products

## Introduction

In most models which simulate soil organic matter turnover, decomposition is calculated using a function such as:

$$\text{Decomposition} = k \times T_m \times W_m \times \text{Other factors}$$

where,

$k$  = potential decomposition rate

$T_m$  = mathematical function which demonstrates the relative rate of microbial activity with increasing soil temperature, usually between a value of 0 and 1

$W_m$  = mathematical function which demonstrates the relative rate of microbial activity with increasing water availability, usually between a value of 0 and 1

Other factors = C:N ratio factor, contact factor etc., usually between a value of 0 and 1

In this paper, various  $T_m$  and  $W_m$  functions are described and compared. Particular attention is paid to the models chosen for comparison at this workshop. Potential problems regarding the 'scaling-up' of these functions (i.e. application in a national carbon accounting model) are also briefly discussed.

## Temperature

The  $T_m$  functions used in the models reviewed for this workshop are given in Table 1 and Figure 1. Over a limited temperature range, many models (e.g. GRAZPLAN and GRASP) assume a linear relationship with microbial activity. Most models use simple exponential or power  $T_m$  function (e.g. APSIM, CENTURY, Socrates) that assume a constant microbial sensitivity to temperature. Other models have a more sophisticated  $T_m$  function, allowing for an adjustment of microbial sensitivity with temperature (e.g. CenW, G'day).

There are no specific  $T_m$  functions in the models that had sophisticated algorithms for predicting decomposition of litter. For the litter decomposition model *GENDEC*,  $T_m$  needs to be entered into the model by the user on a monthly basis

Model	Time -step	Soil/ air	$T_m$ function used	References
GrazPlan & GRASP	D	A	$= T/T_{ref}$	McCaskill and Blair (1990); Cooksley <i>et al.</i> (1993)
APSIM	D	S	$= (T/T_{opt})^2$	Probert <i>et al.</i> (1998)
CENTURY	M	S	$= 0.125 \cdot \exp(0.07 \cdot T)$	Cater (20001) pers. com.
CenW and G'day	D	S	$= \exp[3.36 (T - 40) / (T + 31.79) ]$	Kirschbaum (1995, 2000a)
G'Day (option 2)	D-M	S	$= 0.0326 + 0.00351 \cdot T^{1.652} - (T/41.748)^{7.19}$	Comins and McMurtrie (1993)
Roth-C	M	A	$= 47.9 / [1 + \exp(106 / (T + 18.3))]$	Jenkinson (1990)
Socrates	Y	A	$= 0.177 \cdot \exp(0.069 T)$	Grace <i>et al.</i> (2001)

where,

$T$  is the average temperature (soil or air),

$T_{ref}$  is a reference temperature.

$T_{opt}$  is the optimal temperature for decomposition,

Table 1: Description of  $T_m$  functions used by various models in the calculation of decomposition rates. The time-step of the models may be daily (D), weekly (W) monthly (M) and annually (Y), and the  $T_m$  functions use either soil temperature (S) or air temperature (A).

(Moorhead *et al.* 1999). *Linkages* modifies leaf litter decomposition according to evapotranspiration and litter quality (Keenan 2001, pers. com., Table 2). In this model, woody litter has a specified percentage weight loss.

Microbial activity is generally predicted to increase rapidly up to a temperature of about 30°C. An optimal temperature for microbial activity is reached between 35 and 45°C. Although all biological reactions clearly have optimum temperatures, this is neglected in most models because even average daily temperatures within the surface 5 cm of soil are unlikely to reach this optimum. Furthermore in the field, such extreme temperatures generally coincide with periods of moisture limitation so the decomposition is largely unaffected by temperature.

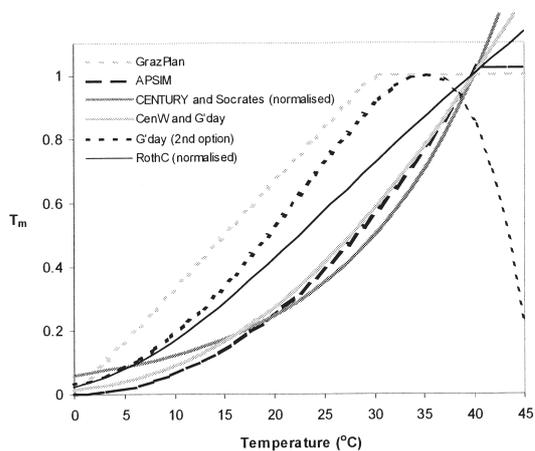


Figure 1:  $T_m$  functions used by various models in calculation of decomposition rates. Where necessary, functions have been normalized such that  $T_m$  equals 1 at a temperature of 40°C.

Models have indicated that decomposition (and CO<sub>2</sub> release) from mineral soils may be enhanced as a result of global warming (Jenkinson *et al.* 1991; Wang and Polglase 1993; Kirschbaum 2000a). This prompted review of  $T_m$  functions (Lloyd and Taylor 1994; Kirschbaum 1995; Rodrigo *et al.* 1997). These reviews showed that commonly used functions, which imply constant temperature sensitivity or activation energy across any temperature range (i.e. Van't Hoff and Arrhenius functions), systematically underestimated decomposition at low temperatures and overestimated decomposition at high temperatures. It was shown that over a large temperature range, a  $T_m$  function that provided accurate estimates of microbial activity across a wide range of soils was the Lloyd and

Taylor (1994) function. This function effectively gave an increase in activation energy with decreasing temperature. Kirschbaum (1995, 2000a) normalised the Lloyd and Taylor at a reference temperature of 40 °C and calibrated the function using an even wider range of soils.

In order to compare  $T_m$  functions and their suitability for application across a wide range of soils, data were collated from laboratory incubation experiments that demonstrated the influence of temperature on net N mineralisation. Figure 2 shows the relationship between relative rates of N mineralisation ( $T_m$ ) and soil temperature for 15 different soils. The rate of N mineralisation was expressed relative to N mineralised under optimal conditions of temperature and moisture. The function used by Kirschbaum (2000a) gave the best fits to the observed data ( $R^2=0.87$ ).

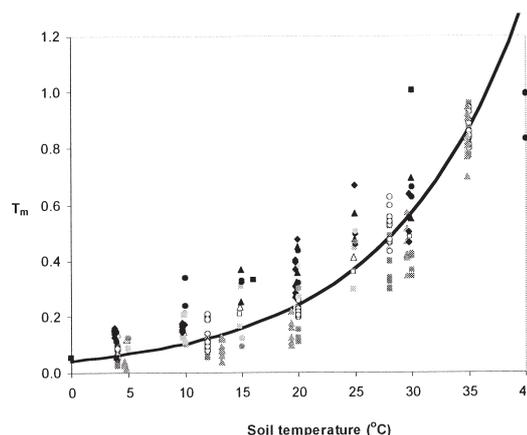


Figure 2: The universal soil  $T_m$  function derived using the laboratory incubation datasets. Solid line represents the function fitted by Kirschbaum (2000a).

## Soil water

In addition to directly affecting microbial activity, several physical processes that can affect microbial activity vary with soil water content, particularly water movement, and gas and solute diffusion. As a consequence, the relationship between soil water content and microbial processes in soils is complex because this relationship varies between soils, depending on the soil moisture-retention curve, porosity, concentration of organic matter, pH and soil depth (Goncalves and Carlyle 1994; Rodrigo *et al.* 1997; Leiros *et al.* 1999). These issues raise the question as to the most appropriate means of expressing soil

water content in a  $W_m$  function which is to be universally applied across a range of soil types.

The argument of  $W_m$  functions are usually volumetric soil water content, percent of an optimal water content, relative water content, or an indicator of soil water availability (i.e. ratio of rainfall to evaporation) (Table 2). Other  $W_m$  functions use percent water-filled pore space or soil water pressure potential. Estimation of a least limiting water content range may be a useful measure of water stress on decomposition in soils (Zou *et al.* 2000).

In order to assess the most appropriate argument of a universal  $W_m$  function, data was collated from laboratory incubation experiments where microbial activity was related to soil water content. Figure 3 shows the relationship between relative rates of N mineralisation ( $W_m$ ) and soil water content for 28

different soils (comprising 40 different soil layers). Various ways of expressing soil water content were explored. In all cases, the rate of N mineralisation was expressed relative to N mineralised under optimal conditions. Although there was a lot of variation between soils regardless of the way in which soil water content was expressed, the best relationship was obtained using a water content relative to the upper and lower limit of water observed in the field (i.e.  $RWC=(W-LL)/(UL-LL)$ ). This allows comparison soils of different textures.

There are various forms of functions used to describe the influence of water content on decomposition (Table 2). As these functions use different ways of expressing soil water content, comparison between them was made using two different scenarios: (i) a sandy soil in a relatively low rainfall mediterranean climate, and (ii) a clay loam soil in a relatively high rainfall temperate climate (Table 3).

Model	Time	Argument	$W_m$ function used	References
GRAZPLAN	D	$\theta_v$	If $W \leq DUL$ , then $= W/DUL$ , else $= 1 - (W - DUL)/(SAT - DUL)$	Simpson and Moore (2001) pers. com.
GRASP	D	RWC	$= RWC$	Cooksley <i>et al.</i> (1993)
APSIM	D	$\theta_v$	Increases from 0 to 1 between LL and $0.5*(LL + DUL)$ , then 1 until DUL. Then decreases to 0.5 at SAT	Probert <i>et al.</i> (1998)
CENTURY	M	S	If $S < 1.5$ , $= 1/[1 + 30 \cdot \exp(-8.5 S)]$ , else $= 1 - 0.7 \cdot (S - 1.5)/1.5$	Parton <i>et al.</i> (1987, 1994)
CENTURY	M	RWC	$= 1/[1 + 4 \cdot \exp(-6 \cdot RWC)]$	Carter (2000) pers. com.
CenW	D	W/WHC	If $W/WHC < Max = \sqrt{(W/WHC) / Max}$ , else $= 1$	Kirschbaum (2000b)
G'Day	D, W	W/WHC	If $W/WHC < 0.6$ , then $= ((W/WHC) - LL)/(UL - LL)$ , else 1	Comins and McMurtrie (1993)
Roth-C	M	TSMD	$= \text{MIN}(1, 0.2 + 0.8 \cdot (\text{ClayFactor} - \text{TSMD}) / 16.53)$	Jenkinson (1990)
Linkages	M	ET	$= 0.9804 + 0.09352(ET) + [0.4956 - 0.001927(ET)] \cdot (\text{lignin:N})$	Keenan (2001) pers. com.
Socrates	Y	R	Empirical crop factors	Grace <i>et al.</i> (2001)

where,

$W$ =soil water content

$\theta_v$ =volumetric water content

RWC=relative water content

UL= upper limit of water content

SAT= saturation, assumed to be about -10 kPa

DUL or FC or WHC=drained upper limit, field capacity or water holding capacity, assumed to be about -25 kPa

PWP or LL=Permanent wilting point or lower limit of water content, assumed to be about -1,500 kPa

S=stored water + rainfall/PET (mm)

TSMD=total soil moisture deficit (mm)

PET= potential evapotranspiration (mm)

R=rainfall (mm)

ET=evapotranspiration (mm)

Table 2: Description of the  $W_m$  functions used by various models in the calculation of decomposition rates. The time-step of the models is either daily (D), weekly (W) or monthly (M).

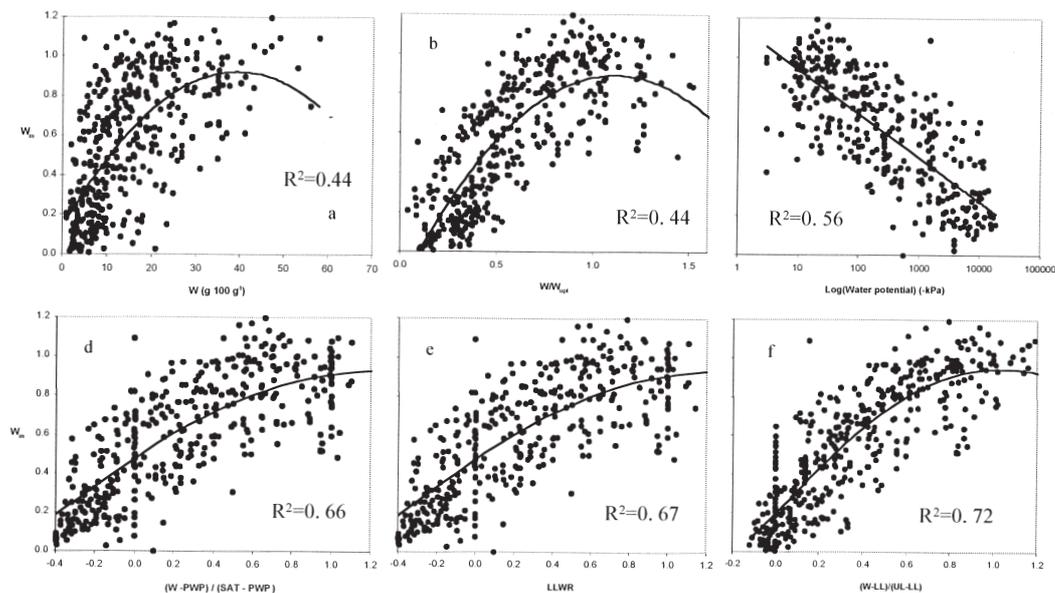


Figure 3: Relationship between  $W_m$  and the water content (a); water content as a percent of optimal water content for  $N$  mineralisation (b); water potential (c); relative water content expresses as water content in terms of water content at permanent wilting point ( $-1500$  kPa) and saturation ( $-10$  kPa) (d); least limiting water range (LLWR, Zou et al. (2000)) (e), and; relative water content expresses as water content in terms of the upper and lower water content observed in the field (f). Lines represent quadratic functions of best fit.

Characteristic	Sand	Clay
Region	SW Western Australia	Tasmania
Climate	Mediterranean	Temperate
Annual rainfall (mm)	632	1,214
Annual pan evaporation (mm)	1,448	699
Clay content (%)	7	33
LL ( $g\ 100g^{-1}$ )	5	25
DUL or FC ( $g\ 100g^{-1}$ )	27	38
UL ( $g\ 100g^{-1}$ )	40	52
Range of TSMD (mm)	0-40	0-40
Range of S (mm)	0.06-2.16	0.61-7.07

Abbreviations have been previously described (Table 2)

Table 3: Site, climate and soil characteristics of the scenarios used for  $W_m$  testing in Figures 3 to 7.

The simplest  $W_m$  functions describe a linear relationships in the "available" moisture range (e.g. APSIM and GRAZPLAN, Figure 4). Power, sigmoidal, exponential and quadratic  $W_m$  functions are also used (Figures 5-8).

Most of the  $W_m$  functions do not describe a decline in microbial activity at very high water contents. The only exception was APSIM and the original version of CENTURY. These functions are

most suitable for soils subject to water logging. However for most soils it is probably not necessary to define a  $W_m$  function over the full range of possible moisture conditions if the principle aim is to predict field rates of decomposition.

In both scenarios, there were vast discrepancies between the  $W_m$  functions at relatively low soil water contents. This is of concern in Australia, where soil water content is often sub-optimal for decomposition. Given the data shown in Figure 3, and the fact that a  $W_m$  function argument of relative water content gave the best universal description of water on the microbial activity, the new  $W_m$  function of CENTURY appears to be a suitable  $W_m$  function for application in models applied across a range of soil types.

## Issues with respect to 'scaling-up' the application of $T_m$ and $W_m$ functions

To minimise the need for site calibration, most models aim to have a  $T_m$  and  $W_m$  function which can be universally applied to a range of litter and soil types and climatic conditions. However, there are a number of potential problems we need to consider when applying the same  $T_m$  and  $W_m$  function across a range of

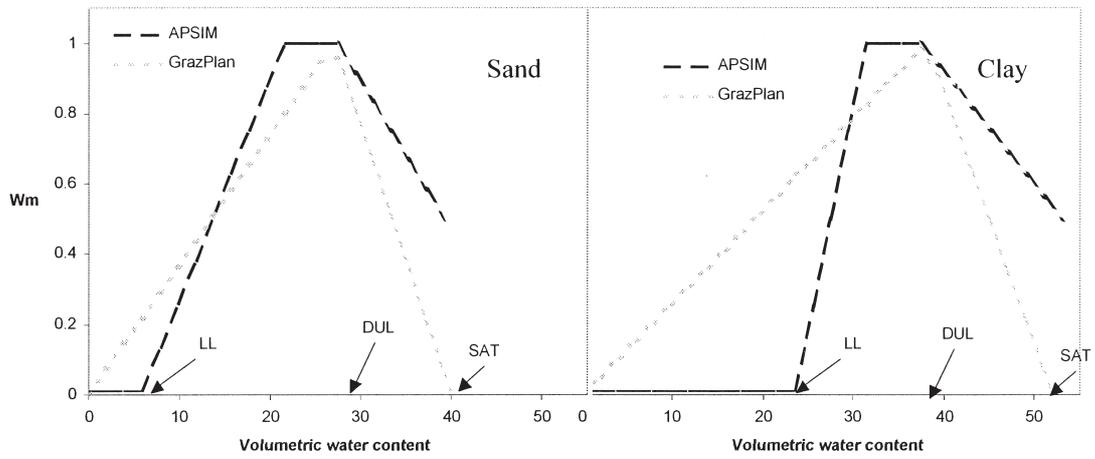


Figure 4:  $W_m$  functions used in APSIM and GRAZPLAN for sand and clay soil scenarios.

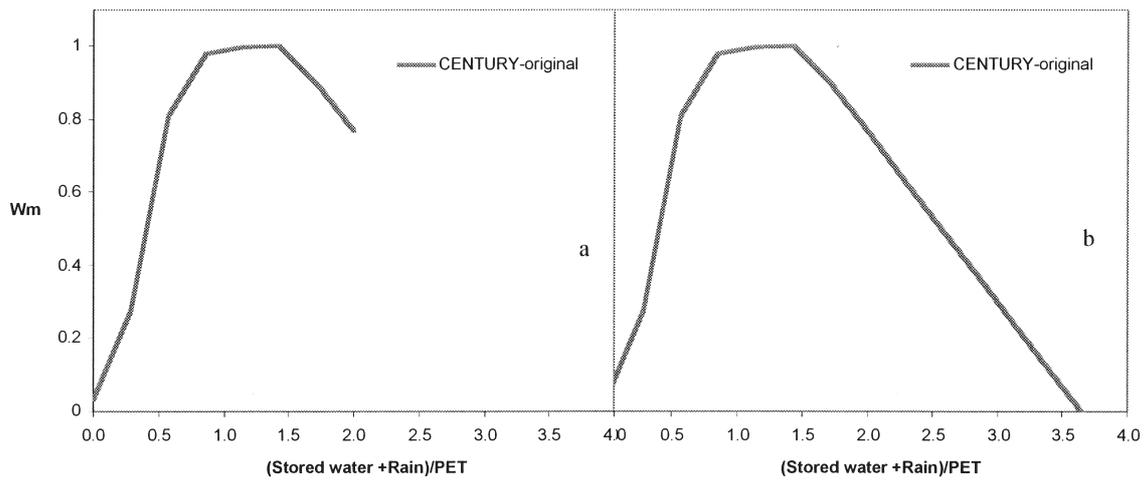


Figure 5:  $W_m$  functions used in the original version of CENTURY for sand and clay soil scenarios.

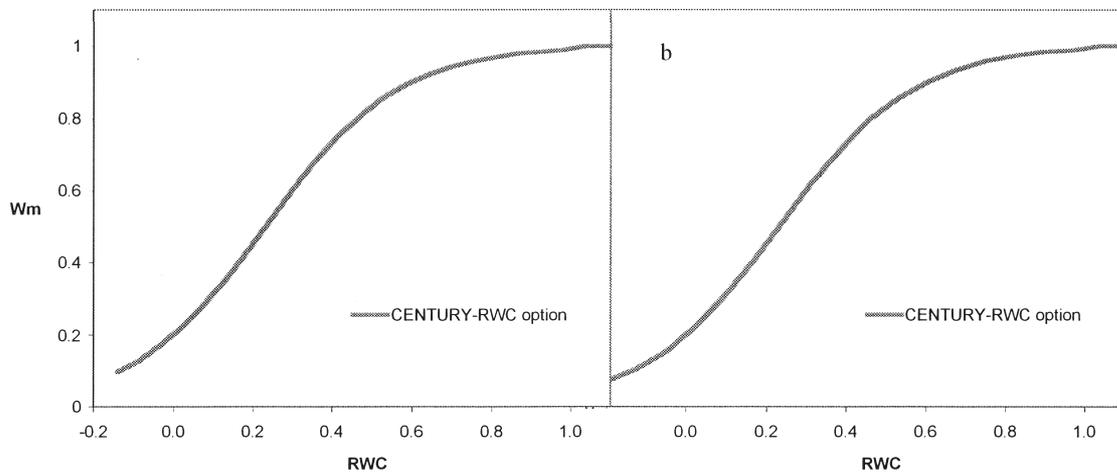


Figure 6:  $W_m$  functions used in the RWC version of CENTURY for sand and clay soil scenarios.

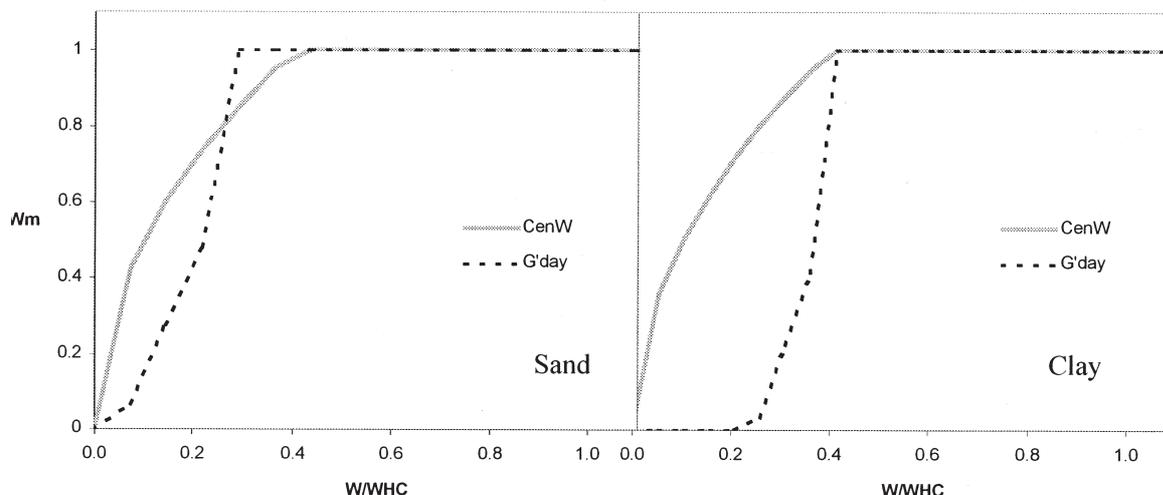


Figure 7:  $W_m$  function used in CenW and G'day for sand and clay soil scenarios.

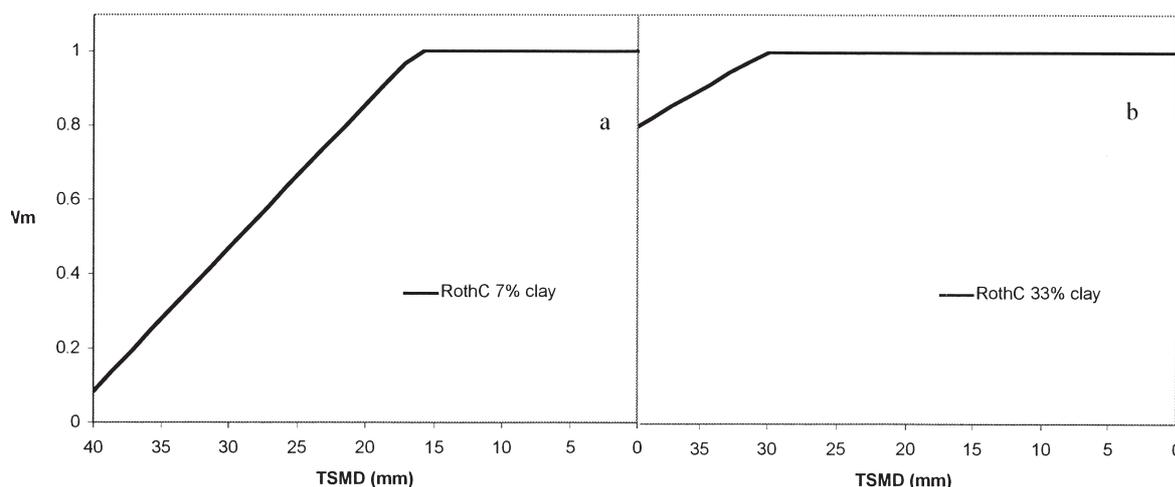


Figure 8:  $W_m$  function used in RothC for sand and clay soil scenarios.

sites. These include: (i) data availability, (ii) substrate quality and, (iii) microbial adaptation to climatic conditions.

Data availability is an issue when considering the most appropriate argument of the  $W_m$  function. It was suggested above that the most appropriate argument is a RWC defined in terms of an upper and lower water content observed in the field. We need to ascertain whether this information can be accurately estimated based on soil information available on a national scale.

The  $T_m$  and  $W_m$  functions may be dependent on substrate quality. The more easily decomposable the substrate is, the more sensitive decomposition is likely to be to temperature and water (e.g. Vigil and Kissel 1995). Difference in substrate quality may explain why microbial activity in the litter layer and soil are not

similarly affected by temperature and water (Quemada and Cabrera 1997), and why the effects of temperature and water on microbial activity was greater in the soil surface layer than in the underlying mineral soil layers (Leiros *et al.* 1999). This is of concern given that  $T_m$  and  $W_m$  functions are usually calibrated using short-term laboratory incubations. During such short-term laboratory incubations, we may only be measuring the influence of temperature and water on decomposition of the 'active', or 'decomposable', soil organic matter pool (Giardina and Ryan 2000). If so, most models may incorrectly assume that decomposition of all soil organic matter is as sensitive to temperature as decomposition of 'active' soil organic matter.

It is unlikely that microbes in a very warm-wet environment will be as equally sensitive to changes in temperature and moisture as microbes in a cold-dry environment. It is often suggested that sensitivity of microbial communities generally decreases with increasing mean annual temperature and rainfall (e.g. Kirschbaum 1995). This may be why turnover was similar across 82 sites of different annual temperature (Giardina and Ryan 2000). Indeed, both the population and metabolism of the microbial population changes with water content (e.g. Sulkava *et al.* 1996), and microbes may adapt to the variations in the frequency of wetting and drying cycles (Paul *et al.* 1999).

## Conclusion

Further work is required to test whether or not significant improvements can be made to prediction of decomposition by having: (i) different  $T_m$  and/or  $W_m$  functions for soil organic matter pools of differing substrate quality, or (ii) an allowance for adaptation to climate. Perhaps the most important issue relating to 'scaling-up' the application of the  $T_m$  and  $W_m$  functions is to ensure that these functions have been calibrated using data obtained from a wide range of soil types or appropriate depth. If  $T_m$  and  $W_m$  functions are also to be applied to litter decomposition algorithms, additional calibration will be required since microbial sensitivity to temperature and water are unlikely to be the same in litter as in soil.

## Acknowledgments

John Carter, Marc Corbeels, Peter Grace, Rod Keenan, Miko Kirschbaum, Andrew Moore, Dave Pepper, Merv Probert, Richard Simpson are thanked for their help in preparing this paper. Partap Khanna, Tony O'Connell, Phil Polglase, Philip Smethurst and are also thanked for the use of their unpublished data.

## References

- Comins, H.N., and McMurtrie, R.E. (1993). Long-term response of nutrient-limited forests to CO<sub>2</sub> enrichment: Equilibrium behavior of plant-soil models. *Ecological Applications*, 3: 666-681.
- Cooksley, D.G., Prinsen, J.H., Paton, C.J., Lisle, A.T. (1993). Rate of decomposition and release of nutrients for litter in a *Heteropogon contortus-Bothriochloa bladhii* dominant native pasture. Proceedings of the XVII International Grasslands Congress. pp. 1557-1559.
- Giardina, C.P., Ryan, M.G. (2000). Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, 404: 858-861.
- Goncalves, J.L.M., Carlyle, J.C. (1994). Modelling the influence of moisture and temperature on net nitrogen mineralization in a forested sandy soil. *Soil Biology Biochemistry*, 26: 1557-1564.
- Grace, P.R., Georgis, K., Reeves, T.G., Altston, A. (2001). Simulating changes in soil organic carbon in cropping systems of the semi-arid Mallee region of Australia. *Agricultural Systems*. In Press.
- Jenkinson, D.S. (1990). The turnover of organic carbon and nitrogen in soil. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*; 329:p361-368
- Jenkinson, D.S., Adams, D.E., Wild, A. (1991). Model estimates of CO<sub>2</sub> emissions from soil in response to global warming. *Nature*, 351: 304-306.
- Kirschbaum, M.U.F., 1995. The temperature dependence of soil organic matter decomposition and the effect of global warming on soil organic carbon storage. *Soil Biology and Biochemistry* 27, 753-760.
- Kirschbaum, M.U.F., 2000a. Will changes in soil organic matter act as a positive or negative feedback on global warming? *Biogeochemistry* 48, 21-51.
- Kirschbaum, M.U.F., 2000b. CenW: a generic forest growth model that links carbon, nutrient and water cycles. *New Zealand Journal of Forestry* 45, 15-19.
- Leiros, M.C., Trasar-Cepeda, C., Seoane, S., Gil-Sotres, F. (1999). Dependence of mineralization of soil organic matter on temperature and moisture. *Soil Biology Biochemistry*, 31: 327-335.
- Lloyd, J., Taylor, J.A. (1994). On the temperature dependence of soil respiration. *Functional Ecology*, 8: 315-323.
- McCaskil, MR, and Blair, GJ. (1990). A model of S, P and N uptake by perennial pasture. Model construction. *Fertilizer Research*, 22: 161-172.
- Moorhead, D.L., Reynolds, J.F. (1991). A general model of litter decomposition in the northern Chihuahuan Desert. *Ecological Modelling*, 56: 197-219.
- Moorhead, D.L., Currie, W.S., Rastetter, E.B., Parton, W.J., Harmon, M.E. (1999). Climate and litter quality controls on

- decomposition: An analysis of modelling approaches. *Global Biogeochemical cycles*, 13: 575-589.
- Rodrigo, A., Recous, S., Neel, C., Mary, B. (1997). Modelling temperature and moisture effects on C-N transformations in soils: comparison of nine models. *Ecological Modelling*, 102: 325-339.
- Probert, M.E., Dimers, J.P., Keating, B.A., Dalal, R.C., Strong, W.M. (1998). APSIM's water and nitrogen modules and simulation of the dynamics of water and nitrogen in fallow systems. *Agricultural Systems*, 56, 1-28.
- Paul K I, Black A S and Conyers MK 1999 Influence of moist-dry cycles on pH changes in surface soils. *Australian Journal of Soil Research*, 37: 1057-1072.
- Parton WJ; Schimel DS; Cole CV, and Ojima DS. (1987). Analysis of factors controlling soil organic matter levels in Great Plains Grasslands. *Soil Science Society of America Journal*, 51: 1173-1179.
- Parton, WJ, Schimel, D.S., Ojima, D.S., Bryant, R.B., and Arnold, R.W., (1994). A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. Quantitative modeling of soil forming processes: proceedings of a symposium sponsored by Divisions S-5 and S-9 of the Soil Science Society of America in Minneapolis, Minnesota, USA, 2 Nov. 1992. Madison, USA: Soil Science Society of America Inc.; pp. p147-167.
- Quemada, M., Cabrera, M.L. (1997). Temperature and moisture effects on C and N mineralization from surface applied clover residue. *Plant and Soil*, 189: 127-137
- Sierra, J. (1997). Temperature and soil moisture dependence of N mineralization in intact soil cores. *Soil Biology Biochemistry*, 27: 1557-1563.
- Sulkava, P., Huhta, V., Laakso, J. (1996). Impact of soil faunal structure on decomposition and N-mineralisation in relation to temperature and moisture in forest soil. *Pedobiologia*, 40: 505-513.
- Vigil, M.F., Kissel, D.E. (1995). Rate of nitrogen mineralized from incorporated crop residues as influenced by temperature. *Soil Science Society of America Journal*, 59: 1636-1644.
- Wang, Y.P., Polglase, P.J. (1993). Carbon balance in the tundra, boreal forest and humid tropical forest during climate change: scaling up from leaf physiology and soil carbon dynamics. *Plant, Cell and Environment*, 18: 1226-1244.
- Zou, C., Sands, R. Buchan, G. Hudson, I. (2000) Least limiting water range: a potential indicator of physical quality of forest soil. *Australian Journal of Soil Research*, 38: 947-958.

# Soil Texture Effects on Decomposition and Soil Carbon Storage

---

Evelyn Krull, Jeff Baldock and Jan Skjemstad  
CRC for Greenhouse Accounting  
CSIRO Land and Water

## Introduction

---

The biological stability of soil organic carbon (SOC) is influenced by the chemical structure of SOC and the existence of various mechanisms of protection offered by soil minerals and their spatial arrangement within the soil matrix (Baldock and Skjemstad, 2000). In addition to defining the potential availability of SOC to decomposer organisms living in soils, the chemical structure of SOC also defines the strength with which mineral and organic soil components interact. The degree of physical protection of SOC is mainly a factor of soil texture, specific mineral surface area, and soil mineralogy. However, other soil parameters (e.g. water holding capacity, pH, porosity) can act as rate modifiers in attaining the protective capacity, set by the mineral matrix of the soil. Therefore, maximum protective capacity can only be achieved under "ideal" conditions because other soil properties, together with the parameters established by the soil mineral matrix, affect whether carbon will accumulate in soil up to its maximum capacity. Thus, a realistic assessment of the degree of protection of SOC by soil minerals is possible only through a collective analysis of the individual physical, chemical, and textural properties of a soil. Bearing these limitations in mind, the aim of this paper was threefold:

- 1 to review the 3 major controls of physical protection of SOC in soil (1. chemical nature of the soil mineral fraction, 2. physical nature of soil mineral fraction, and 3. architecture of soil matrix)
- 2 to examine the concept that soils have a maximum protective capacity, and
- 3 to briefly evaluate the parameters used to account for the physical protection of SOC in several current soil carbon cycling simulation models.

## Chemical nature of the soil mineral fraction: the importance of clays and cations

---

A comparison of the organic C contents of different types of mineral soils indicates that the presence of multivalent cations such as Ca (as Ca-containing minerals or exchangeable cation), Al or Fe (as amorphous Al and Fe minerals) leads to accumulations of organic C in comparison to other soil types (Spain *et al.* 1983, Oades 1988, Sombroek *et al.* 1993). Studies by Spain *et al.* (1983) and Oades (1988) demonstrated a positive relationship between soil organic C contents and either high base status or the presence of substantial contents of Al and Fe oxides. Particularly the presence of reactive CaCO<sub>3</sub> in soils has been shown to lead to a biological stabilization of both particulate organic carbon (POC) and humus (Duchaufour, 1976). The mechanisms for stabilization of SOC by addition of Ca include precipitation of thin carbonate coatings, particularly on fresh residues, and the formation of Ca-organic linkages on more decomposed humus. Stabilization of OC in high base status soils with less reactive CaCO<sub>3</sub> must result primarily from the formation of Ca-organic linkages. The ability of a source of Ca<sup>2+</sup> cations to protect soil organic matter from mineralisation has been well demonstrated. Sokoloff (1938) showed that addition of salts containing Ca reduced the solubility and mineralisation of organic C relative to the addition of either no salt or Na<sup>+</sup> salts. Muneer and Oades (1989c) also observed a decreased solubility of SOC on addition of Ca<sup>2+</sup> salts, and additional studies (Linhares 1977, Muneer and Oades 1989a,b) have noted a decreased mineralisation of C from an added substrate or native organic matter on addition of salts containing Ca to soils.

Studies by Juste and Delas (1970), Juste *et al.* (1975), Gaiffe *et al.* (1984), and Nelson *et al.* (1996) showed that most of the protection was due to the formation of Ca-organic linkages rather than from indirect effects of Ca<sup>2+</sup> on colloidal dispersibility. Positively charged Ca<sup>2+</sup> cations are assumed to provide bridges between negatively charged organic functional groups or between negatively charged clay surfaces and negatively charged organic groups (Sollins *et al.*, 1996).

Soils derived from volcanic ash (Andisols) are characterized by large accumulations of organic C with mean SOC contents of 25.4 kg m<sup>-2</sup> in the upper 100 cm (Batjes, 1996). Such large accumulations of organic matter are commonly explained by the protection of SOM by allophane (Mizota and Van Reeuwick, 1989). The source of the Al may be Al<sup>3+</sup>, Al-hydroxy cations or terminal Al atoms available for bonding within allophanic minerals. However, even non-allophanic andisols (pH < 5) show high accumulation of organic matter, suggesting that protection involves not only Al-containing allophanic clays but also organo-metallic complexes between Al<sup>3+</sup> and organic functional groups (Boudot *et al.*, 1988; Aran *et al.*, 2001). The ability of Al<sup>3+</sup>/Al-hydroxy cations to form biologically stable Al-organic complexes was demonstrated in incubation experiments where oxygen consumption and C mineralisation rates from a variety of Al and Fe saturated organic compounds were measured (Martin *et al.* 1966, Martin *et al.* 1972, Juste *et al.* 1975).

The role of allophanic minerals in protecting OC against biological attack was demonstrated in studies where C mineralisation was measured from allophanic soil, nonallophanic soil, and nonallophanic soil amended with allophane (Zunino *et al.* 1982, Boudot *et al.*, 1988, Boudot *et al.*, 1989). In each of these studies, mineralisation of C derived from added substrates was reduced by the presence of allophane. Zunino *et al.* (1982) also demonstrated that the chemical structure of the substrate contributed to the degree of biological stabilization imparted by the presence of allophane (Fig. 1). The role of Al-complexes in protecting SOC in non-allophanic andisols was demonstrated by Nanzyo *et al.* (1993) where high Al, non-allophanic andisols were able to protect a greater amount of OC than allophanic andisols and the degree of protection increased with increasing Al concentrations.

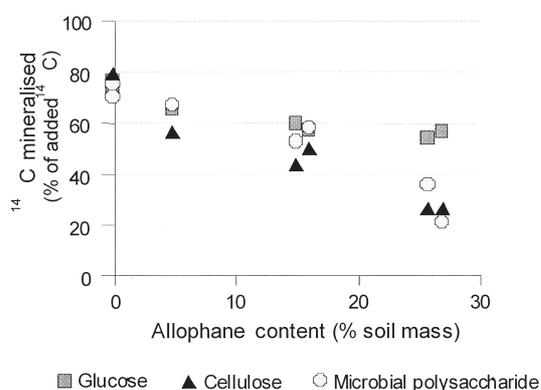


Fig. 1: Influence of allophane content on the amount of <sup>14</sup>C-labelled glucose, cellulose and microbial

polysaccharide carbon that was mineralised in a laboratory incubation (Zunino *et al.* 1982).

Apart from the direct effect of cations as bridging agents between SOC, multivalent cations can also indirectly impact the biological stability of OC in soils. Clay particles saturated with multivalent cations tend to remain in a flocculated state reducing the exposure and mineralisation of OC adsorbed on clay particle surfaces or existing as globules between packets of clays within a clay matrix. In addition, the three-dimensional orientation of organic macromolecules containing carboxyl functional groups may be altered in the presence of multivalent cations. The structures will become more condensed and the orientation of functional groups will be altered (Oades 1988). Such changes may alter the efficiency of enzymatic attack.

## Physical nature of the soil mineral fraction: the importance of surface area

The specific surface area (SSA) of soil mineral particles increases in progressing from large to small particles. Ransom *et al.* (1998) demonstrated the significant effect that even small amounts of high SSA (100 m<sup>2</sup> g<sup>-1</sup>) clay-size (<2 mm) material can have on the total SSA of mineral particle mixtures. The presence of 1 wt% of high-SSA clay in 1 mm diameter sand grains with a SSA of 0.001 m<sup>2</sup> g<sup>-1</sup>, increases total SSA by three orders of magnitude. To increase the SSA of 2-4 mm silt particles by 50% approximately 5 wt% of high-SSA clay is required. Thus, it becomes apparent that the presence of clay particles in soil provides the most significant surface area onto which OC may be adsorbed.

The mineralogy, surface charge characteristics, and precipitation of amorphous Fe and Al oxides on clay mineral surfaces defines the capacity of clay minerals to adsorb and potentially protect OC. However, it is important to note that surface charge varies among clay types. On hydroxylated surfaces (e.g. in kaolinite, sesquioxides and amorphous aluminosilicates) net surface charge varies and becomes progressively more negative with increasing pH. Clays with a permanent negative surface charge such as smectite, illite, and other layer silicate clays, are unaffected by pH (Sollins *et al.*, 1996). An important aspect to bear in mind is that sorption of OC has been studied dominantly on cleaned or artificially produced clays, whereas in the natural environment the surface properties and thus sorption capacity of clays may be altered by pre-existing amorphous

organomineral deposits (Sollins *et al.*, 1996). Sorption of negatively charged organic groups through cation bridging is probably the most common mechanism that allows for stabilization of organic matter against biological attack.

It is generally assumed that there is a positive correlation between clay content and preservation of SOC as documented in studies by Ladd *et al.* (1985), Schimel *et al.* (1985a,b), Spain (1990), Feller *et al.* (1991), Amato and Ladd (1992), and summarized by Oades (1989). Recent studies by Schønning *et al.* (1999) and Thomsen *et al.* (1999) reported differences in the rate of degradability of soil carbon which was strongly correlated with water holding capacity and volumetric water content. Furthermore, in a 6-year experiment by Saggar *et al.* (1996), monitoring the amount of residual  $^{14}\text{C}$ -labelled carbon in four mineralogically different soils, a strong correlation was found between the mean residence time of added  $^{14}\text{C}$  labeled C with specific surface area (SSA) but not with clay content (Fig. 2). In fact, the significance of SSA on the preservation of organic carbon has been documented in recent studies in marine sediments (Mayer 1994a,b, Keil *et al.* 1994). Ransom *et al.* (1998) demonstrated, by using data from Keil *et al.* (1994) from the Washington State continental margin, that TOC in the sediments was linearly related to SSA as well as to the content of high surface area minerals present (smectite + illite + opal). Furthermore, the low smectite sediments showed little variation in TOC with increasing SSA, whereas the high smectite sediments showed much larger variations in TOC. The linear but significantly different relationships obtained between clay-TOC and clay-SSA for each type of sediment mineralogy indicated that a relationship existed between SSA and protection of organic C, but that mineralogy exerted an additional control.

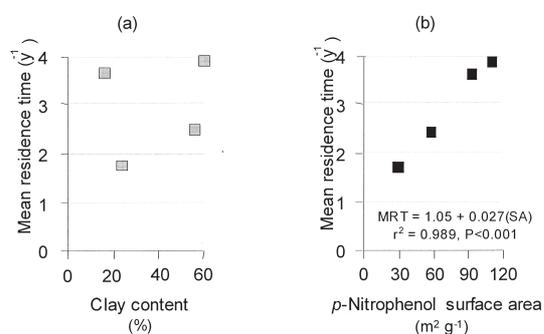


Fig. 2: Relationship between mean residence time of  $^{14}\text{C}$ -labelled ryegrass incubated for 6 years in soils with a variable mineralogy and (a) soil clay content and (b) soil surface area as determined by *p*-nitrophenol (Saggar *et al.* 1996).

Mayer (1994a,b) and Keil *et al.* (1994) proposed that the organic C associated with mineral grains in marine sediments existed as a monolayer spread evenly over the entire surface. Using transmission electron microscopy Ransom *et al.* (1997) showed that the organic matter existed in patches associated with and often encapsulated by mineral surfaces and was not uniformly spread over all surfaces. In experimental studies by Mayer (1999) he also reported a lack of homogenous dispersal of OM over mineral surfaces and instead thicker, isolated patches of organic matter. Subsequent work by Bock and Mayer (2000) showed that most of the surface area of clay particles is contained within small mesopores of  $< 10 \text{ nm}$  width, suggesting enclosure and protection of organic matter within intergranular pores.

## Architecture of the soil matrix: the importance of aggregates

The architecture of the soil mineral matrix refers to the arrangement of pores and soil particles. Almost all organic carbon in soil is located within pores between mineral grains either as discrete particles or as molecules adsorbed onto the surfaces of mineral particles. Soil architecture can influence the biological stability of organic materials through its effects on water and oxygen availability, entrapment and isolation from decomposers, and through the dynamics of soil aggregation.

The pore space of soil is composed of a continuum of pores ranging in size from micropores  $< 0.1 \text{ mm}$  in diameter through to macropores  $> 20 \text{ mm}$  with an upper size limit on the order of centimeters. Adequate quantities of available water and oxygen are required to optimize the processes of decomposition and mineralisation. With increasing water content, water becomes more available to decomposer organisms; however, oxygen availability decreases. An optimum air-filled porosity exists at which the processes of decomposition and mineralisation of OC will be optimized for a given soil (Fig. 3). Changes in the pore size distribution towards a greater proportion of large pores, such as noted in progressing from a clay to sand, are accompanied by higher rates of OC mineralisation at equivalent values of air filled porosity (Franzluebbers 1999) (Fig. 3).

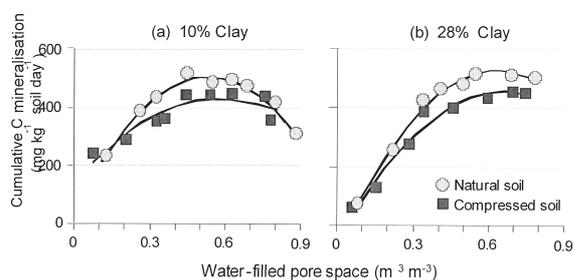


Fig. 3: Changes in mineralisation of C with changes in air-filled porosity and for uncompressed and compressed soils with (a) 10 % clay and (b) 28 % clay (modified from Franzleubbers 1999).

Most importantly, the pore size distribution of a soil also influences the ability of decomposer organisms to reach potential organic substrates. Kilbertus (1980) suggested that bacteria can only enter pores >3 mm. Within pore sizes less than this lower limit, decomposition of OC can only occur via diffusion of extracellular enzymes away from organisms towards a substrate and then diffusion of the products of enzyme reactions back to the organisms. With increasing clay content, the proportion of the total porosity found in small pores increases, and the potential stabilisation of OC against biological attack due to the exclusion of decomposer organisms increases. Van der Linden *et al.* (1989) showed that protozoa and nematodes are excluded from pores <5 mm and <30 mm, respectively. Thus OC residing in pores smaller than these diameters in the form of molecules, small particles, or bacterial or fungal tissues will not be susceptible to decomposition or predation by soil fauna.

Scanning electron micrographs of clay-organic matrices in soil indicate that OC is not uniformly distributed in soil matrices and that much of the OC is not in direct contact with or intimately associated with mineral surfaces. OC can exist as discrete particles, masses of amorphous materials typified by the mucilage exuded by microorganisms, or individual molecules adsorbed to mineral particles (Ladd *et al.* 1993, Ransom *et al.* 1997). Thus, encapsulation of OC by flocculation of clay particles, adsorption of mineral particles around organic particles, or formation of stable aggregates will influence the biological stability of OC as it places a physical barrier between potential substrates and decomposer organisms or their extracellular enzymes. Encapsulation can occur at size scales ranging from nanometres (e.g. encapsulation of OC into pores between packets of clay particles) to centimeters (e.g. encapsulation of a piece of plant residue by mineral particles).

Soil mineral particles are typically bound together into larger secondary particles referred to as aggregates. Chemical, microbial, plant, and physical processes affect the degree of soil aggregation. Microbes and soil animals promote aggregation by excreting binding agents and forming fecal pellets (Lynch and Bragg, 1985) and root exudates may flocculate colloids to bind or stabilize aggregates (Glinski and Lipiec, 1990). The intimate association between mineralogy, aggregation, and protection of organic matter is suggested by the observation that Fe-oxide rich soils and allophanic soils constitute the most firmly micro-aggregated soils (Churchman and Tate, 1986, 1987) and that aggregation increased and C mineralisation decreased with the addition of  $\text{Ca}^{2+}$  (Muneer and Oades, 1989a,b).

Soil aggregation is a transient property and aggregates are continually being formed and destroyed. The protection of OC against biological attack by encapsulation within an aggregate will be greatest where aggregate stability is high and aggregate turnover is low. Amelung and Zech (1996) demonstrated the influence of aggregation on the biological stability of OC. OC buried within aggregates was associated with organic materials having a higher C/N ratio, higher content of less biologically altered lignin, and a higher content of neutral sugars than OC associated with the 0–0.5 mm external layer of aggregate surfaces.

## Maximum capacity of soils to protect organic matter

The three mechanisms involved in the protection of OC against biological attack in soil are determined by the mineralogy and size distribution of soil mineral particles. For each mechanism, only a finite amount of OC can be protected (e.g. Hassink, 1996; Hassink *et al.*, 1997). As a result, each soil will have a finite capacity to protect OC against biological attack. The proportion of OC added to a soil that can be protected will depend on the extent of saturation of the protective capacity. In soils where the protective capacity is not saturated, further additions of OC will increase soil OC contents. Where the protective capacity is saturated, OC added to the soil will remain in a biologically available form, be mineralized provided the appropriate suite of decomposer organisms and environmental conditions are present, and contribute little to soil OC content.

It is important to recognise that protection rarely equates to a permanent and complete removal of OC from the decomposing pool, but rather equates to a reduction in the rate of decomposition relative to the same form of OC existing in an

unprotected state. One exception to this generalization may be the potential trapping of OC within the interlayer spaces of layer silicate clay minerals (Theng *et al.* 1986). As protected OC is slowly mineralized, its position in the protected pool is filled with new OC provided a source of the correct type of OM exists.

## Physical protection in soil carbon models

The soil carbon simulation models that will be examined in this paper include APSIM, Soil Carbon Manager/SOCRATES, CENTURY, CenWY, and ROTH-C. All of the models include algorithms that attempt to account for the influence of soil texture on OC mineralisation, and thus SOC protection, in a direct (as individual parameters such as clay content) or indirect way (included within other parameters, such as rate of produced CO<sub>2</sub>).

APSIM ([www.apsim-help.tag.csiro.au](http://www.apsim-help.tag.csiro.au)) does not consider directly the physical parameters of the soil and consists of only two SOM pools: BIOM (organic carbon associated with the labile soil microbial biomass and microbial products) and HUM (remaining SOC). It is assumed that some of the HUM pool, which is specified at initialization as the amount of inert carbon, is not subject to mineralisation. This inert carbon is similar to the "passive pool" in other models, such as CENTURY, and is considered the most recalcitrant fraction that remains after long periods of decomposition (Probert *et al.*, 1998). In order to adjust for soil texture effects on rate of decomposition, the proportion of HUM that includes inert C would need to be manipulated. This is a somewhat unsatisfactory solution because:

- 1 the user has to gather substantial information about the protective capacities of a soil to decide on an appropriate adjustment of inert carbon (alternatively, the user might be tempted into "making the curve fit" by "blindly" adjusting the inert carbon to achieve the desired outcome),
- 2 physical protection of OC is not equivalent to an inert carbon pool as it is a transient phenomenon that can include relatively labile OC and in turn is also subject to destabilization and release of SOC (Baldock and Skjemstad, 2000),
- 3 physical protection is highly depended on attributes such as water holding capacity, clay content, and mineralogy, which have to be taken into account.

By comparison, SOCRATES does not use an inert pool whereas its successor (Soil Carbon Manager) includes an inert or

charcoal pool. Soil Carbon Manager directly attempts to model SOM protection by including clay content, CEC or soil texture parameters, which alter the decay rate of the labile carbon pools and determine how much carbon is released as CO<sub>2</sub> and how much goes into the humus (stable) and microbial biomass pools (regression relationship between organic recycling and CO<sub>2</sub> evolution based on the CEC vs CO<sub>2</sub>/biomass data of Amato and Ladd (1992) and Ladd *et al.* (1995). A greater amount of clay (or higher CEC) is considered to physically "protect" SOM and is calculated by estimating a value "pcorg" from CEC of the soil. When % clay or texture (clay, silty clay, sandy loam, etc.) is entered, CEC is calculated from the empirical formula

$$\text{CEC} = 11.46 * \text{clay \%} - 51.3$$

$$\text{If CEC is } > 100, \text{pcorg} = (0.04 * \text{CEC} + 34.4)/100$$

$$\text{If CEC is } < 100, \text{pcorg} = (0.14 * \text{CEC} + 15.0)/100$$

These calculations allow for a more direct estimate of the physical protection of OC if the amount of clay is considered to be a reliable estimate. As outlined in this paper, clay content by itself might not fully describe protection of SOC but these parameters together with climatic data probably allow for a reasonable approximation.

The latest version of the CENTURY model (Century 5) also accounts for protection of SOC by including site parameters for texture for each soil layer (e.g. SAND (1...10), SILT (1...10)) which influences the turnover rate of the active SOC and the efficiency of stabilizing active SOC into slow SOC. Century 5 also accounts for changes in texture due to erosion and deposition events as well as for homogenization with cultivation, which is related to the degree of disturbance and therefore to rate of decomposition.

CenW accounts for decomposition rates by using a modified formulation based on the original CENTURY model, which includes an input variable for soil texture (Kirschbaum, 1999, 2000).

Roth-C 26.3 does not adjust for soil texture by using a rate modifying factor but by altering the partitioning between CO<sub>2</sub> evolved and the sum of BIO and HUM formed during decomposition. The ratio CO<sub>2</sub>/(BIO + HUM) = x is calculated from the clay content of the soil:

$$X = 1.67 (1.85 + 1.60 \exp(-0.0786 \% \text{clay}))$$

This function results in an asymptotic decline of CO<sub>2</sub> with increasing clay content, approaching equilibrium at 30% clay content. It is worthwhile noting that this equation differs from the one given in Jenkinson (1990), which preferably uses CEC

instead of clay content to account for differences in kaolinitic vs smectitic clay.

To conclude, the incorporation of physical protection of SOC in most soil models is only dealt with in a simplified way as clay content or CEC. Furthermore, there is no feedback mechanism included from other parameters such as water content or pH, which would enhance or reduce the protective mechanism, nor is the finite protective capacity of soil addressed. Unfortunately, models that tried to include physical protection in a more detailed way (such as the Verberne model: Verberne *et al.*, 1990; Whitmore *et al.*, 1997) do not achieve comparably good results as for example CENTURY or Roth-C (Smith *et al.*, 1997). Future models might benefit in their estimate of physical protection by including feedback mechanisms that acknowledge the intimate relationships that define the physical protective capacity of soil, namely water holding capacity, specific surface area, and clay content.

## References

- Amato, M.A. Ladd, J.N., 1992. Decomposition of <sup>14</sup>C-labelled glucose and legume material in soils: properties influencing the accumulation of organic residue C and microbial biomass C. *Soil Biology and Biochemistry* 24, 455-464.
- Amelung, W., Zech, W., 1996. Organic species in ped surface and core fractions along a climosequence in the prairie, North America. *Geoderma* 74, 193-206.
- Aran, D., Gury, M., and Jeanroy, E., 2001. Organo-metallic complexes in an Andosol: a comparative study with a Cambisol and Podzol. *Geoderma* 99, 65-79.
- Baldock, J.A., Skjemstad, J.O., 2000. Role of the soil matrix and minerals in protecting natural organic materials against. *Organic Geochemistry* 31, 697-710.
- Batjes, N.H., 1996. Total carbon and nitrogen in the soils of the world. *European Journal of Soil Science* 47, 151-163.
- Bock, M.J., Mayer, L.M., 2000. Mesodensity organo-clay associations in a near-shore sediment. *Marine Geology* 163, 65-75.
- Boudot, J.P. Bel Hadi Brahim, A., Chone, T., 1988. Dependence of carbon and nitrogen mineralisation rates upon amorphous metallic constituents and allophanes in highland soils. *Geoderma* 42, 245-260.
- Boudot, J.P., Bel Hadi Brahim, A., Steiman, R., Seigle-Murandi, F., 1989. Biodegradation of synthetic organo-metallic complexes of iron and aluminium with selected metal to carbon ratios. *Soil Biology and Biochemistry* 21, 961-966.
- Churchman, G.J., Tate, K.R., 1986. Aggregation of clay in six New Zealand soil types as measured by disaggregation procedures. *Geoderma* 37, 207-220.
- Churchman, G.J., Tate, K.R., 1987. Stability of aggregates of different size grades in allophonic soils from volcanic ash in New Zealand. *Journal of Soil Science* 38, 19-27.
- Duchauffour, P., 1976. Dynamics of organic matter in soils of temperate regions: its action on pedogenesis. *Geoderma* 15, 31-40.
- Feller, C., Fritsch, E., Poss, R., Valentin, C., 1991. Effets de la texture sur le stockage *et al.* dynamique des matieres organique dans quelque sols ferrugineux et ferrallitiques (Afrique de l'Ouest, en particulier). *Cahiers ORSTOM, Serie Pedologie* 26, 25-36.
- Franzleubbers, A.J., 1999. Microbial activity in response to water-filled pore space of variably eroded southern Piedmont soils. *Applied Soil Ecology* 11, 91-101.
- Gaiffe, M., Duquet, G., Tavant, H., Tavant, Y., Bruckert, S., 1984. Stabilité biologique et comportement physique d'un complet argilo-humic placé dans différentes condition de saturation en calcium ou en potassium. *Plant and Soil* 77, 271-284.
- Glinski, J., Lipiec, J., 1990. Soil physical conditions and plant roots. CRC Press, Boca Raton, FL.
- Hassink, J., 1996. Preservation of plant residues in soil differing in unsaturated protective capacity. *Soil Science Society of America Journal* 60, 487-491
- Hassink, J., Whitmore, A.P., Kubát, J., 1997. Size and density fractionation of soil organic matter and the physical capacity of soils to protect organic matter. *European Journal of Agronomy* 7, 189-199.
- Jenkinson, D.S., 1990. The turnover of organic carbon and nitrogen in soil. *Philosophical Transactions of the Royal Society of London B* 329, 361-368.
- Juste, C. Delas, J., 1970. Comparaison par une méthode respirométrique, des solubilités biologiques d'un humate de calcium et d'un humate de sodium. *Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences, D* 270, 1127-1129.
- Juste, C., Delas, J., Langon, M., 1975. Comparaison de la stabilité biologique de différents humates métalliques. *Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences, D* 281, 1685-1688.

- Keil, R.G., Tsamakis, E., Fuh, C.B., Giddings, C., Hedges, J.J., 1994. Mineralogical and textural controls on the organic composition of coastal marine sediments: Hydrodynamic separation using SPLITT-fractionation. *Geochemica et Cosmochimica Acta* 58, 879-893.
- Kilbertus, G., 1980. Microhabitats in soil aggregates. Their relationship with bacterial biomass and size of procaryotes present. *Revue d'Ecologie et de Biologie du Sol* 17, 543-557.
- Kirschbaum, M.U.F., 1999. CenW, a forest growth model with linked carbon, energy, nutrient and water cycles. *Ecological Modelling* 181: 17-59.
- Kirschbaum, M.U.F., 2000. CenW: a generic forest growth model that links carbon, nutrient and water cycles. *New Zealand Journal of Forestry* 45: 15-19
- Ladd, J.N., Amato, M., Oades, J.M., 1985. Decomposition of plant materials in Australian soils. III Residual organic and microbial biomass C and N from isotope-labelled legume materials and soil organic matter decomposing under field conditions. *Australian Journal of Soil Research* 23, 603-611.
- Ladd, J. N., Foster, R.C., Skjemstad, J.O., 1993. Soil structure: carbon and nitrogen metabolism. *Geoderma* 56, 401-434.
- Ladd, J.N., Amato, M., Grace, P.R., Van Veen, J.A., 1995. Simulation of  $^{14}\text{C}$  turnover through the microbial biomass in soils incubated with  $^{14}\text{C}$ -labelled plant residues. *Soil Biology and Biochemistry* 27, 777-783.
- Linhares, M., 1977. Contribution de l'ion calcium à la stabilisation biologique de la matière organique des sols. Thèse Doc. Spéc., Université de Bordeaux III.
- Lynch, J.M., Bragg, E., 1985. Microorganisms and soil aggregate stability. *Australian Journal of Soil Research* 27, 411-423
- Martin, J.P., Ervin, J.O., Shepard, S.J., 1966. Decomposition of the iron, aluminium, zinc, and copper salts or complexes of some microbial and plant polysaccharides in soils. *Soil Science Society of America Proceedings* 30, 196-200.
- Martin, J.P., Ervin, J.O., Richards, S.J., 1972. Decomposition and binding action of some mannose containing microbial polysaccharides and their Fe, Al, Cu, and Zn complexes. *Soil Science* 113, 322-327.
- Mayer, L.M., 1994a. Surface area control of organic carbon accumulation in continental shelf sediments. *Geochimica et Cosmochimica Acta* 58, 1271-1284.
- Mayer, L.M., 1994b. Relationships between mineral surfaces and organic carbon concentrations in soils and sediments. *Chemical Geology* 114, 347-363.
- Mayer, L.M., 1999. Extent of coverage of mineral surfaces by organic matter in marine sediments. *Geochim. Cosmochim. Acta* 63, 207-215.
- Mizota, C., Van Reeuwijk, L.P., 1989. Clay mineralogy and chemistry of soils formed under volcanic material in diverse climatic regions. *Soil Monograph* 2, ISRIC, Wageningen.
- Muneeer, M., Oades, J.M., 1989a. The role of Ca-organic interactions in soil aggregate stability. 1. Laboratory studies with  $^{14}\text{C}$ -glucose,  $\text{CaCO}_3$ ,  $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ . *Australian Journal of Soil Research* 27, 389-399.
- Muneeer, M., Oades, J.M., 1989b. The role of Ca-organic interactions in soil aggregate stability. 2. Field studies with  $^{14}\text{C}$ -labelled straw,  $\text{CaCO}_3$ ,  $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ . *Australian Journal of Soil Research* 27, 401-409.
- Muneeer, M., Oades, J.M., 1989c. The role of Ca-organic interactions in soil aggregate stability. 3. Mechanisms and models. *Australian Journal of Soil Research* 27, 411-423.
- Nanzyo, M., Dahlgren, R., and Shoji, S., 1993. Chemical characteristics of volcanic ash soils. In: Nanzyo, M., Dahlgren, R., and Shoji, S., eds., *Volcanic Ash Soils. Genesis, Properties and Utilisation*. Dev. Soil Sci. 21 Elsevier, Amsterdam, Netherlands, 145-187.
- Nelson, P.N., Ladd, J.N., Oades, J.M., 1996. Decomposition of  $^{14}\text{C}$ -labelled plant material in a salt affected soil. *Soil Biology and Biochemistry* 28, 433-441.
- Oades, J.M., 1988. The retention of organic matter in soils. *Biogeochemistry* 5, 35-70.
- Oades, J.M., 1989. An introduction to organic matter in mineral soils. In Dixon, J.B., Weed, S.B. (Ed.) *Minerals in Soil Environments*, 2<sup>nd</sup> Edition. Soil Science Society of America, Madison, WI, USA. pp. 89-159
- Probert, M.E., Dimes, J.P., Keating, B.A., Dalal, R.C., and Strong, W.M., 1998. APSIM's water and nitrogen modules and simulation of the dynamics of water and nitrogen in fallow systems. *Agricultural Systems* 56, 1-28.
- Ransom, B., Bennett, R.H., Baerwald, R., 1997. In situ organic matter in recent marine sediments: A TEM investigation of organic matter preservation on continental margins and the monolayer hypothesis. *Marine Geology* 138, 1-9.
- Ransom, B., Kim, D., Kastner, M., Wainwright, S., 1998. Organic matter preservation on continental slopes: Importance of mineralogy and surface area. *Geochimica et Cosmochimica Acta* 62, 1329-1345.
- Saggar, S., Parshotam, A., Sparling, G.P., Feltham, C.W., Hart, P.B.S., 1996.  $^{14}\text{C}$ -labelled ryegrass turnover and residence

- times in soils varying in clay content and mineralogy. *Soil Biology and Biochemistry* 28, 1677-1686.
- Schimel, D.S., Coleman, D.C., Horton, K.A., 1985a. Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. *Geoderma* 36, 201-214.
- Schimel, D.S., Stillwell, M.A., Woodmansee, R.G., 1985b. Biogeochemistry of C, N, and P in a soil catena of the short grass steppe. *Ecology* 66, 276-282.
- Schjønning, P., Thomsen, I.K., Møberg, J.P., de Jonge, H., Kristensen, K., Christensen, B.T., 1999. 1. Turnover of organic matter in differently textured soils: I. Physical characteristics of structurally disturbed and intact soils. *Geoderma* 89, 177-198.
- Smith, P., Smith, J.U., Powlson, D.S., McGill, W.B., Arah, J.R.M., Chertov, O.G., Coleman, K., Franko, U., Frolking, S., Jenkinson, D.S., Jensen, L.S., Kelly, R.H., Klein-Gunnewick, H., Komarov, A.S., Li, C., Molina, J.A.E., Mueller, T., Parton, W.J., Thornley, J.H.M., Whitmore, A.P., 1997. A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. *Geoderma* 81, 153-225.
- Sokoloff, V.P., 1938. Effect of neutral salts of sodium and calcium on carbon and nitrogen in soils. *Journal of Agricultural Research* 57, 201-216.
- Sollins, P., Homann, P., and Caldwell, B.A., 1996. Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma* 74, 65-105
- Sombroek, W.G., Nachtergaele, F.O., Hebel, A., 1993. Amounts, dynamics and sequestering of carbon in tropical and subtropical soils. *Ambio* 22, 417-426.
- Spain, A., 1990. Influence of environmental conditions and some soil chemical properties on the carbon and nitrogen contents of some Australian rainforest soils. *Australian Journal of Soil Research* 28, 825-839.
- Spain, A.V., Isbell, R.F., Probert, M.E., 1983. Soil organic matter. In *Soils, an Australian Viewpoint*. CSIRO, Melbourne, Australia/Academic Press, London, UK. pp. 551-563
- Theng, B.K.G., Churchman, G.J., Newman, R.H., 1986. The occurrence of interlayer clay-organic complexes in two New Zealand soils. *Soil Science* 142, 262-266.
- Thomsen, I.K., Schjønning, P., Jensen, B., Kristensen, K., Christensen, B.T., 1999. Turnover of organic matter in differently textured soils. II. Microbial activity as influenced by soil water regimes. *Geoderma* 89, 199-218.
- van der Linden, A.M.A., Jeurisson, L.J.J., Van Veen, J.A., Schippers, G., 1989. Turnover of soil microbial biomass as influence by soil compaction. In Attanssen, J., Henriksen, K. (Ed.) *Nitrogen in Organic Wastes Applied to Soil*. Academic Press, London, UK. pp. 25-36.
- Verberne, E.L.J., Hassink, J., de Willigen, P., Groot, J.J.R., van Veen, J.A., 1990. Modelling organic matter dynamics in different soils. *Netherlands Journal of Agricultural Science* 38, 221-238.
- Whitmore, A.P., Klein-Gunnewiek, H., Crocker, G.J., Klir, J., Körschens, M., Poulton, P.R., 1997. Simulating trends in soil organic carbon in long-term experiments using the Verberne/MOTOR model. *Geoderma* 81, 137-151.
- Zunino, H., Borie, F., Aguilera, S., Martin, J.P., Haider, K., 1982. Decomposition of <sup>14</sup>C-labeled glucose, plant and microbial products and phenols in volcanic ash-derived soils of Chile. *Soil Biology and Biochemistry* 14, 37-43.

# Acidic Soil pH, Aluminium and Iron Affect Organic Carbon Turnover in Soil

---

Dr Ram C Dalal  
CRC for Greenhouse Accounting  
Department of Natural Resources and Mines,  
Queensland

## Abstract

---

Turnover of organic matter (OM) in soil affects its distribution in different carbon pools, CO<sub>2</sub> (and other gases such as oxides of nitrogen) emissions to the atmosphere, and physical, chemical and biological effects on soil. Although temperature, soil moisture and the quality of carbon and nutrient input determine the overall organic carbon turnover in soil, soil matrix characteristics (such as clay content, aluminium and iron contents, and soil pH) moderate carbon turnover rates in soil. As the soil pH decreases, soil surfaces are increasingly occupied by organic carbon. Also, microbial activity decreases as pH decreases, resulting in overall decrease in organic carbon turnover in soil. Provided significant carbon inputs occur, decreasing soil pH in natural ecosystems results in increasing organic carbon in soil. However, if the carbon inputs are reduced such as in cropping systems, and as the organic C oxidises, more mineral surfaces are exposed, which are then get dissolved through protonation of aluminium and iron, thus creating further acidity and lower biomass productivity. Most affected soils by this process are Kandosols and Podosols. Below pH 6, the influence of soluble and exchangeable Al increases as pH decreases. In such an environment, Al forms Al-OM complexes through solubilization, condensation, precipitation, aggregation and occlusion, with decreasing turnover rates and increasing organic matter stability in soil.

Most current soil carbon dynamics models do not account for the effect of Al-OM complexation on C turnover in soil. In New Zealand, where Andosols form a major soil group, the quantity of pyrophosphate extractable Al is used as a surrogate for Al-OM complexes effects in soil C modelling. Soil pH effects are considered in GRAZPLAN but not in other models such as CENTURY and ROTH-C. A number of other models (APSIM, CenW and FullCAM) are essentially similar to the two latter models. It is suggested that in acidic soils, the effect of Al-OM complexation on C turnover must be quantified on C turnover

and such effects should be explicitly included in soil C models, which consider C dynamics in Andosols, Podosols, Kandosols, Ferrosols, and acidic Chromosols.

It is estimated that 29 million ha of mainly agricultural land is regarded as significantly acidified, at least in the topsoil layers. Thus, consideration of acidic soil pH and Al effects on C turnover (and nutrient dynamics) in soil C research and modelling is important for an accurate national greenhouse gas inventory in Australia.

## Introduction

---

In the terrestrial carbon cycle, organic matter (OM) in soil is a major sink and source of greenhouse carbon; for example, soil, vegetation, and atmosphere account for 2011 Gt C, 466 Gt C, and 760 Gt C, respectively (Watson *et al.* 2000). Drivers of soil carbon stocks and turnover are climate (temperature, precipitation, potential evapotranspiration, CO<sub>2</sub>, radiation, etc.), topography, vegetation, parent material (soil matrix characteristics) and time (Jenny 1941). The soil matrix affects C turnover in numerous ways, through soil moisture relationships, microbial associations and protection, and carbon protection and stabilisation.

Clay stabilises part of OM through clay-OM complexes and cation bonding (Oades 1995). For example, sorption of humic acid on illite, montmorillonite, and kaolinite varied with the cation added, decreasing in the order Al > Ca > Mg > K > Na (Varadachari *et al.* 1991). Acidic soil pH increases Al in the soil solution through dissolution of soil mineral surfaces, and solubilization and complexation of Al in the soil solution. It is suggested that soil Al occurs mainly as Al-OM complexes rather than as a constituent of clay and clay-like minerals (Boudot *et al.* 1988), and such interaction should reduce the soil C turnover. Parton *et al.* (1989) identified the limitations of the CENTURY model for C turnover in Ferrosols, Podosols and Andosols due to the lack of information on soil pH and Al effects on C turnover, and Al (and Fe) effects on organic matter formation, complexation and decomposition in soil.

It is estimated that 29 million ha of mainly agricultural land in Australia is regarded as significantly acidified, at least in the

surface layers (State of the Environment Advisory Council 1996). Thus, consideration of acidic soil pH and Al effects on C turnover (and nutrient dynamics) in soil C research and modelling is important for an accurate national greenhouse gas inventory in Australia. In this paper, we examine the effect of acidic soil pH and aluminium on carbon turnover in soil, and consideration of such effects in soil carbon modelling.

## Acidic soil pH effects

Soil pH affects microbial activity in soil as well as hydrolysis and protonation. Microbial activity is optimum in the range of pH 6 to pH 8. Similarly, wide range of proteolytic and carbon-compound degrading enzymes, both cellular and extra-cellular, are active within a similar pH range. Protonation causes solubilization and complexation of mineral-OM surfaces by controlling dissolution of mineral surfaces, sorption-desorption of organic C on mineral surfaces, precipitation, aggregation and occlusion.

## Microbial activity

Bacterial growth rates are generally more sensitive to low pH than fungal growth rates (Walse *et al.* 1998). Microbial biomass and lignin and cellulose decomposition appears to be not significantly affected by soil acidity at pH range of 4.5-6.5 (Donnelly *et al.* 1990). However, in acidic pH <4.5, microbial activity as well as nutrient turnover is greatly reduced (Santa 2000). The combined impact of H<sup>+</sup> and Al<sup>3+</sup> on microbial activity and OM decomposition could be modelled with ion exchange expression, such as Vanselow expression (Walse *et al.* 1998).

## Physico-chemical effects

Acidic soil pH dissolves Al and other metals from the mineral soil surfaces, which enter the soil solution. In Podosols, Al is mobilised in the alluvial horizons under the predominant influence of organic acidity, then leaches down the profile as organic bound Al, Al-OM complexes, where Al is apparently bound to bidentate organic sites (Nissinen *et al.* 1999). However, as the carbon input is maintained higher than carbon decomposition and loss due to lower microbial activity, soil mineral surfaces become increasingly occupied by carbon, thus reducing the dissolution of Al from mineral surfaces. Mayer and Xing (2001) found that the amount of C sorbed increased from

<1 mg m<sup>-2</sup> of soil surface above pH 5 to approximately 6 mg m<sup>-2</sup> at pH 3.5 (Fig. 1)

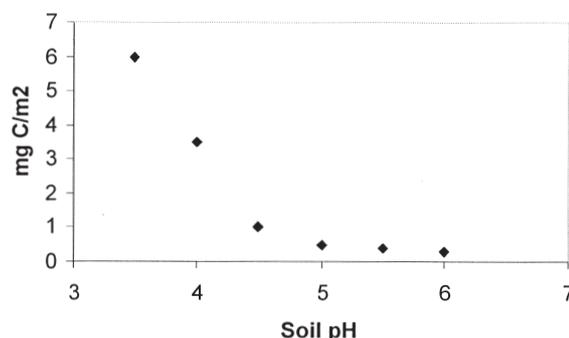


Figure 1. Effect of soil pH on carbon retained by soil surfaces (estimated from Mayer and Xing 2001).

Thus, at pH 3.5, almost 90% of the mineral surfaces could be covered by organic C (Fig. 2). Generally, occluding OM is present in a low-surface area configuration, such as organoclay aggregates, rather than as dispersed coatings on mineral soil surfaces (Mayer and Xing 2001).

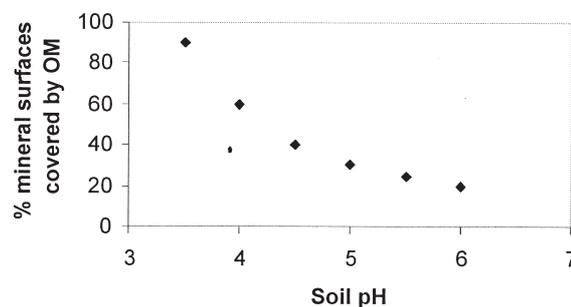


Figure 2. Percentage of all mineral surfaces covered by organic matter in soil (estimated from Mayer and Xing 2001).

The negative and positive charges of soil OM and Al and Fe compounds significantly influence aggregation of soil clays. Thus, as the soil's negative charge decreases with decreasing pH, especially in low activity clay and pH-dependent cation exchange capacity soils, aggregation becomes stronger, and C turnover rate decreases.

## Aluminium-Organic Matter Complexes

In acidic soils and Andosols, pyrophosphate extractable Al is correlated with organic matter; presumably as Al-OM complexes. Pyrophosphate extractable Al appears to originate

from the dissolution and dispersion of Al and Al hydroxides (and Fe hydroxides) associated with organic matter (Skjemstad 1992; Kaiser and Zech 1996; Sollins *et al.* 1996). Percival *et al.* (2000) found that pyrophosphate extractable Al strongly related to soil C across all soils in New Zealand grasslands.

The Al-OM complexes are formed through the processes of solubilization of Al and C, condensation, precipitation, and aggregation of Al-OM complexes and their occlusion within the soil matrix. The stability of Al-OM complexes increases as Al-OM complexes become aggregated and occluded within the soil matrix. Conversely, C turnover rate decreases as the extent of aggregation and occlusion of Al-OM complexes increases in soil.

Boudot (1992) showed that C mineralisation decreased as the Al: C ratio increased in Al-C complexes. Similarly, Tate (1992) found that soils with very high pyrophosphate extractable Al had very low soil C turnover, and it has been suggested that Al-OM complexes, as determined by pyrophosphate extraction should have a 25-year C turnover time (Veldkemp 1994).

At lower pH, Al is released from oxides, hydrous-oxides and mineral surfaces due to dissolution and then Al complexes with organic matter; O-alkyl sites are preferred over the alkyl sites. Stevenson (1982) listed the major Al-OM sites, in order of affinity, as follows: -C-OH > -NH<sub>2</sub> > -N=N- > -COOH > -C-O-C- >> -C=O. For aromatic C, Al-OM complexes are in the order of affinity: -COOH-OH > -OH-OH- > -COOH-COOH > -COOH (Tam and McColl 1990). Aluminium increases precipitation of not only Al-OM complexes but also increases their sorption and precipitation on other soil mineral surfaces. Moreover, Al (and Fe) forms polyvalent cationic bonding with OM and mineral surfaces and thereby increases aggregation (Oades 1995), for example in Andosols, Ferrosols, Kandosols and Chromosols. Aggregation is stabilised further through fungal activity, producing biopolyphenols and polysaccharides. Furthermore, Al-OM complexes become occluded within aggregates, high in clay such as in Podosols, whereas in low clay soils, mineral particles are occluded within Al-OM complexes.

However, refined analytical techniques are required which can differentiate in soil the range of Al-OM complexes (Kaiser and Zech 1996) before the C turnover rates could be studied. Currently, decomposition rates are inferred from analytical procedures since it is difficult to isolate intact Al-OM complexes (Salm *et al.* 2000)

The Al-OM complexes are disaggregated by mechanical disturbance, tree clearing and cultivation, loss in organic matter, accessibility to interaggregated OM and decreased input of

aggregate stabilisers. For example, Al: C ratio declines rapidly as the OM is lost from a pasture soil when it is converted to cropping. Unfortunately, turnover rates of carbon in such aggregates are not known since dynamics of these aggregates is poorly understood.

In summary, we know about Al-OM complexes from synthetic complexes such as Al-fulvic acid complexes, and Al-citrate complexes. There is an indirect evidence of Al-OM complexes in soil from regression analysis, pyrolysis and extraction procedures but little direct evidence of Al-OM turnover rates in soil. We know that Al-OM complexes are very important in Ferrosols, Andosols, Chromosols and Podosols, but they play an important role in C turnover in all soils. Hence, it is the least understood area in OM fluxes, both in terms of C inputs and C fluxes.

Soil carbon modelling needs to include pH and Al effects both on Net Primary Production and C turnover. Some progress to include pH effects has been made in GRAZPLAN (Moore *et al.* 1997; Andrew Moore, CSIRO Plant Industry, pers. comm.), Gendec (Moorhead and Sinsagaugh 2000) and APSIM (Probert *et al.* 1998) on nitrogen transformation but not explicitly on Al effects on C turnover. New Zealand soil C models consider pyrophosphate extractable Al in their C simulations to account for passive pool in ROTH-C, based on <sup>14</sup>C data of soil carbon (Kevin Tate, Manaaki Whenua Landcare Research, N.Z., pers. comm.) although explicit dynamic C turnover in Al-OM complexes is unknown.

For example, in the current version of the GRAZPLAN, soil pH affects C decomposition and nitrification processes. Decomposition rates are multiplied by a modifier in the range of 0 or 1 as follows:

$$\begin{aligned} Z(\text{pH}) &= 0 & \text{pH} \leq 3.2 \\ Z(\text{pH}) &= (\text{pH}-3.2)/(4.5-3.2) & 3.2 < \text{pH} \leq 4.5 \\ Z(\text{pH}) &= 1 & \text{pH} > 4.5 \end{aligned}$$

Nitrification rates are multiplied by a similar modifier as follows:

$$\begin{aligned} Z(\text{pH}) &= 0 & \text{pH} \leq 3.5 \\ Z(\text{pH}) &= (\text{pH}-3.5)/(6.0-3.5) & 3.5 < \text{pH} \leq 6.0 \\ Z(\text{pH}) &= 1 & 6.0 < \text{pH} \leq 8.5 \\ Z(\text{pH}) &= 1 - (\text{pH}-8.5)/(9.0-8.5) & 8.5 < \text{pH} \leq 9.0 \\ Z(\text{pH}) &= 0 & \text{pH} > 9.0 \end{aligned}$$

pH values are taken in 1:5 CaCl<sub>2</sub>. These functions are crude representations of the combined effects of pH and Al (Andrew

Moore and Richard Simpson, CSIRO Plant Industry, pers. comm.).

Since, Australia has an estimated 29 million ha of acidic soils, it is important to include the effects of pH and Al in C turnover in soil C modelling and research to improve the national greenhouse gas inventory as well as organic matter management in these soils.

## Acknowledgements

---

I am thankful to Andrew Moore and Kevin Tate for sharing their ideas and information on inclusion of pH and Al in soil C modelling.

## References

---

- State of the Environment Advisory Council (1996) Land resources. Pp.6: 31-32. *Australia State of the Environment 1996*. CSIRO Publishing, Collingwood, Victoria.
- Boudot JP (1992) Relative efficiency of complexed aluminium, non-crystalline Al hydroxides, allophane, and imogolite in retarding the biodegradation of citric acid. *Geoderma* **52**, 29-39.
- Boudot JP, Bel Hadj BA, Chone T (1988) Dependence of carbon and nitrogen mineralisation rates upon amorphous metallic constituents and allophanes in highland soils. *Geoderma* **42**, 245-260.
- Donnelly PK, Entry JA, Crawford DL, Cromack K Jr (1990). Cellulose and lignin degradation in forest soils: response to moisture, temperature, and acidity. *Microbial Ecology* **20**, 289-295.
- Jenny H (1941) 'Factors of soil formation'. (McGraw-Hill, New York.)
- Kaiser K, Zech W (1996) Defects in estimation of aluminium in humus complexes of podsol soils by pyrophosphate extraction. *Soil Science* **161**, 452-458.
- Mayer LM, Xing B (2001) Organic matter-surface area relationships in acid soils. *Soil Science Society of America Journal* **65**, 250-258.
- Moore AD, Donnelly JR, Freer M (1997) GRAZPLAN: decision support systems for Australian Grazing enterprises. III. Pasture growth and soil moisture sub models, and the GrassGro DSS. *Agricultural Systems* **55**,535-582.
- Moorhead DL, Sinsabaugh RL (2000) Simulated patterns of litter decay predict patterns of extracellular enzyme activities. *Applied Soil Ecology* **14**, 71-79.
- Nissinen A, Ilvesniemi H, Tanskanen N (1999) Equilibria of weak acids and organic Al complexes explain activity of H<sup>+</sup> and Al<sup>3+</sup> in a salt extract of exchangeable cations. *European Journal of Soil Science* **50**, 675-686.
- Oades JM (1995) Recent advances in organomineral interactions: implications for carbon cycling and soil structure. In 'Environmental impact of soil component interactions'. Vol. 1 (Eds PM Huang, J Berthelin, JM Bollag, WB McGill, AL Page) pp. 119-134. (Lewis Publishers: Boca Raton, FL)
- Parton WJ, Sanford RL, Sanchez PA, Stewart JWB, Bonde T, Crosley D, van Veen H, Yost R (1989) Modelling soil organic matter dynamics in tropical soils. In 'Dynamics of soil organic matter in tropical soils'. (Eds. DC Coleman, JM Oades, G Uehara) pp. 153-171. (University of Hawaii: Honolulu USA.)
- Percival HJ, Parfitt RL, Scott NA (2000) Factors controlling soil carbon levels in New Zealand grasslands: Is clay content important? *Soil Science Society of America Journal* **64**, 1623-1630.
- 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.
- Salm C van der, Westerveld JW, Verstraten JM (2000) Release rates of Al from inorganic and organic compounds in a sandy podsol, during laboratory experiments. *Geoderma* **96**, 173-198.
- Santa RI (2000) Biomass estimation and nutrient pools in four *Quercus pyrenaica* in Sierra de Gata Mountains, Salamanca, Spain. *Forest Ecology and Management* **132**, 127-141.
- Skjemstad JO (1992) Genesis of podzols on coastal dunes in southern Queensland: III. The role of aluminium-organic complexes in profile development. *Australian Journal of Soil Research* **30**, 645-665.
- Sollins P, Homann P, Caldwell BA (1996) Stabilization and destabilization of soil organic matter: Mechanisms and controls. *Geoderma* **74**, 65-105.
- Stevenson FJ (1982) 'Humus chemistry genesis, composition, reactions'. p. 339 (John Wiley & Sons: New York.)
- Tate KR (1992) Assessment, based on a climosequence of soil in tussock grasslands, of soil carbon storage and release in

- response to global warming. *Journal of Soil Science* **43**, 697-707.
- Tam SC, McColl JG (1990) Aluminium- and calcium-binding affinities of some organic ligands in acidic conditions. *Journal of Environmental Quality* **19**, 514-520.
- Varadachari C, Mondal AH, Ghosh K (1991) Some aspects of clay humus complexation: Effects of exchangeable cations and lattice charge. *Soil Science* **151**, 220-227.
- Veldkemp E (1994) Organic carbon turnover in three tropical soils under pasture after deforestation. *Soil Science Society of America Journal* **58**, 175-180.
- Walse C, Berg B, Sverdrup H (1998). Review and synthesis of experimental data on organic matter decomposition with respect to the effect of temperature, moisture, and acidity. *Environmental Reviews* **6**, 25-40.
- Watson RT, Noble IR, Bolin B, Ravindranath NH, Verardo DJ, Dokken DJ (2000) 'Land Use, Land-use Change, and Forestry: A Special Report of the IPCC'. (Cambridge University Press: Cambridge, U.K.)

# Charcoal and Other Resistant Materials

---

Jan Skjemstad  
CRC for Greenhouse Accounting  
CSIRO Land & Water

## Introduction

---

Most models dealing with the turnover of soil organic carbon include a soil carbon pool that is either inert or has a turnover time measured in centuries or millennia. The strongest evidence of the presence of such a pool or pools comes from radiocarbon dating of soils that shows that in some cases, even in surface horizons, the mean residence time (MRT) for organic carbon can exceed 1000 years (Anderson and Paul, 1984). Since modern carbon in the form of plant residues is constantly being added to active surface soils, these soils must contain some organic carbon which is much older than the MRT of the soil as a whole.

Several mechanisms for imparting resistance (recalcitrance) have been evoked. These mechanisms range from strong interaction with the mineral matrix (Hassink, 1997), chemical recalcitrance imparted through strong humification processes (Anderson and Paul, 1984) and the presence of significant quantities of finely-divided charcoal (Skjemstad et al., 1998). Despite the inclusion of inert or resistant pools in many models, few define the nature of this material (McGill, 1996). Some attempts have been made to measure these "old" resistant pools with varying degrees of success. All of these methods assume that chemical recalcitrance is the most significant factor for long-term protection. Clay content is included in many models and is considered to reduce decomposition rates, but only in respect to more active pools.

In this presentation, the role of the resistant/inert/recalcitrant pools in five specific models (APSIM, Century, CenW, RothC and SOCRATES) is discussed along with issues of measurement both by chemical and isotopic means.

## Models and Approaches

---

The five models considered and means by which a highly resistant pool is considered is given below.

- APSIM considers an inert carbon (INERT-C) pool which is uncoupled from soil carbon decomposition processes.

Profile distribution of OC has been used as an indicator of the size of the INERT-C pool.

- Century and CenW consider a passive or resistant pool, coupled to both the slow and active pools. Carbon flow from the slow and active pools to the passive pool is moderated by clay content, temperature and soil water while the decomposition of the passive pool is influenced only by temperature and soil water. The turnover time of the passive pool is in the order of 1000 years.
- The RothC and SOCRATES models also consider an inert organic matter (IOM) pool uncoupled from soil carbon decomposition processes. In the RothC model, the inert pool is considered to be radiocarbon "dead" with a turnover time of at least 50,000 years.

## Measurement of Resistant Pools

---

In almost all cases, the size of the resistant pool is determined by fitting the model to available site data or by regression. In some cases, estimates of the other pools are made and the resistant pool determined by subtraction. Radiocarbon dating has been used in conjunction with the RothC model to estimate the IOM pool. Here, an age is given to each of the pools and from the radiocarbon age of the total soil carbon, the contribution of each pool can be proportioned. In some cases, direct measurement or estimation of this pool has been attempted.

Estimates of the INERT-C pool of the APSIM model have been made using the total carbon in the deeper horizons of profiles. This assumes that the INERT-C of each horizon of the profile is relatively constant and that almost all the carbon in the lower profile is inert (Merv Probert pers. comm.). This approximation probably provides data of the correct magnitude and could be useful where no other information is available. It could however, clearly have difficulties in soils with complex profiles such as podzols and alluvial soils.

The passive pool of the Century model has been equated to the non-hydrolysable soil carbon fraction (Paul *et al.*, 1997). Acid hydrolysis (reflux with 6M HCl) effectively removes carbohydrate and protein materials, leaving largely intact the more biologically recalcitrant alkyl and aryl materials. Paul *et al.* (1997) demonstrated that, on average, the non-hydrolysable

carbon comprised between 23 and 70% of the soil carbon and was about 1500 years older than the bulk soil carbon.

Soil charcoal measurements have been used as estimates of the IOM pool in both the RothC and SOCRATES models (Skjemstad and Janik, 1996). Charcoal, measured by  $^{13}\text{C}$  NMR spectroscopy following photo-oxidation, seems to fit well with the IOM pools of these models and although charcoal would not be expected to be completely inert, its turnover would be expected to be at least as slow as the Century passive pool. The difference is that a charcoal pool would need to be uncoupled from the other soil carbon pools but would be directly influenced by the rate and mass of biomass burning.

## Controversies

---

### *Inert?*

A major issue with a number of the models discussed above is whether any organic based material can in fact be inert or even turn over in time spans of tens of millennia in a biologically active surface soil. The radiocarbon age of surface soil samples rarely exceeds 2,000 years and is often no more than a few hundred years (Leavitt *et al.* 1996). This suggests that very old, inert pools can not be significant in most surface soils and should not show a high degree of variability among different soil types. Evidence suggests that this is not so however, and that equilibrium values for soil carbon under exploitive cropping conditions can be highly variable (Dalal and Mayer, 1984).

### *Chemical or Physical?*

The only major mechanisms that can provide a high degree of protection to soil organic matter are chemical recalcitrance, a strong interaction with the mineral matrix in such a way that the protected material is effectively removed from the biosphere or a combination of both. The former mechanism suggests the formation of organic moieties that are chemically different to the more labile pools or at least contain functional groups that impart recalcitrance. Both aromatic (Skjemstad *et al.*, 1996) and long-chained alkyl (Baldock *et al.*, 1992) structures have been suggested as candidates for imparting biological recalcitrance to soil organic matter.

During exploitive cultivation, plant residue inputs are low and soil carbon levels can be reduced to as little as 30% of the carbon in the initial undisturbed surface horizon (Dalal and Mayer, 1986). Under these conditions, any highly recalcitrant organic moiety should be concentrated as the more active soil

carbon pools decrease. Using solid-state  $^{13}\text{C}$  NMR spectroscopy, Skjemstad *et al.* (2001) showed that the only functional group that showed a relative increase with prolonged cropping was the aryl-C and this could be attributed to the presence of charcoal. The alkyl carbons remained constant or declined.

It therefore seems unlikely that physical processes are involved in the long-term protection of soil organic matter. Adsorption processes such as clay-OM and metal-OM interactions can be demonstrated to slow decomposition processes (Martin and Haider, 1986), but it is unlikely that these processes can slow decomposition enough to give the high MRTs measured in biologically active surface soils.

### *Radiocarbon dating*

Since charcoal is highly resistant to biological decomposition and other oxidative processes, the presence of aryl carbon in the form of finely-divided (<53  $\mu\text{m}$ ) charcoal is a significant factor in determining the turnover of soil carbon. Few attempts have been made to measure the age of finely divided soil charcoals. Skjemstad *et al.* (1996) showed for one Australian soil that the photo-oxidation resistant carbon fraction, which was >70% charcoal, was in fact ~1,300 years older than the bulk soil. Similarly, charcoal separated by photo-oxidation from a set of German soils was shown to be as much as 4000 years older than the bulk soil (unpublished data). In one case, the differences were not large but here the MRT of the bulk soil was ~5,000 years.

Leavitt *et al.*, (1996) showed for 30 surface soil samples that reflux with 6M HCl also increased the radiocarbon age of the organic matter by about 1000 y. Both acid hydrolysis and photo-oxidation therefore appear to selectively remove younger carbon and preserve older carbon. Either method therefore probably effectively separates a fraction which could be used as a passive or "inert" fraction in soil carbon modelling, at least in surface soils.

Invariably, soil organic carbon age increases with depth, indicating that turnover rates also increase with depth. In most soils, there is very little change in the chemistry of soil organic matter with increasing depth. Polysaccharides often decrease with depth reflecting a decrease in plant residues but this decrease is not sufficient to account for the large increases in radiocarbon age. With increasing depth, microbial biomass and activity decline leaving larger volumes of soil with very low, if any, biological activity. Organic materials that survive the initial processes of decomposition would be effectively removed from contact with the biosphere and coupled with physical

protection mechanisms that prevent their movement in the soil, could remain isolated from the biosphere for many years perhaps even millennia. Both of the methods discussed above assume recalcitrance inferred through chemical structure of the substrate and therefore would be inadequate for establishing a soil carbon pool structure in subsoils. Here, it might be more appropriate to decrease turnover rates of the slower pools to compensate for reduced biological activity.

For models like Century where the passive pool is coupled to the turnover of the other pools, a high radiocarbon age for the passive pool would be expected. Material is cycled through the slow and passive pools repeatedly so that the most recalcitrant "old" material accumulates. If charcoal is considered however, fire history and transport processes may be more important. For ecosystems with long fire histories, charcoal should form the basis of an "old" pool but if fire history was only recent, then this recalcitrant pool could have a relative young radiocarbon age.

### Methodologies

A comparison of the amount and nature of the material remaining after acid hydrolysis or photo-oxidation treatments for a <53 mm fraction from a duplex soil showed that the acid hydrolysis method recovered about 40% of the original carbon whereas the photo-oxidation method recovered only 25% (unpublished data). Similarly, the chemical nature of the two fractions were different. The hydrolyzed fraction consisted of a mixture of aryl (including charcoal) and long-chained alkyl materials while the photo-oxidized fraction was dominated by aryl carbon (charcoal). The two methods therefore clearly recover different organic moieties and are not interchangeable.

Even with the measurement of charcoal or black carbon (BC), methods and recoveries vary considerably. Schmidt *et al.* (2001) compared five different methods of BC estimation and found that the photo-oxidation method could recover >500 times more BC than some of the thermal methods. Since BC is a continuum of combustion products from lightly charred biomass to refractory soot, it is likely that the different methods determine different windows in the continuum. Many of the thermal methods, which are thought to determine soot, showed little variation in BC between soil types and so would have little value for soil carbon modelling purposes. It is clear however, that better comparisons of analytical techniques are required together with better definitions of what is being determined.

## Conclusions

---

Soil carbon turnover models require a pool with a turnover time probably exceeding 1,000 years to account for the relative old radiocarbon ages measured in some surface soils. Although a number of "old" recalcitrant fractions of organic carbon can be separated from soil and can show radiocarbon ages much older than the bulk soil, none of these can be defined as truly inert. Chemical recalcitrance appears to be the only mechanism by which soil organic carbon can be protected for long periods of time in active surface soils. <sup>13</sup>C NMR studies show that the only chemical structures that appear to survive decomposition processes are aryl in nature and are mostly due to finely-divided charcoal. For longer-term modelling, some estimates of the rate of charcoal production will need to be considered. Some long-chained alkyl materials may also be resistant to decomposition.

Of the techniques used to measure resistant soil organic matter, only two, photo-oxidation and acid hydrolysis, appear to show promise. These methods both recover relatively old pools but appear to determine different fractions of carbon and are not interchangeable. A combination of these techniques may be more informative, but better estimates of the turnover times of these fractions are needed.

## References

---

- Anderson, D.W. and Paul, E.A. (1984). Organo-mineral complexes and their study by radiocarbon dating. *Soil Science Society of America Journal* 48: 298-301.
- Baldock, J.A., Oades, J.M., Waters, A.G., Peng, X., Vassallo, A.M. and Wilson, M.A. (1992). Aspects of the chemical structure of soil organic materials as revealed by solid-state <sup>13</sup>C NMR spectroscopy. *Australian Journal of Soil Research* 28: 213-225.
- Dalal, R.C. and Mayer, R.J. (1986). Long-term trends in fertility of soils under continuous cultivation and cereal cropping in southern Queensland. II Total organic carbon and its rate of loss from the soil profile. *Australian Journal of Soil Research* 24: 281-292.
- Hassink, J. (1997). The capacity of soils to preserve organic C and N by their association with clay and silt particles. *Plant and Soil* 191: 77-81.
- Leavitt, S.W., Follett, R.F. and Paul, E.A. (1996). Estimation of slow- and fast-cycling soil organic carbon pools from 6N HCl Hydrolysis. *Radiocarbon* 38: 231-239.

- Martin, J.P. and Haider, K. (1986). Influence of mineral colloids on turnover rates of soil organic matter. In "Interactions of Soil Minerals with Natural Organics and Microbes." Eds. P.M. Huang and M. Schnitzer. pp.283-304. SSSA Special Publication Number 17. (SSSA, Inc. Madison, Wisconsin, USA).
- McGill, W.B. (1996). Review and classification of ten soil organic matter models. In "Evaluation of Soil Organic Matter Models." Eds. D.S. Powlson, P. Smith and J.U. Smith. pp. 111-132. NATO ANSI Series no 1, vol 38. (Springer Verlag).
- Paul, E.A., Follett, R.F., Leavitt, S.W., Halvorson, A., Peterson, G.A. and Lyon, D.J. (1997). Radiocarbon dating for determination of soil organic matter pool sizes and dynamics. *Soil Science Society of America Journal* 61: 1058-1067.
- Schmidt, M.W.I., Skjemstad, J.O., Czimczik, C.I., Glaser, B., Prentice, K.M., Gelin, Y. and Kuhlbusch, T.A.J. (2001). Comparative analysis of black carbon in soils. *Global Biogeochemical Cycles*. 15: 163-168.
- Skjemstad, J.O., Clarke, P., Taylor, J.A., Oades, J.M. and McClure, S.G. (1996). The chemistry and nature of protected carbon in soil. *Australian Journal of Soil Research* 34: 251-271.
- Skjemstad, J.O., Dalal, R.C., Janik, L.J. and McGowan, J.A. (2001). Changes in chemical nature of soil organic carbon in Vertisols under wheat in southeastern Australia. *Australian Journal of Soil Research* 39: 343-359.
- Skjemstad, J.O. and Janik, L.J. (1996). Climate change: determining the potential for carbon sequestration in Australian soils. Final Report for RIRDC Project CSO-5A.
- Skjemstad, J.O., Janik, L.J. and Taylor, J.A. (1998). Non-living soil organic matter: what do we know about it? *Australian Journal of Experimental Agriculture* 38: 667-680.

# Effect of Mechanical Disturbance (Cultivation) on Soil Carbon Dynamics

Phil Polglase  
CSIRO Forestry and Forest Products

Mechanical disturbance is often thought to significantly affect (deplete) stocks of soil C, yet solid evidence for direct effects on soil biological activity, versus other related and indirect effects, is scant. Here, some evidence is presented and reviewed to illustrate the main issues and to highlight potentially confounding factors that make interpretation of data at times difficult.

Soil C can be lost from cultivated systems either through respiration (decomposition), erosion and transport off-site by wind or water (surface run-off), or through leaching of C in either particulate form or in solution (dissolved organic C). Most models and concerns primarily centre around respiratory losses (rightly or wrongly), and for the most part that is the mechanism considered here. Finally, how models of soil C describe the effects of disturbance is reviewed.

Most evidence and expectation for loss of soil C after disturbance comes from studies such as those of Dalal and Mayer (1986), Mann (1986), Davidson and Ackerman (1993), Tiessen *et al.* (1994), Whitbread *et al.* (1998) and Kirschbaum *et al.* (2000) where it has been clearly demonstrated that conversion of forest to repeatedly cultivated (cropped) land can greatly deplete soil C stocks. In Australia, data of Dalal and Mayer (1986) nicely illustrate the point (Fig. 1). In southern Queensland, native vegetation had been cleared and the soil cultivated for a varying number of years. At one of the sites the initial concentration of soil C was decreased by up to 70% after more than 40 years of cultivation, but what caused such marked change?

The direct effects of disturbance in stimulating decomposition is often invoked as the main mechanisms, but in uncontrolled studies such as those of Dalal and Mayer (1986) one needs to be mindful of other factors at work. An obvious contributing factor is the difference between cultivated soil and the preceding forest in both the quantity and quality of residue inputs. Crops are bred and managed to maximise above-ground growth – and if this is removed from the site the amount of plant material available to build soil C is greatly diminished. Furthermore, tree residues are more resistant to decomposition

(more lignified) than agricultural residues and this leads to higher stocks of litter and soil C.

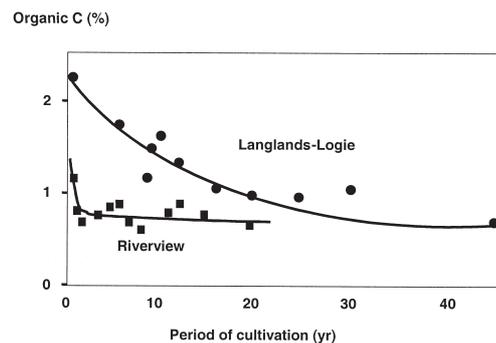


Fig. 1. Change in soil C with period of cultivation at two sites in southern Queensland (adapted from Dalal and Mayer, 1986).

To separate the effects of plant inputs from direct effects of mechanical disturbance, one needs to look at controlled experiments. A study published 44 years ago by Rovira and Greacen (1957) is typical of some more contemporary results (Fig. 2). A Lismore clay-loam was artificially cultivated in the laboratory over a period of days and O<sub>2</sub> uptake measured. Note that this is a better measure of biological activity because it has been observed that, immediately upon disturbance of soil, there can be an outgassing of CO<sub>2</sub> that was previously held in soil micropores. Results showed that disturbance quickly and dramatically increased biological activity, but that the effect was short-lived. Each simulated tillage was calculated to cause loss in soil C of about 0.02 t C/ha. Assuming 4 tillages per year, every 10 years of cultivation would mean loss in soil C of about 0.8 t/ha.

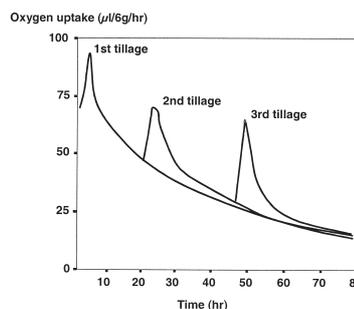


Fig. 2. Effect of successive tillage treatments in the laboratory on rate of oxygen uptake (adapted from Rovira and Greacen, 1957).

Uptake of  $O_2$  was closely related to the level of soil disaggregation, and this is the main mechanism proposed for cultivation causing depletion in soil C. Soil aggregates are broken up, increasing aeration, affecting water availability, and exposing more surfaces to invasion by bacteria and fungi. An example of soil disaggregation caused by tillage comes from Chan *et al.* (1992). Three levels of cultivation in the field were imposed on a Wagga red earth under wheat/ lupin rotation. Conventional cultivation was 3 cultivations/yr, reduced tillage was 1 cultivation /yr, and direct drilling was no cultivation. After 10 years soil C concentration was significantly decreased in the 2 cultivated soils (Fig. 3). The percent aggregation of soil was also decreased in these treatments (Fig. 4), as determined by wet sieving to  $< 250 \mu m$ . It is noteworthy that the authors observed some inversion of soil under cultivation (another confounding factor) and that they did not ascribe a direct effect of cultivation to loss of soil C. Rather, they speculated that incorporation of stubble in cultivated treatments may have increased rates of decomposition. Erosion by wind and water should also not be discounted.

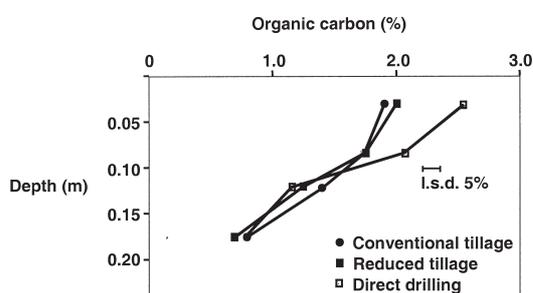


Fig. 3. Effect of cultivation frequency on change in soil C after 10 years at Wagga Wagga (adapted from Chan *et al.*, 1992).

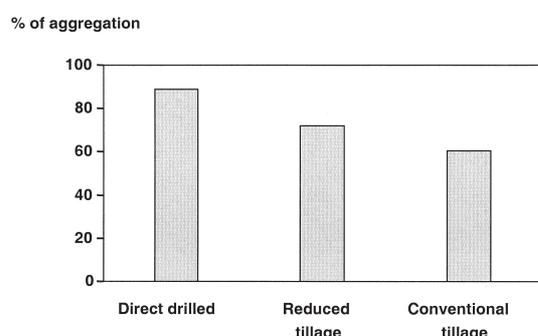


Fig. 4. Effect of cultivation frequency on level of soil aggregation after 10 years at Wagga Wagga (adapted from Chan *et al.*, 1992).

More evidence for the direct effects of disturbance on decomposition comes from a synthesis of laboratory N mineralisation data (Paul *et al.*, 2001). Here, N mineralisation in intact soil cores collected from soils throughout south-eastern Australia (covering a range of textures) was compared with mineralisation in soil sieved to  $< 2 mm$  (Fig. 5). Although there is some scatter in the data, there is close fit between mineralisation measured in undisturbed and disturbed soil.

In forestry there seems to be a popular perception that site preparation of agricultural land leads to substantial loss of soil C. As part of a global review of the effects of afforestation on change in soil C, Polglase *et al.* (2000) examined the effects of mechanical disturbance and could not determine any significant effect (Fig. 6). However, results need to be interpreted with some caution (see below).

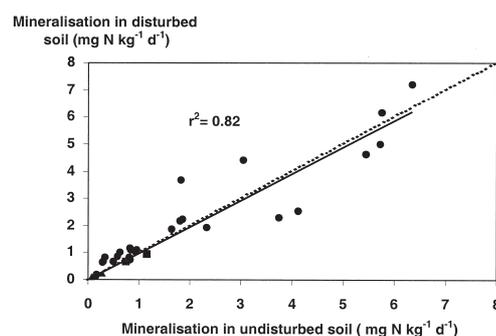


Fig. 5. Comparison of laboratory rates of mineralisation in undisturbed (intact) soil cores and in sieved soil ( $< 2mm$ ) (from Paul *et al.*, 2001). The solid line is the line-of-best fit, the broken line is the 1:1 relationship.

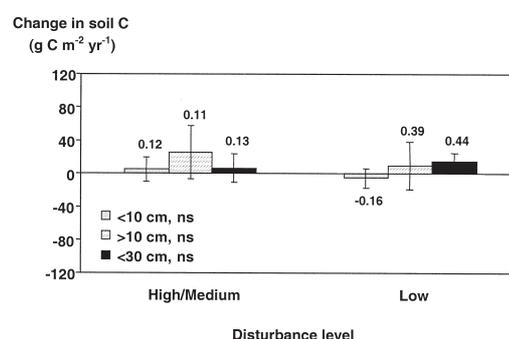


Fig. 6. Effect of level of mechanical disturbance on change in soil C after afforestation of agricultural sites throughout the world (from Polglase *et al.*, 2000). Numbers on top of bars are the rates of change in soil C relative to the initial amount ( $\%C ha^{-1} yr^{-1}$ ).

Fig. 7 shows an example of site preparation for plantations in Australia where the site has been deep ripped and mounded, with planting lines typically 3 to 4 m apart. Spatial heterogeneity is greatly increased with much mixing and potential inversion of soil within mounds, and a decrease in soil bulk density. Weeds are often left to grow in the inter-row, but in mounds weeds are controlled and residues left to decompose. Thus, when trees are young, soil in the mound has few inputs from fresh residues whereas older residues continue to decompose, in a somewhat inverted soil. It should not therefore be surprising that soil C would decrease in mounded soil, but not necessarily due to the direct effects of mechanical disturbance, rather it is equally likely to be caused by temporary cessation of plant inputs.

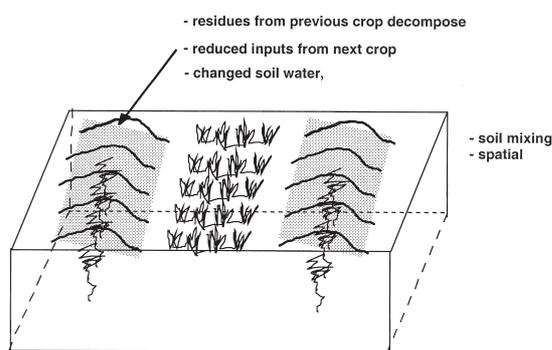


Fig. 7. Spatial heterogeneity in a field cultivated in preparation for tree planting.

The heterogeneity resulting from site preparation highlights the difficulty in sampling soil to detect statistically differences in soil C. It is common for soil in plantations to be sampled from the inter-row, away from the zone of major disturbance, and it is likely that this was the case for many of the studies reviewed by Polglase *et al.*, (2000, Fig. 6). In mounded and ripped soil, changes in bulk density need to be carefully monitored when interpreting results.

Of the 11 process-based models reviewed, 6 explicitly tried to account for the effects of disturbance on decomposition. Invariably this was done empirically by adjusting the rate constant for decomposition of each soil pool. This is a simple procedure and would be easily incorporated into all soil decomposition models. Some models such as CENTURY and SOCRATES also attempt to explicitly describe erosion processes. As is often the case, model algorithms for disturbance effects remain largely unverified.

In summary,

- Evidence for disturbance causing direct depletion of soil C through increased biological activity is at the best equivocal.
- There are many confounding factors, the most important of which are disruption of plant inputs to soil under cultivation, and soil inversion.
- An informal survey of model builders and users revealed that most felt modelling disturbance effects was not a priority. The potential for confounding influences and lack of convincing data was widely recognised.
- There is little evidence for site preparation in forestry directly causing large loss of C that could not otherwise be explained by decrease in plant uptake, soil inversion, or inherent variability.
- Finally, all models considered had their genesis in agricultural systems. In harvested forests we should perhaps note the special case where heavy machinery trafficks soil, often causing considerable, if localised, disturbance. Under these conditions there is potential for significant transport and loss of soil C by erosion. Whether or not such movement of soil across the landscape needs to be considered in models of terrestrial C balance is another question.

## Acknowledgment

I thank Kris Jacobsen (CSIRO Forestry and Forest Products) for adapting the Figures from their original sources.

## References

- Chan, K. Y., Roberts, W.P. and Heenan, D.P. (1992). Organic carbon and associated soil properties of a red earth after 10 years of rotation under different stubble and tillage practices. *Aust. J. Soil Res.*, **30**, 71-83.
- Dalal, R.C. and Mayer, R.J. (1986). Long-term trends in fertility of soils under continuous cultivation and cereal cropping in southern Queensland. II Total organic carbon and its rate of loss from the soil profile. *Aust. J. Soil Res.*, **24**, 281-292.
- Davidson, E.A. and Ackerman, I.L. (1993). Changes in soil carbon inventories following cultivation of previously amended soils. *Biogeochem.*, **20**, 161-193.
- Kirschbaum, M.U.F., Murty, D., McGilvray, H. and McMurtrie, R.E. (2000): How does soil organic carbon change after

- conversion from forest to agricultural land uses? Climate Change Newsletter, Bureau of Resource Sciences 12: 5-7.
- Mann, L.K. (1986). Changes in soil carbon storage after cultivation. *Soil Sci.*, **142**, 279-288.
- Paul, K.I., Polglase, P.J., O'Connell, A.M. , and Carlyle, J.C. (2001). Soil Nitrogen Availability Predictor (SNAP): A method to estimate nitrogen mineralisation in forest soils. Divisional Report. CSIRO Forestry and Forest Products, Canberra.
- Polglase, P.J., Paul, K, I, Khanna, P.K., Nyakuengama, J.G., O'Connell, A.M., Grove, T.S., and Battaglia, M. (2000). Change in soil carbon following afforestation or reforestation: Review of experimental evidence and development of a conceptual framework. National Carbon Accounting System Technical Report No. 20. Australian Greenhouse Office:Canberra. 102 p.
- Rovira, A. D. and Greacen, E.L. (1957). The effect of aggregate disruption on the activity of microorganisms in the soil. *Aust. J. Agric. Res.*, **8**, 659-679.
- Tiessen, Cuevas, E., and Chacon, P. (1994). The role of soil organic matter in sustaining soil fertility. *Nature*, **371**, 783-785.
- Whitbread, A.M., Lefroy, R.D.B., and Blair, G.J. (1998). A survey of the impacts of cropping on soil physical and chemical properties in north-western New South Wales. *Aust. J. Soil. Res.*, **36**, 669-681.

# Plant Litter and Decomposition: General Concepts and Model Approaches

---

Marc Corbeels  
CSIRO Forestry and Forest Products

## Introduction

---

The global terrestrial heterotrophic respiration is estimated at about 60 Gt C yr<sup>-1</sup> (Schlesinger, 1991). Plant litter produced during senescence processes and plant residues left on site after harvest operations are the primary substrate for heterotrophic respiration in plant-soil ecosystems. They constitute both of aboveground and belowground plant parts. Substrate quality, together with the physico-chemical environment and the decomposer community, is one of the three interacting factors regulating decomposition rates (Swift *et al.*, 1979). Thus, the quantity and quality of plant litter are key factors controlling carbon (C) loss in the plant-soil ecosystem.

In the context of predicting net C exchange at ecosystem level, a fundamental topic is the influence of plant litter decomposition on the longer-term soil C balance. A key question is how substrate quality affects the transformations of plant residues into stable soil organic matter (SOM).

This paper describes plant substrate effects on the decomposition process and discusses briefly the various attributes of litter quality. I review and compare how existing ecosystem models deal with plant litter decomposition and how they incorporate different aspects of substrate quality. Finally, I show the sensitivity of some models to litter quality.

## Litter quantity and decomposition

---

The total amount of C produced by decomposition of plant litter is primarily determined by the amount of litter present. Carbon loss from litter decomposition is largely determined by the amount of decomposing litter. In steady state conditions, the rate of C loss from the soil system through decomposition over a year or more must be equal to the rate of C input by litter decomposition over the same period. Data from published studies monitoring *in situ* soil respiration provide evidence that at the biome scale, C losses from soil (soil respiration) correlate

positively with rates of litter input to the soil system (Raich and Tufekcioglu, 2000).

At a smaller scale, experiments under both field and laboratory conditions suggest that under non nutrient limiting conditions the rate of decomposition per unit C added is relatively independent of the quantity added, provided litter is not added in excessive amounts (e.g. Green *et al.*, 1995).

## Litter quality and decomposition

---

In the last two decades, an extensive amount of experimental research has been published on plant substrate decomposition and on the relationship between plant litter quality and decomposition in particular. A recent comprehensive review of various aspects of plant litter quality in relation to decomposition can be found in Heal *et al.* (1997).

The quality of plant litter with respect to decomposition can be defined as its relative ease of mineralisation by decomposing organisms (Paustian *et al.*, 1997). Plant litter quality involves intrinsic characteristics of plant material that affects its assimilation by decomposers. These characteristics are both of chemical and physical nature. Most of the experimental studies on plant litter quality defined chemical quality indices using various ratios of C, N, lignin and polyphenols (see Vanlauwe *et al.*, (1997) for detailed discussion on these indices).

From these studies, at least two general paradigms have emerged. First, the C:N ratio is accepted as a general index of quality (Seneviratne, 2000): mineralisation rates tend to decrease with increasing C:N ratio. Second, lignin contributes to the recalcitrance of plant litter to decomposition by occluding more easily decomposable polysaccharides (e.g. Melillo *et al.*, 1982). Other chemical compounds like polyphenols, may interfere in enzyme functions or decomposer metabolism, resulting in the reduction in decomposition rate of other litter constituents (e.g. Palm and Sanchez, 1991).

Physical components of litter quality have received somewhat less attention in research on litter quality. Recent research has shown that particle size and surface area to mass characteristics

can markedly affect decomposition rates (Angers and Recous, 1997).

Most of the studies have searched for quantitative indicators for litter quality that can predict decomposition, generally in terms of N mineralisation. It has resulted in simple empirical regression-type models, with highly variable litter quality indicators and regression coefficients. However, no unique relationship have yet been found between mineralisation and litter quality (Vanlauwe *et al.*, 1997).

A decrease in quality or decomposability of plant substrate as decomposition progresses is a general concept. The decomposing material becomes enriched in recalcitrant chemical compounds, due to direct chemical changes in the substrate itself and the succession in microorganisms able to assimilate the substrate (Berg and Staaf, 1980). This means also that there is a shift in relative importance of the different quality parameters in regulating decomposition as it progresses. The early stages of decomposition are dominated by the easily decomposable carbohydrates, while at later stages, lignin exerts the major control on decomposition rate. Consequently, indices based on initial litter quality will have limitations in predicting longer-term decomposition rates.

## Integration of plant litter decomposition into plant-soil ecosystem models

Representation of plant litter and its decomposition in ecosystem models has started as early as the late 1970s (e.g. Hunt, 1977, Jenkinson and Rayner, 1977). In those early models, plant litter was represented by two or more organic matter pools (a rapidly and a slowly-decomposing plant fraction). Decomposition was simulated according to first order kinetics through C flows from the litter pools to microbial biomass and recalcitrant SOM pools with production of CO<sub>2</sub>. These early multi-pools simulation models still form the basis for the vast majority of the current soil C cycling models.

I will examine the assumptions regarding litter quantity and quality effects on decomposition in the 12 models, which are considered in this workshop (see Table 1).

The models PROMOD and 3PG do not represent decomposition of plant litter. All other models, with the exception of the GRASP model, simulate plant litter decomposition as C flows through a catenary sequence of pools of increasing recalcitrance. The GRASP model simulates litter decomposition, but not as part of soil C cycling.

Model <sup>a</sup>	No. of litter pools	Type	Comments
APSIM	1	-	for above-ground plant litter; C:N ratio effect on k
	3	chemical	for belowground (root) litter; determined analytically
CENTURY	2	functional	pool sizes function of initial lignin:N
CenW	2	functional	as in CENTURY
FullCAM	3	chemical/	as in GENDEC (above-ground litter) and
	2	kinetic	Roth-C (belowground litter)
G'DAY	2	functional	as in CENTURY
Gendec	3	chemical	determined analytically
GRASP	1	-	litter type specific k
GRAZPLAN	2	functional	pool sizes function of initial C:N
Linkages	- <sup>b</sup>	-	proportional mass loss as a function of initial lignin:N
Roth-C	2	kinetic	fitting to plant residue decomposition data
Socrates	2	kinetic	as in Roth-C

<sup>a</sup> PROMOD and 3PG do not consider the decomposition process

<sup>b</sup> litter as continuum of cohorts

Table 1. Model characteristics on non-woody litter decomposition

Plant substrate for decomposition is represented as a single C pool in the APSIM (in the case of above-ground litter) and GRASP models. In those models, the only option to incorporate litter quality is by varying the specific decomposition rate  $k$  as a function of litter type. For example, simulations with APSIM suggest that the  $k$  value for *E. grandis* litter ( $0.025 \text{ day}^{-1}$ ) is considerable lower than a default value ( $0.1 \text{ day}^{-1}$ ) proposed by Probert *et al.* (1998) for simulations of mineralisation dynamics in grain and/or legume cropping systems. This is despite the incorporation of a decay rate modifier, which is a function of the initial residue C:N ratio. Also, simulation of the decomposition of sugar cane residues indicated that the C:N factor on decomposition did not describe the litter quality effects satisfactorily (Thorburn *et al.*, 2001). These results suggest the need for a more complex description of plant litter decomposition to overcome the requirement of residue-specific  $k$  values.

The Linkages model considers plant substrate for decomposition as a continuum of cohorts, which represent annual inputs of species-specific litter at various stages of decomposition. For non-woody litter, the lignin:N ratio is used as a quality attribute and it is assumed that percent mass loss for a given site is linearly related to this ratio. The Linkages model is an empirical regression-type model and, hence, limited to the conditions for which it has been developed. Once a litter cohort reaches an advanced critical stage of decomposition, it is transferred to a combined pool of soil humus.

The other simulation models represent plant substrates by two or more discrete C pools, but differ in their criteria of compartmentalisation (Table 1). These criteria can be chemically, kinetically or functionally defined.

One of the first multi-pool decomposition models was developed by Minderman (1968) and included several analytically determined chemical fractions of plant substrates. Chemically defined pools recognize the discrete chemical components of litter, but the question arises whether the individual chemical fractions decompose independently. The Gendec and APSIM (for root litter) models distinguish three discrete chemical components of plant litter: labile carbohydrates (water-soluble), holocellulose and acid-insoluble (lignin-like) compounds. These pools can be analytically determined through a proximate analysis, e.g. the Van Soest Acid Detergent Fiber method. Simulations with models adopting this approach indicated that for short-term C decomposition of plant residues under laboratory conditions, litter quality can be well represented by the Van Soest fractions,

provided that interactions are considered between different compounds (Corbeels *et al.*, 1999; Henriksen and Breland, 1999).

Kinetically defined pools are conceptual substrate fractions that are determined by fitting the decomposition model to experimental data on substrate decomposition. Double exponential decay models are an example of models with kinetically defined pools (e.g. O'Connell, 1997). The combination of a relative small labile pool with a larger, more resistant pool is a good description of the two phase decomposition of most plant residues: a rapid initial loss, followed by a slower mass loss rate. This type of models generally fit short-term decomposition of plant residues well. Kinetically defined pools do not directly correspond to experimentally verifiable fractions. Therefore, it may lead to uncertainties on how to transpose these conceptual pools to different types of plant litter. The Roth-C and Socrates model distinguish two kinetically defined pools of plant litter: decomposable (DPM) and resistant plant material (RPM). In these models the DPM/RPM is the sole attribute for litter quality. Values for the DPM/RPM ratio refer to biomes and were estimated by fitting the Roth-C model to measured data of plant material decomposition (Jenkinson *et al.*, 1991). Recently, Skjemstad *et al.* (2001) showed that the particulate organic C (>53 $\mu\text{m}$ ) fraction in soil could represent the RPM fraction in Roth-C, provided that the decomposition rate constant of the RPM pool was reduced 3-fold.

The functionally or morphologically defined compartmentalisation of plant litter defines a metabolic (a labile or rapidly decomposing fraction) pool versus a structural (a resistant or slowly decomposing fraction) pool of plant litter. The metabolic component constitutes the cell cytoplasmic compounds of the plant cells, whereas the structural pool represents cell wall compounds with bound proteins and lignified structures. This concept of litter compartmentalisation recognizes that both cell structures decompose somewhat independently and that the physical structure of plant material at the micro-scale is an important attribute to quality. The size of these functional pools is determined by a regression type function of litter quality attributes. Examples of this type of litter characterisation are found in the CENTURY and GRAZPLAN models. CENTURY divides plant residues into a metabolic and structural pool as a function of the initial lignin:N ratio of the litter, such that the fraction of litter going into the structural pool increases with increasing lignin:N ratio. GRAZPLAN adopts the concept of Hunt (1977) and uses the initial residue C:N ratio as litter quality attribute to divide litter into a metabolic and structural pool. The regression-type functions allow extrapolation of the functional

pool concept to other litter types. Parton *et al.* (1994) showed that the structural litter pool in CENTURY is closely correlated to the cellulose plus lignin fraction as determined by proximate analysis.

The CENTURY model incorporates two other effects of litter quality on the decomposition process. First, the decay rate of the structural material is a function of its lignin content, such that increasing lignin content slows the decay rate. Second, the lignin fraction of the structural pool is directly incorporated into the pool of slow organic matter with a relatively low proportional C loss. CENTURY also differentiates between above-ground and belowground litter, and assume a 20% slower decomposition rate for the above-ground litter fractions compared to the belowground.

The models CenW and G'DAY incorporate slightly modified versions of the CENTURY model, but with the same assumptions regarding the litter quality attributes. The FullCAM model incorporates the Gendec model to simulate decomposition of above-ground litter and the Roth-C model for decomposition of belowground litter.

In these models, physical litter quality attributes are only considered in an indirect way by including separate litter pools for woody debris. The Linkages model considers 3 size classes for woody litter, with decay rates related to size class. From the other models, only CENTURY (the forestry version), CenW, G'DAY (new version) and FullCAM consider woody litter pools (above- and belowground) explicitly as 2 or more size classes, each with a specific decay rate.

All models, with the exception of APSIM assume that there is no litter quantity effect on the specific rate of decay. In APSIM, the

rate of decomposition is modified by a 'contact factor' depending on the initial residue mass. It is presumed that the material in immediate contact with the soil decomposes more rapidly than material in the upper mulch layer.

Table 2 shows the potential decomposition rates (k-values) of the litter fractions represented in some of the models considered. These potential rates vary considerably between similar litter fractions of different models. The k-values are *strictu sensu* transformation rates to other (more recalcitrant) SOM pools. This finding indicates that the various models differ significantly in the assumptions on the litter pools and –more importantly– on the microbial turnover and formation of secondary products.

## Model sensitivity to litter quality

Paustian *et al.* (1997) showed by calculating total and individual pool C levels under steady state conditions as function of litter quality, how CENTURY and Roth-C behave differently in responding to litter quality effects on soil C sequestration. Soil C level predicted by Roth-C increases in direct proportion to the size of the RPM pool. In CENTURY, soil C increases curvilinearly with increasing lignin content. The largest difference between the models is, however, in the responses of the individual pools to litter quality. In Roth-C, litter quality does not affect the size of the secondary SOM pools (microbial biomass and humus). Only the amount of undecomposed litter increases proportionally with increased RPM. This is because the C transformed from both DPM and RPM both flow into microbial biomass and humus.

Model	Pools	k	Comments
CENTURY	Metabolic	6.1 yr <sup>-1</sup>	fitting against decomposition data from 1 yr incubations of plant residues (Pinck <i>et al.</i> , 1950)
	Structural	1.5 yr <sup>-1</sup>	
Gendec	Labile	36 yr <sup>-1</sup>	values from Paul and Juma (1981)
	Holocellulose	15 yr <sup>-1</sup>	
	Lignin	1.8 yr <sup>-1</sup>	
Roth-C	DPM	19 yr <sup>-1</sup>	fitting against decomposition data (10 yr, labelled ryegrass) under field conditions (Jenkinson and Rayner, 1977)
	RPM	0.6 yr <sup>-1</sup>	
Socrates	DPM	22 yr <sup>-1</sup>	fitting against decomposition of <sup>14</sup> C labelled plant residues (Ladd <i>et al.</i> , 1995)
	RPM	1.5 yr <sup>-1</sup>	

Table 2. Pools and decomposition rate constants (for first-order kinetics at 15°C and optimal moisture conditions) for litter pools in some models

In CENTURY, all secondary pools respond to lignin content. Both the slow and passive pool show a linear response to lignin content, mainly as a consequence of the fact that the lignin fraction of the structural pool is directly incorporated in the slow pool. These different assumptions in the models raise the question of litter quality effects on the chemical nature of SOM. Experimental results are not clear on the importance of plant lignin as precursors of soil humic substances. The role of phenolic compounds from plant sources in reacting with other organic compounds to form stable complexes is generally accepted, but does not account for the wide variety of structures found in humic substances (Cadish and Giller, 2001).

## Conclusions and some omissions

Substrate quality is a key factor regulating the decomposition of litter and transformation of litter C into soil humus. Largely based on results from short-term decomposition studies, most models include biochemical composition or chemical attributes (initial C:N or lignin:N ratio) as litter quality parameter. The Roth-C and SOCRATES models define two conceptual litter pools by fitting the model to long-term decomposition data.

Uncertainty exists on how litter quality affects transformations of litter C into stable soil organic matter. The effect of litter quality on transformation processes is not well considered in the simulation models. Only CENTURY considers the direct effect of recalcitrant compounds such as lignin on C sequestration by allocating the lignin fraction of litter directly to the slowly-decomposing SOM pool. Whether this concept adequately represents the reality is not known and remains to be thoroughly tested. New analytical techniques, such as nuclear magnetic resonance (NMR) spectroscopy may contribute to a better mechanistic understanding of litter quality effects on SOM chemistry.

## References

- Angers D and Recous S (1997) Decomposition of wheat straw and rye in soil as affected by particle size. *Plant Soil* 189: 197-203.
- Berg B and Staaf H (1980) Decomposition rate and chemical changes of Scots pine needle litter. II. Influence of chemical composition. In: Persson T (Ed.), *Structure and Function of Northern Coniferous Forests- An ecosystem study*. Ecological Bulletins (Stockholm) 32: 373-390.
- Cadish G and Giller KE (2001) Soil organic matter management: the roles of residue quality in C sequestration and N supply. In: Rees RM, Ball BC, Campbell CD and Watson CA (Eds.), *Sustainable management of soil organic matter*. pp 97- 111. CAB International.
- Corbeels M, Hofman G, Van Cleemput O (1999) Simulation net N immobilisation and mineralisation in substrate-amended soils by the NCSOIL computer model. *Biology and fertility of Soils* 28: 422-430.
- Green CJ, Blackmer AM and Horton R (1995) Nitrogen effects on conservation of carbon during corn residue decomposition in soil. *Soil Science Society of America Journal* 59: 453-459.
- Heal OW, Anderson JM, Swift MJ (1997) Plant litter quality and decomposition: An historical overview. In Cadish G and Giller KE (Eds.), *Driven By Nature. Plant Litter Quality and Decomposition*. pp 3-30. CAB International, Wallingford.
- Henriksen TM and Breland TA (1999) Evaluation of criteria for describing crop residue degradability in a model of carbon and nitrogen turnover in soil. *Soil Biology and Biochemistry* 31: 1135-1149.
- Hunt HW (1977) A simulation model for decomposition in grasslands. *Ecology* 58: 469-484.
- Jenkinson DS, Adams DE and Wild A (1991) Model estimates of CO<sub>2</sub> emissions from soil in response to global warming. *Nature* 351: 304-306.
- Jenkinson DS and Rayner JH (1977) The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Science* 123:298-305.
- Ladd JN, Amato M, Grace PR and Van Veen JA (1995) Simulation of <sup>14</sup>C turnover through the microbial biomass in soils incubated with <sup>14</sup>C labelled plant residues. *Soil Biology and Biochemistry* 27: 777-783.
- Melillo JM, Aber JD and Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63: 621-626.
- Minderman G (1968) Addition, decomposition and accumulation of organic matter in forests. *Journal of Ecology* 56: 355-362.
- O'Connell AM (1997) Decomposition of slash residues in thinned regrowth eucalypt forest in Western Australia. *Journal of Applied Ecology* 34: 111- 122.

- Palm CA and Sanchez PA (1991) Nitrogen release from the leaves of some tropical legumes as affected by their lignin and polyphenolic contents. *Soil Biology Biochemistry* 23: 83-88.
- Parton WJ, Ojima D.S. Cole CV and Schimel DS (1994) A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. In: Bryant RB and Arnold RW (Eds.), *Quantitative modeling of soil forming processes*. pp147-167. SSSA Special Publication n<sup>o</sup> 39. SSSA, Madison, Wisconsin, USA.
- Paul EA and Juma NG (1981) Mineralization and immobilization of soil nitrogen by microorganisms. In: Clark FE and Rosswall T (Eds.), *Terrestrial nitrogen cycles*. *Ecological Bulletins (Stockholm)* 33: 179-199.
- Paustian K, Ågren GI and Bosatta E (1997) Modelling litter quality effects on decomposition and soil organic matter dynamics. In: Cadisch G and Giller KE (Eds.), *Driven by nature: plant litter quality and decomposition*. pp 313-335. CAB International.
- Pinck LA, Allison FE and Sherman MS (1950) Maintenance of soil organic matter:II Losses of carbon and nitrogen from young and mature plant material during decomposition in soil. *Soil Science* 69: 391-401.
- Probert MP, Dimes JP, Keating BA, Dalal RC and Strong WM (1998) APSIM's water and nitrogen modules and simulation of the dynamics of water and nitrogen in fallow systems. *Agricultural Systems*: 56, 1-26.
- Raich JW and Tufekcioglu A (2000) Vegetation and soil respiration: correlations and controls. *Biogeochemistry* 48: 71-90.
- Schlesinger WH (1991) *Biogeochemistry: an analysis of global change*. Academic Press, New York.
- Seneviratne G (2000) Litter quality and nitrogen release in tropical agriculture: a synthesis. *Biology and Fertility of Soils* 31: 60-64.
- Skjemstad JO, Dalal RC, Janik LJ and McGowan JA (2001) Changes in chemical nature of soil organic carbon in Vertisols under wheat in south-eastern Queensland. *Australian Journal of Soil Research* 39: 343-359.
- Swift MJ, Heal OW and Anderson JM (1979) *Decomposition in terrestrial ecosystems*. Blackwell Oxford, UK, 372pp.
- Thorburn PJ, Probert ME, Robertson FA (2001) Modelling decomposition of sugar cane surface residues with APSIM-Residue. *Field Crops Research* 70: 223-232.
- Vanlauwe B, Diels J, Sanginga N. And Merckx R. (1997) Residue quality and decomposition: an unsteady relationship? In: Cadisch G and Giller KE (Eds.), *Driven by nature: plant litter quality and decomposition*. p 157-166. CAB International.

# Rapporteur Reports

---

*S. Roxburgh, C. Barton, M. Battaglia,  
M. Corbeels, D. Eamus, J. Evans, R. Gifford,  
B. Henry, R. Keenan, E. Krull, B. Medlyn,  
D. Pepper, J. Skjemsted, K. Tate.*

## Overview

---

Over the course of the workshop the rapporteurs provided summaries of the discussions that took place at the end of each session, as well as highlighting some of the major results to emerge from the presentations.

The summary reports below focus predominantly on the issues raised during discussion, but also include those results that were particularly relevant to the overall aims of the workshop:

- (1) to describe the specific processes that together control net ecosystem exchange;
- (2) to highlight current controversies or remaining unresolved issues;
- (3) detail how various processes are dealt with in the various models of interest in modelling carbon exchange for Australia;
- (4) discuss what processes should be included in continental-scale models of the Australian biosphere.

## Day 1—Wednesday 18 April 2001

---

**Morning Session** (Radiation interception, Radiation conversion, Respiration)

**Chair:** Craig Pearson  
**Rapporteurs:** David Pepper, Jan Skjemsted  
**Presenters:** Yingping Wang, Belinda Medlyn, Roger Gifford

The first two presentations in this session summarised current methodologies used in modelling radiation interception and radiation conversion. With respect to radiation interception it was noted that many models use Beer's law to calculate radiation extinguishment through plant canopies, and that the calculations are based on the assumption that all radiation is considered to be 'direct beam'. However, the importance of splitting radiation into direct beam and diffuse fractions was highlighted, and that diffuse light within plant canopies should

be accounted for in order to appropriately quantify the within-canopy light environment. This has important implications for modelling vegetation growth at all scales.

With respect to estimating respiration, it was noted that there are several ways in which respiration can be defined, and a suggestion was put forward that the CRC ought to produce a consensus definition of the components of plant respiration, and after further discussion it was decided that one outcome of the workshop would be the development of a set of definitions of the components of ecosystem gas exchange. Such a set of definitions has been produced and is being published as part of these proceedings. There was some discussion regarding the respiration: gross primary production ratio approach to estimating plant respiration. This is based on the observation of a reasonably conservative respiration: primary production ratio of around 0.4–0.6, measured across a wide variety of plant growth forms. Although it was noted that there are, in the literature, examples which fall outside this range, the overall feeling was that, in particular for continental-scale carbon budget modelling, the conservative nature of the ratio could be effectively utilised.

A general point was made that we can quantify the small-scale analyses quite well, but the real challenge lies in scaling the processes up through time and space.

**Afternoon Session** (Allocation, Mortality and stand age effects on productivity, Other factors (phenology, reproduction, ..))

**Chair:** Graham Farquhar  
**Rapporteurs:** Derek Eamus, Beverly Henry  
**Presenters:** Craig Barton, Michael Battaglia, Chris Beadle (read by M. Battaglia)

There was general agreement that knowledge of these processes is much-less well-known than those in the first session. For example the mechanisms underlying allocation to plant parts remain largely unknown, and therefore we are forced to use empirical relationships. Most current models use either a fixed allocation coefficient or fixed proportionality between certain coefficients with others modified by environmental factors. A similar situation exists for changes in productivity with stand-age – where the patterns of age-related decline in productivity are well documented, but the underlying reasons remain elusive, and rarely appear in current models of NPP. There was a brief discussion on how such effects

could be parameterised across large spatial scales, resulting in a general agreement that better understanding the underlying processes is required.

Much of the discussion focussed on belowground allocation, its potential importance and how it could be measured. Root windows, serial coring and mini-rhizotrons were suggested as some of the available methodologies. To provide some approximate figures, Kevin Tate reported that in NZ, a study in a pine plantation showed about 25% of NPP to be allocated belowground, with a comparable figure of 80% in a tussock grassland. It was noted that the difficulty in measuring allocation lies in the fact that it involves fluxes of material, and to quantify it through examination of standing stocks requires knowledge of the rates of input and the rates of output. This is especially problematic for belowground allocation, given the difficulties involved in quantifying belowground processes in general.

At the end of the discussion Miko Kirschbaum suggested a combined projects to run some common scenarios across the different models under consideration. This was not taken up at the time, but if interest is wide enough this could be the focus for follow-up work.

## Day 2 – Thursday 19 April 2001

**Morning Session** (The impact of ecosystem water balance on NPP, Other soil constraints (impedance, acidity, salinity, water logging), Nutrient uptake and use in plant growth)

**Chair:** Roger Gifford

**Rapporteurs:** Michael Battaglia, Rod Keenan

**Presenters:** Derek Eamus Rob Edis, John Evans

With respect to modelling ecosystem water budgets (and their impact on NPP) it was admitted that while some terms in the water balance equations are well studied, there are many which are poorly understood, yet they are critical for understanding water budget/NPP relations at larger spatial scales. These include groundwater dynamics, lateral flows, canopy interception, and the importance of patterns of rainfall events and their intensity (and not just the averages). Another critical gap in our current knowledge is being able to reconcile the fact that to understand regional water dynamics it is necessary to address water in the soil profile down to and beyond the rooting depth, yet our current methodologies focus on the much smaller soil volume within the first metre or so of the surface.

In the discussion of Other Soil Constraints, it was highlighted that the major constraints of salinity, soil acidity, waterlogging and soil strength are all dependent on correct quantification of the regional water budgets, further highlighting the importance of understanding both small and large-scale water dynamics in Australian ecosystems.

With respect to nutrient uptake and plant growth, the importance of the major limiting nutrients (N, P, S) in Australian ecosystems were considered, and it was noted that all of the models under consideration in the workshop account for nutrient effects on growth to some extent – but that some models handle the relationships better than others. A generalised relationship between N content of leaves and annual NPP was presented. However in discussion it was suggested that variation in this relationship in the range of foliar N contents and NPP where many Australian ecosystems reside may make meaningful extrapolation difficult.

Discussions both during and following the session raised the possibility that savanna ecosystems could be used as an example for cross-model comparisons. This is because tree/grass systems offer many challenges for estimating NEE, such as marked seasonality, the importance of groundwater in determining vegetation patterns, and the importance of disturbance (fire), among others. Particular issues raised included a discussion of the importance of fire in these ecosystems, and what the most important features would be to include in large-scale modelling studies. Two issues emerged. The first was the importance of the tree/grass balance, and in particular understanding tree mortality and canopy death in response to the disturbance. The second was a need to understand the role that fire plays in the cycling of nutrients, particularly with respect to the highly seasonal rainfall patterns which also impact on nutrient loads via. e.g. the flush of nutrients out of the system following the first rains of the season.

The major issues to emerge from the session included the importance of understanding large-scale water budgets – including a better understanding of rooting depth (which usually goes well beyond the ability to take measurements of soil properties, at least over wide areas) and defining effective rooting volumes. Although not addressed by ecosystem models at present, the effects of waterlogging & soil strength, acidity and salinity are all potentially important factors in determining the NEE of Australian ecosystems, and some effort needs to be put into the assessment of their importance, and to develop the methods for explicit descriptions in ecosystem models.

**Afternoon Session 1** (CO<sub>2</sub> concentration, Temperature effects on growth)

**Chair:** Kevin Tate

**Rapporteurs:** Roger Gifford

**Presenters:** Graham Farquhar, Marilyn Ball

A common theme running through the content of the presentations and discussions in this session was the challenge of taking what is well studied and hence well known at the individual-plant level (and other small spatial scales) and using this information to scale up through space, to eventually attain the correct representation of the processes at regional and continental scales. For example, photosynthesis at the leaf/individual level is well understood and well modelled, hence we are in a good position to start scaling up (as indeed has been done in a number of international models). In this case the limitation is not in the model representation of the underlying process, but in determining how that process is affected by all of the other factors that come into play as one moves to the larger scales. In discussion, the point was made that, when interpreting patterns of ecosystem carbon sources and sinks, it is only possible to disentangle historical/stand-age related effects from CO<sub>2</sub> fertilisation effects and recent management if the lasting effects of historical disturbances can be factored out of the analysis. At regional and continental scales this therefore requires some knowledge of the disturbance histories of the vegetation over several decades.

In Marilyn Ball's presentation on 'Temperature effects', and in the discussion that followed, two important points directly related to this scaling issue were made. The first was the concept of 'sensitivity to initial conditions', whereby events which result in seemingly small differences at one time accumulate to eventually result in large effects later on, and that the timing of those events, in this case seasonally extreme frost and heat events, is critical. The second point echoed the earlier discussion on ecosystem water balances, and highlighted that the 'average' climate, rainfall, etc. is often an inappropriate descriptor of the system, as it is the variability, and in particular the occurrence of extreme events, which are critical to determining the system behaviour, especially changes in species composition. This has important implications for modelling NEE at continental scales, as it is often tempting to use e.g. 'averaged' climate values as parameter estimates when little is known about the underlying processes, yet by using such averages introduces the danger of excluding critical drivers of the system.

Of the models under consideration in the workshop only CenW specifically includes the effects of extreme temperature events on NEE processes. None of the models allow for the accumulation of the effects of events occurring earlier in time.

**Afternoon Session 2** (Linking above and belowground processes, Interactions between carbon dynamics and nutrient mineralisation)

**Chair:** Rod Keenan

**Rapporteurs:** Marc Corbeels, Craig Barton

**Presenters:** Miko Kirschbaum, Peter Grace

The importance of including nutrient cycles, and in particular nitrogen, when considering ecosystem carbon gain and loss was further highlighted in the presentations in this session. In particular, the importance of incorporating the feedbacks between plant growth and the flux of nutrients from above- to below ground via litterfall was identified as a feature of NEE modelling that demands attention. For example, using the CenW model, Miko Kirschbaum showed how omitting a negative feedback between growth and N availability can significantly alter predictions of NPP. If growth is enhanced, it can lead to increased litter production, and the increased amount of soil organic carbon can then act to immobilise nitrogen in the soil and thereby reduce nitrogen availability for plants. If this feed-back effect is not simulated, it would increase the expected variability in NPP in response to various perturbations.

The importance of considering the role of soil microbes in nutrient cycling, and in particular their role in fixing and immobilising N was highlighted by Peter Grace, who also spent some time considering more general issues of modelling ecological systems, with particular reference to the distinction between model components and parameters which on the one hand are conceptual and 'modelable' vs. those which are more pragmatic, in the sense that they might not encapsulate all of the detail possible, but are defined in such a way that they can be readily 'measured' and quantified empirically. This provided the impetus for the discussion which followed.

It was generally agreed that when considering soil organic matter, it is not strictly accurate to define separate 'pools' of carbon and nutrients, with each pool having a characteristic turnover time. In reality, soil organic matter constitutes a continuum of turnover times without discrete boundaries, yet in the models in current use the pools are regarded as discrete entities. There was some discussion about the 'minimum requirements' for an effective continental model of carbon

stocks and fluxes. Whilst the general consensus was such a question is difficult to answer, over and above the obvious statement that a model must be as simple as possible but no more, there was general agreement that nutrients (possibly more than just N) should be included as a constraint. It was suggested that obtaining adequate data on N, P and other nutrient cycles at the continental scale could be a limiting factor to progress, although it was pointed out that the tendencies for conservation of mass-ratios among the major elements provides useable constraints. A number of contributors to the discussion highlighted the importance of keeping the modelling as simple as possible, due to both practicalities of running a spatially-explicit simulation exercise over a continent the size of Australia, and also for the data requirements for both model parameterisation and validation.

## Day 3 – Friday 20 April 2001

---

**Morning Session** (Temperature and moisture effects on decomposition rate, Soil texture effects on decomposition and soil C storage, pH, aluminium and other factors that can inhibit decomposition rates, Charcoal and other resistant organic matter)

**Chair:** Martin Schutz

**Rapporteurs:** John Evans, Kevin Tate

**Presenters:** Keryn Paul, Evelyn Krull, Ram Dalal, Jan Skjemstad

Soil carbon dynamics, and in particular the decomposition of organic matter and soil building processes, are of central importance in understanding the carbon cycle, yet it is in these areas that much of our current knowledge is lacking. Sensitivity of decomposition rates to temperature and water is included in all models considered, however the way in which these effects are incorporated is through simple 'modifier' functions - empirical functions which generate a scalar multiplier whose value is dependent upon the current temperature or water status. Given the complexity of the processes involved, and the spatial variability in both temperature and water at all spatial scales, it would seem that this is the only feasible approach to take. However, in discussion it was highlighted that care must be taken to make sure that the underlying empirical relationships are both robust, and are able to be validly applied outside of the experimental conditions within which they were derived.

In the consideration of soil texture effects on decomposition and soil C storage, it is clear that both chemical and physical

'protection' of organic matter in the soil matrix plays an important role in setting absolute decomposition rates, and hence in determining both the stocks and fluxes of belowground carbon. Such effects are not currently considered in NEE models, despite the potential for manipulating the soil's protective capacity as a means of managing terrestrial carbon dynamics. There was some discussion over the current status of Australian soils, the potential to increase their protective capacity, and how this might vary between soils which had undergone prior disturbance, such as agricultural soils, and soils under more natural conditions. Other factors that were considered, and which influence decomposition include pH and aluminium. Australian ecosystems in which these influences might be important, and the capacity for building them into our modelling frameworks, need to be assessed

In the consideration of chemically resistant soil carbon, the distinction was drawn between the different pool definitions that have been used, the various turnover times commonly associated with those pools, and the current methods used in their estimation.

In determining the carbon stocks at large spatial scales two issues were raised. The first considered the data availability for estimating broadscale estimates of bulk-density. At present the best data available are based on general relationships with soil type, particle size distributions etc. The second issue was the potential for large-scale (landscape → regional) lateral spread of carbon via windblown and waterborn material. This may be particularly important in Australia as fires are widespread, resulting in potentially significant lateral transport. There is also evidence that stores of carbon in river sediments, particularly in flooded areas, can be very high. A suggestion was made that the importance of such lateral carbon movement in the Australian context be examined. It was also noted that much of our available data on belowground carbon dynamics comes from grassland/agricultural systems, and that data under forest conditions is under-represented. This is particularly important, given the contribution of Australia's forested ecosystems towards the total continental carbon inventory.

**Afternoon Session** (Soil disturbance (cultivation) effects on decomposition and soil C storage, Litter quality and quantity).

**Chair:** John Raison

**Rapporteurs:** Evelyn Krull, Belinda Medlyn

**Presenters:** Phil Polglase, Marc Corbeels

Mechanical disturbance has many impacts on both the structure and function of soils, and has the potential to

influence the rates of carbon sequestration and loss. One difficulty in studying these effects is that decline in TOC following disturbance is often confounded with changes in the management regime, such as the subsequent planting of crops with different productivities, which leads to changes in the rates of carbon-input to the soil. Although wind and water erosion are potentially important forces, the discussion mostly focussed on agriculture, plantation forestry and other managed systems. The key question is whether cultivation and other management practices result in a loss of carbon from soils, such as whether site preparation before establishing new plantations can lead to a decrease in soil organic carbon. With respect to the practice of direct drilling vs. minimum tillage, under Australian conditions the situation is confounded by other factors, such as lower-input crops that are routinely used under no-till situations. Some results were presented that showed that over long periods of time, disturbed and undisturbed sites did not differ significantly in their rates of carbon loss.

Globally there is a strong relationship between total litterfall in forested ecosystems and total soil respiration. Litter quality, in terms of its chemical properties, the physical sizes of particles, the presence of microbial inhibitory substances and the activity of the decomposers also contribute to determine the effective rates of litter decomposition. With respect to modelling the process, most models assume linear first-order decay processes.

During discussion, the question was raised on what the simplest approach to take would be in terms of a continental modelling capacity. It was suggested that the vegetation could be stratified into a number of biomes (10 was the figure proposed), and that litter qualities and behaviours could be assigned to each. It was the feeling of the presenters that the appropriate information at this scale for the Australian environment is available.

It was noted that larger scale processes, such as climatic change and disturbance, have the potential to cause large changes in the microbial micro-environment, and hence have the potential to override the finer-scaled processes considered here.

# NEE Workshop: CRC Participants

---

Jeffery Baldock  
CSIRO Land and Water  
jeff.baldock@greenhouse.crc.org.au

Marilyn Ball  
Research School of Biological Sciences,  
The Australian National University  
marilyn.ball@greenhouse.crc.org.au

David Barker  
Research School of Biological Sciences,  
The Australian National University  
david.barker@greenhouse.crc.org.au

Michele Barson  
CRCGA & Bureau of Rural Sciences.  
michele.barson@greenhouse.crc.org.au

Craig Barton  
Forest Research & Development Division,  
State Forests of NSW  
craig.barton@greenhouse.crc.org.au

John Carter  
Qld Department of Natural Resources  
and Mines  
john.carter@greenhouse.crc.org.au

Annette Cowie  
Forest Research & Development Division,  
State Forests of NSW  
annette.cowie@greenhouse.crc.org.au

Ram Dalal  
Qld Department of Natural Resources  
and Mines  
ram.dalal@greenhouse.crc.org.au

Ian Davies  
Research School of Biological Sciences,  
The Australian National University  
ian.davies@greenhouse.crc.org.au

Everard Edwards  
The Research School of Biological  
Sciences,  
The Australian National University  
everard.edwards@greenhouse.crc.org.au

John Evans  
Research School of Biological Sciences,  
The Australian National University  
john.evans@greenhouse.crc.org.au

Graham Farquhar  
Research School of Biological Sciences,  
The Australian National University  
graham.farquhar@greenhouse.crc.org.au

Roger Gifford  
CSIRO Plant Industry  
roger.gifford@greenhouse.crc.org.au

Lan Bin Guo  
CSIRO Plant Industry  
lanbin.guo@greenhouse.crc.org.au

Rod Keenan  
Bureau of Rural Sciences  
rod.keenan@greenhouse.crc.org.au

Miko Kirschbaum  
CSIRO Forestry and Forest Products  
miko.kirschbaum@greenhouse.crc.org.au

Evelyn Krull  
CSIRO Land and Water  
evelyn.krull@greenhouse.crc.org.au

Brendan Mackey  
Department of Geography,  
The Australian National University  
brendan.mackey@greenhouse.crc.org.au

Greg McKeon  
Qld Department of Natural Resources  
and Mines  
greg.mckeon@greenhouse.crc.org.au

Angela Newey  
CSIRO Plant Industry  
angela.newey@greenhouse.crc.org.au

Ian Noble (CEO, CRCGA)  
Research School of Biological Sciences,  
The Australian National University  
ian.noble@greenhouse.crc.org.au

Craig Pearson  
Bureau of Rural Sciences  
craig.pearson@greenhouse.crc.org.au

Wayne Phippen  
Research School of Biological Sciences,  
The Australian National University  
wayne.phippen@greenhouse.crc.org.au

John Raison  
CSIRO Forestry and Forest Products  
john.raison@greenhouse.crc.org.au

Kema Ranatunga  
Bureau of Rural Sciences  
kema.ranatunga@greenhouse.crc.org.au

Lucy Randall  
Bureau of Rural Sciences  
lucy.randall@greenhouse.crc.org.au

Michael Roderick  
Research School of Biological Sciences,  
The Australian National University  
michael.roderick@greenhouse.crc.org.au

Stephen Roxburgh  
Research School of Biological Sciences,  
The Australian National University  
stephen.roxburgh@greenhouse.crc.org.au

Martin Schutz  
CRC for Greenhouse Accounting  
martin.schutz@greenhouse.crc.org.au

Jan Skjemstad  
CSIRO Land and Water  
jan.skjemstad@greenhouse.crc.org.au

Julie Styles  
Research School of Biological Sciences,  
The Australian National University  
julie.styles@greenhouse.crc.org.au

# NON-CRC Participants

---

Brian Atwell  
Macquarie University  
batwell@rna.bio.mq.edu.au

Troy Baisden  
Landcare Research, New Zealand  
baisdenT@landcare.cri.nz

Michael Battaglia  
CSIRO Forestry and Forest Products and  
Cooperative Research Centre for  
Sustainable Production Forestry  
michael.battaglia@csiro.au

Chris Beadle  
Cooperative Research Centre for  
Sustainable Production Forestry and  
CSIRO Forestry and Forest Products  
chris.beadle@csiro.au

Nicholas Coops  
CSIRO Forestry and Forest Products  
nicholas.coops@csiro.au

Marc Corbeels  
CSIRO Forestry and Forest Products  
marc.corbeels@csiro.au

Derek Eamus  
Department of Environmental Science,  
University of Technology  
derek.eamus@uts.edu.au

Robert Edis  
Institute of Land and Food Resources,  
University of Melbourne  
roberte@unimelb.edu.au

Peter Grace  
Sinclair Knight Merz  
pgrace@skm.com.au

Beverley Henry  
Qld Department of Natural Resources  
and Mines  
beverley.henry@dnr.qld.gov.au

Brian Keating  
CSIRO Sustainable Ecosystems  
brian.keating@csiro.au

Heather Keith  
CSIRO Forestry and Forest Products  
heather.keith@csiro.au

Joe Landsberg  
Landsberg Consulting  
joe.landsberg@landsberg.com.au

Ray Leuning  
CSIRO Land and Water  
ray.leuning@csiro.au

Beth Loveys  
Visiting Fellow, Research School of  
Biological Sciences,  
The Australian National University  
loveys@rsbs.anu.edu.au

Don McGuire  
Forestry South Australia  
mcguire@saugov.sa.gov.au

Belinda Medlyn  
School of Biological Sciences,  
University of New South Wales  
b.medlyn@unsw.edu.au

Andrew Moore  
CSIRO Plant Industry  
andrew.moore@csiro.au

Keryn Paul  
CSIRO Forestry and Forest Products  
keryn.paul@csiro.au

David Pepper  
School of Biological Science,  
University of New South Wales  
d.a.pepper@unsw.edu.au

Philip Polglase  
CSIRO Forestry and Forest Products  
philip.polglase@csiro.au

Merv Probert  
CSIRO Sustainable Ecosystems  
merv.probert@csiro.au

Gary Richards  
Australian Greenhouse Office  
gary.richards@ea.gov.au

Peter Sands  
CSIRO Forestry and Forest Products and  
Cooperative Research Centre for  
Sustainable Production Forestry  
peter.sands@csiro.au

Kevin Tate  
Landcare Research, New Zealand  
tatek@landcare.cri.nz

Craig Trotter  
Landcare Research, NZ  
trotterc@landcare.cri.nz

Ying Ping Wang  
CSIRO Atmospheric Research  
yingping.wang@csiro.au

Anthony Whitbread  
CSIRO Sustainable Ecosystems  
anthony.whitbread@csiro.au