Balances of Water, Carbon, Nitrogen and Phosphorus in Australian Landscapes: (2) Model Formulation and Testing

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Executive Summary

This report is a scientific and technical description of the formulation of a model for the long-term average or "statistical steady state" balances of water, carbon, nitrogen and phosphorus over large land regions. The report is a companion to another [Raupach et al. (2001), Landscape Balances of Water, Carbon, Nitrogen and Phosphorus: (1) Project Description and Results (CLW Technical Report 40/01), hereafter Report 1], which describes the main results. The work was undertaken under Project 5.4a of the National Land and Water Resources Audit, "Landscape Nutrient Flux and Water Balance".

A new model of the landscape dynamics of water, C, N and P has been developed for this work. The model, called Bios, is founded on the mass balances for water, C, N and P, together with "phenomenological equations" for the coupled water, C, N and P fluxes at large scales. Two versions of the model have been constructed: an evolving or time-dependent model with a time step of 1 day (BiosEvolve) and an equilibrium or statistically steady-state model (BiosEquil). All results presented in Report 1 are from BiosEquil. The governing equations in both models are identical, with the exceptions that BiosEquil uses a simplified treatment of the water balance and time-averaged forms of equations for some C, N and P fluxes.

This report concentrates on BiosEquil. It first defines some general properties of landscape biogeochemistry models, and formalises them as dynamical systems (Section 2). Then (in Section 3) it formulates the balance equations for water, carbon, nitrogen and phosphorus. The phenomenological equations for the fluxes are then set out. These include Net Primary Productivity (NPP) of carbon (Section 4); the steady-state solutions for NPP and mineral nutrients, including estimation of nutrient fluxes due to disturbance (Section 5); the fluxes of C, N and P through litter and soil pools (Section 6); and the water fluxes (Section 7). Section 8 outlines the input data and model operation. Section 9 describes the model calibration and testing process, and presents some sample results. Section 10 gives a concluding summary.

The major results are presented in Report 1. In brief, they are:

Net Primary Production: The most important driver of the coupled balances of water, carbon and nutrients is NPP, equal to plant photosynthesis less plant respiration. This is the carbon or biomass yield of the landscape, available for use by animals and humans. On the Australian continent the spatial distribution of NPP broadly follows rainfall, but with additional influences from saturation deficit or air dryness (through its effect on water use efficiency), and also from light. The influence of light is significant only in Tasmania, because light is not a limiting resource elsewhere. The influence of saturation deficit implies that there is less NPP per unit rainfall in the north of the continent (where the air is dry on average) than in the south. This is a basic physiological constraint on plant growth and thence on agricultural productivity. NPP is also strongly increased in agricultural regions by nutrient inputs, and by water inputs through irrigation.

Carbon stores: The C stores in biomass, litter and soil are strongly controlled by NPP (hence rainfall and saturation deficit). In addition, C stores are modulated by temperature: for a given NPP, there is less C storage in the tropics than in temperate regions because tropical C stores decay faster.
**N and P stores:** The stores of plant-available N and P, including both organic and mineral stores, are strongly coupled with NPP like the C stores. Only a small fraction (of order 1%) of the plant-available N and P is in mineral form.

**Dissolved N and P Concentrations in Soil Water:** Dissolved N and P concentrations in soil water have a completely different spatial pattern to NPP, as the main climate driver on these concentrations is saturation deficit (air dryness) rather than rainfall. Hence, the N and P concentrations in soil water decrease as the climate-average air dryness increases from temperate to semi-arid tropical environments.

**Effects of agriculture on NPP and the landscape stores of C, N and P:** Agricultural nutrient inputs (including N and P from fertilisation and N from sown legumes) have led to regional-scale increases (relative to pre-agricultural conditions) of up to a factor of 2 for NPP and the stores of C, organic N and organic P, and up to a factor of 5 for mineral N, plant-available mineral P and the N and P concentrations in soil water. These increases are concentrated in southern agricultural regions in WA, SA, Victoria and NSW. The influence of irrigation on NPP and the stores of N and P is locally large (especially in economic terms because of the prevalence of high-value commodities in irrigated areas) but its effect on continental aggregate stores and fluxes is relatively small because the irrigated area of the continent is small. Likewise, there is only a small influence at continental-aggregate scale on NPP and C, N and P stores from offtakes of agricultural products, though local effects may be significant.

**N Balance:** Before the advent of European-style agriculture, the N balance was dominated by input of N from natural fixation, with a small contribution from atmospheric N deposition. The balancing losses of N occurred through a mixture of volatilisation, leaching and disturbance (herbivory and fire). The spatial distributions of all these N fluxes were closely connected with the NPP distribution. With the advent of European-style agriculture, the N budget changed substantially: the largest term remains fixation, greatly enhanced in agricultural areas by sown legumes. Losses occur through disturbance (primarily herbivory by stock), leaching and volatilisation. The contribution of agricultural offtakes is negligible continentally but can be significant locally.

**Continental-aggregate stores and fluxes of C, N and P:** We estimate that the mean continental NPP is 0.96 GtC/year, and that nearly 60 Gt of carbon is stored on the continent in biomass and soil. Agricultural nutrient inputs have increased the continental NPP by 5%, the continental mineral N store by 13% and the continental mineral P store by 8%.

**Uncertainties:** On regions of around 100 km by 100 km, the NPP has an uncertainty of around 30%, the organic C, N and P stores around 50%, and the mineral N and P stores around 100%. Estimates of change (current / pre-agricultural ratios) have uncertainties of around 50%. The predictions should never be interpreted at single-cell (5 km) scale, but rather should be used to analyse large patterns.
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1 Introduction

This is the second of two technical reports summarising the outcome of Project 5.4a of the National Land and Water Resources Audit, "Landscape Nutrient Flux and Water Balance". It is a supplement to a companion report, Landscape Balances of Water, Carbon, Nitrogen and Phosphorus: (1) Project Description and Results (Raupach et al. 2001, hereafter Report 1), which provides a non-mathematical account of the framework and results of the project. The present report (Report 2) describes in detail the hypotheses, mathematical formulation and testing of the model used to deliver the results.

A new model of the landscape dynamics of water, C, N and P has been developed for this work. The model, called Bios, is founded on the mass balances for water, C, N and P, together with "phenomenological equations" for the coupled water, C, N and P fluxes at large scales. Two versions of the model have been constructed: an evolving or time-dependent model with a time step of 1 day (BiosEvolve) and an equilibrium or statistically steady-state model (BiosEquil). All results presented in Report 1 are from BiosEquil. The structure of the governing equations in both models is identical, with the exceptions that BiosEquil uses a simplified treatment of the water balance and time-averaged forms of some of the equations for fluxes in the C, N and P cycles. This report describes the structure of both models, concentrating mainly on BiosEquil but including reference to BiosEvolve as appropriate for completeness.

The report is organised as follows: Section 2 defines some general properties of landscape biogeochemistry models, and formalises them as dynamical systems. Section 3 formulates the balance equations used in both BiosEvolve and BiosEquil. The next sections set out the equations for the fluxes, concentrating on the Net Primary Productivity (NPP) in Section 4, the steady-state solutions for NPP and mineral nutrients (including estimation of nutrient fluxes due to disturbance) in Section 5; the fluxes of C, N and P through litter and soil pools, in Section 6; and water fluxes in Section 7. Section 8 outlines the input data and model operation. Section 9 describes the model calibration and testing process, and presents some sample results. A summary and conclusions are given in Section 10.

2 Biogeochemical Structure

2.1 Pools, Stores, Pathways and Fluxes

The aim is to determine the dynamical behaviour of the water, C, N and P in a landscape. This is done by defining a set of "pools", each being a functional component of the matter in a landscape, such as the C, N or P in leaves, wood or roots. A "store" is the amount of matter (water, C, N or P) in a given pool (with the dimension of mass or moles per unit ground area). A "pathway" is a functional route by which matter is transferred between pools, and a "flux" is the amount of matter per unit time transferred through a given pathway (with the dimension of mass or moles per unit ground area per unit time).

Each pool is defined by three attributes: a chemical species (such as water, C, N or P); a biogeochemical function (for instance the C in leaves or soil microbes); and a control volume (a region of space such as the leaves, woody tissue, roots or soil in a specified layer, on a piece of landscape with specified boundaries in the horizontal).
In this work, the horizontal boundaries of individual control volumes are defined by a 0.05° (approximately 5 km) grid. There are 278190 such grid cells in the spatial domain considered here, spanning the Australian continent including Tasmania and near-shore islands.

Appendix A outlines the general mathematical formulation of the model. Briefly, the stores and fluxes are governed by two kinds of equation: conservation equations of the general form \( dX/dt = \sum(F) \) where \( X \) is a set of stores and \( F \) is the set of fluxes causing matter to enter (or leave) these stores, with the sum running over fluxes acting on individual stores; and phenomenological equations which specify the fluxes \( F \) as functions \( F(X,M,P) \) of the stores \( X \), the external forcing variables \( M \) acting on the system (including meteorological, land use and land management variables) and process parameters \( P \). The conservation equations depend only on mass conservation, are linear, scale-independent, and differential in time. The phenomenological equations are empirical statements of the processes governing the fluxes. They are nonlinear, scale-dependent in general, and algebraic. *BiosEvolve* is a time-differential model in which the in which the stores \( X \) and fluxes \( F \) are solved as functions of time, using the conservation and phenomenological equations together with specified time-dependent forcing variables \( M \) and parameters \( P \). *BiosEquil* is a statistically steady-state model in which all variables \( (X,F,M,P) \) are averaged over a time long enough for storage changes to be small relative to fluxes. In this case the conservation equations reduce to algebraic forms: \( \sum[F(X,M,P)] = 0 \). Hence the whole model becomes algebraic. The phenomenological equations in this formulation describe the averaged fluxes rather than their short-term counterparts.

### 2.2 Total Landscape Balances

Figure 1 gives a schematic, highly aggregated view for the pools of water, C, N and P stores considered in this work, and the pathways that connect them to each other and the external environment. From this figure, the following mass balance equations can be written for the total landscape stores of water and biologically active or available C, N and P (in units of mass or moles per unit area) stored in plants, litter and soil to the plant rooting depth:

**Water:**

\[
\begin{align*}
W_{Tot} & = [\text{Plant Water}] + [\text{Soil Water}] \\
\frac{dW_{Tot}}{dt} & = [\text{Rain}] - [\text{Canopy Transpiration}] - [\text{Soil Evaporation}] \\
& - [\text{Interception Evaporation}] - [\text{Runoff}] - [\text{Drainage}]
\end{align*}
\]

(2.1)

**Carbon:**

\[
\begin{align*}
C_{Tot} & = [\text{Plant C}] + [\text{Litter C}] + [\text{Soil C}] \\
\frac{dC_{Tot}}{dt} & = [\text{Net Primary Production (NPP)}] - [\text{Heterotrophic Respiration}] \\
& - [\text{Transport (Water, Wind)}] - [\text{Disturbance (Herbivory, Fire, Offtake)}]
\end{align*}
\]

(2.2)
Nitrogen:

\[
N_{tot} = [\text{Plant N}] + [\text{Litter N}] + [\text{Soil Organic N}] + [\text{Plant-Available Mineral N}]
\]

\[
\frac{dN_{tot}}{dt} = [\text{N Fertilisation}] + [\text{N Fixation}] + [\text{Atmospheric N Deposition}]
- [\text{Gaseous N Loss}] - [\text{N Leaching}]
- [\text{Transport (Water, Wind)}] - [\text{Disturbance (Herbivory, Fire, Offtake)}]
\]

Phosphorus:

\[
P_{tot} = [\text{Plant P}] + [\text{Litter P}] + [\text{Soil Organic P}] + [\text{Plant-Available Mineral P}]
\]

\[
\frac{dP_{tot}}{dt} = [\text{P Fertilisation}] + [\text{Atmospheric P Deposition}] + [\text{Weathering of P}]
- [\text{P Leaching}] - [\text{Exchange with Soil-Bound P}]
- [\text{Transport (Water, Wind)}] - [\text{Disturbance (Herbivory, Fire, Offtake)}]
\]

The total mass balances are defined here in a control volume consisting of the plants and soil root zone on a specified piece of landscape. This control volume deliberately excludes several components of the terrestrial system: (1) aquifers below the plant rooting depth; (2) waterways, rivers and estuaries; and (3) repositories of harvested product in warehouses, dwellings and towns. Each of these additional components can be subjected to mass balance analysis by defining appropriate control volumes.

2.3 Functional Pools and Pathways for Carbon, Nitrogen and Phosphorus

The aggregate pools and pathways for C, N and P shown in Figure 1 are resolved for modelling purposes into a number of components. These are shown in Figure 2 for carbon and in Figure 3 for nitrogen and phosphorus. Figure 4 shows the pathways into and out of the mineral N and P pools.

**Pools:** For C, N and P, the landscape pools are broadly divided into living plants, litter, soil organic matter (SOM), and inorganic or mineral N and P. Within these broad classes, several finer functional distinctions are resolved as follows (see Figures 2 and 3):

- **Plant pools** \((\text{Pla} = \text{Lea} + \text{Woo} + \text{Roo})\):
  
  - **Lea:** living leaf, including all cohorts from first growth to senescence;
  - **Woo:** all above-ground living wood including stem, heartwood, branches and twigs;
  - **Roo:** all fine and coarse living roots, subdivided into two soil layers;

- **Litter pools** \((\text{Lit} = \text{Res} + \text{Met} + \text{Str})\):
  
  - **Res:** a plant residue pool which collects all detritus resulting from death of living material in the plant (leaf, wood, root) pools;
  - **Met:** a metabolic or fast-turnover litter pool;
  - **Str:** a structural litter or slow-turnover litter pool;
SOM pools (SOM = Act + Hum + Pas):
  Act: an active or microbial pool for SOM;
  Hum: a slow or humic SOM pool;
  Pas: a pool for passive or inert SOM.

Inorganic N and P pools:
  Mnl: the mineral nitrogen pool (N_{Mnl}), including mineral N in all oxidation states;
  Pri: the primary, plant-available or soluble phosphorus pool (P_{Pri});
  Sec: the secondary pool of insoluble phosphorus (P_{Sec});
  Occ: the occluded pool of insoluble phosphorus (P_{Occ}).

Note that:

- All pools are designated by three-letter identifiers.
- The organic (plant, litter and soil) pools are defined for each of C, N and P, with an identical pool structure in each case.
- All below-ground pools (Roo, Res, Met, Str, Act, Hum, Pas, Mnl, Pri, Sec, Occ) are defined for two soil layers, corresponding to the A and B soil horizons.
- A key property of all organic pools is that the ratios among C, N and P are constrained to well-defined ranges, different for each pool.
- The litter and SOM pools are chosen to correspond fairly closely with those defined in the Century model for biogeochemical cycling in the soil (Parton et al. 1987, 1988, 1993). Century is a widely-used model which is the parent of numerous other biogeochemical models developed since about 1990. It has been extensively parameterised, giving initial guidance on parameter choices in Bios.
- Three mineral phosphorus pools are defined, corresponding to different levels of plant availability or chemical reactivity (Figure 5). These are (1) the primary mineral P pool (Pri), consisting mainly of soluble PO$_4^{3-}$ either in solution or electrostatically bound to soil particle surfaces; (2) the secondary mineral P pool (Sec), consisting mainly of insoluble P which is ionically bound to soil particle surfaces; and (3) the occluded mineral P pool, consisting mainly of insoluble P which is both ionically bound and physically protected by being inside soil particles rather than on their surfaces. We assume that the plant-available and soluble P pools are identical, though in reality the question of how much of the P in a landscape is plant-available is complex and is affected by a variety of strategies used by plants to mobilise P (for instance the exudation of organic acids from roots). A further complication is that the various chemical extraction methods used to determine P in laboratory soil tests do not completely align with the primary, secondary and occluded pools as defined above (Figure 5).
- The stores for C, N and P are denoted C_{Aaa}, N_{Aaa}, P_{Aaa}, with units of mass per unit area. The generic form is X_{Aaa,j} where X is one of C, N and P, Aaa is one of the above three-letter identifiers for a particular pool, and j is the number of the soil layer (for in-ground pools only).
- The total landscape stores in Equations (2.2) to (2.4) are defined as the total landscape C, N and P available for participation in the plant cycle. Thus:
\[
C_{\text{Tot}} = C_{\text{Lea}} + C_{\text{Woo}} + \sum_{j=1}^{2} \left\{ C_{\text{Roo}} + C_{\text{Lij}} + C_{\text{Somj}} \right\}
\]
\[
= C_{\text{Lea}} + C_{\text{Woo}} + \sum_{j=1}^{2} \left\{ C_{\text{Roo}} + C_{\text{Resj}} + C_{\text{Meij}} + C_{\text{Strj}} + C_{\text{Actj}} + C_{\text{Humj}} + C_{\text{Pasj}} \right\} \tag{2.5}
\]
\[
N_{\text{Tot}} = N_{\text{Lea}} + N_{\text{Woo}} + \sum_{j=1}^{2} \left\{ N_{\text{Roo}} + N_{\text{Lij}} + N_{\text{Somj}} \right\}
\]
\[
= N_{\text{Lea}} + N_{\text{Woo}} + \sum_{j=1}^{2} \left\{ N_{\text{Roo}} + N_{\text{Resj}} + N_{\text{Meij}} + N_{\text{Strj}} + N_{\text{Actj}} + N_{\text{Humj}} + N_{\text{Pasj}} \right\} \tag{2.6}
\]
\[
P_{\text{Tot}} = P_{\text{Lea}} + P_{\text{Woo}} + \sum_{j=1}^{2} \left\{ P_{\text{Roo}} + P_{\text{Lij}} + P_{\text{Somj}} \right\} + \sum_{j=1}^{2} P_{\text{Prij}}
\]
\[
= P_{\text{Lea}} + P_{\text{Woo}} + \sum_{j=1}^{2} \left\{ P_{\text{Roo}} + P_{\text{Resj}} + P_{\text{Meij}} + P_{\text{Strj}} + P_{\text{Actj}} + P_{\text{Humj}} + P_{\text{Pasj}} \right\} + \sum_{j=1}^{2} P_{\text{Prij}} \tag{2.7}
\]

where the contributions from the upper and lower soil layers are shown explicitly. The mineral stores include only the plant-available mineral components, that is, \(N_{\text{Mnl}}\) in the case of nitrogen and \(P_{\text{Pri}}\) in the case of phosphorus. The total P store as defined here excludes the slower, more inert mineral P pools (\(P_{\text{Sec}}, P_{\text{Occ}}\)) which are assumed here to be not directly available for plant uptake. These pools buffer the plant-available P pool (\(P_{\text{Pri}}\)), and also contribute at least partly to the mineral P measured by most laboratory soil tests (Figure 5). Mineral carbon pools, such as char, are considered to be inert.

- It is also useful to define the total plant-available nitrogen (\(N_{\text{Avl}}\)) and plant-available phosphorus (\(P_{\text{Avl}}\)) in the soil root zone encompassing both soil layers.

\[
N_{\text{Avl}} = \sum_{j=1}^{2} \left\{ N_{\text{Lij}} + N_{\text{Somj}} \right\} + \sum_{j=1}^{2} N_{\text{Meij}} \tag{2.8}
\]
\[
P_{\text{Avl}} = \sum_{j=1}^{2} \left\{ P_{\text{Lij}} + P_{\text{Somj}} \right\} + \sum_{j=1}^{2} P_{\text{Prij}} \tag{2.9}
\]

so that \(N_{\text{Tot}} = N_{\text{Pla}} + N_{\text{Avl}}\) and \(P_{\text{Tot}} = P_{\text{Pla}} + P_{\text{Avl}}\).

**Pathways:** Figures 1 to 4 show (at different levels of detail) the pathways by which C, N and P are transferred between the above pools. These pathways are either external or local-cycling. External pathways transfer C, N and P between the external environment and the total landscape stores \(C_{\text{Tot}}, N_{\text{Tot}}\) and \(P_{\text{Tot}}\) (see Equations (2.5), (2.6) and (2.7)), while local-cycling pathways transfer matter locally among the various landscape pools. The major pathways of both kinds are as follows:

- **Net Primary Production** is an external pathway transferring C from the atmosphere into the plant (\(\text{Lea, Woo, Roo}\)) pools, representing plant growth.
- As plants grow, they also take up N and P from the mineral (\(N_{\text{Mnl}}, P_{\text{Pri}}\)) pools in the soil, to maintain the tightly constrained ratios among C, N and P in the \(\text{Lea, Woo and Roo}\) pools. This is a local-cycling pathway.
• Plants return C, N and P to the soil through litterfall via the litter (Res, Met and Str) pools, in a set of local-cycling pathways. Of the litter pools, Res is a very rapid-turnover holding pool with no dynamic significance, used to collect litter for partitioning into Met (metabolic litter) and Str (structural litter). The pathway through the Met pool describes the decay of soft plant tissue, and the pathway through Str the decay of woody, lignified material.

• In a further set of local-cycling pathways, microbial activity breaks down litter from the Met and Str pools into the soil organic (Act, Hum, Pas) pools. These are distinguished by different turnover times and different ratios among C, N and P.

• Microbial activity is accompanied by Heterotrophic Respiration, an external pathway returning C to the atmosphere.

• Also, the microbial activity is accompanied by Mineralisation which transfers N and P from the organic to the mineral (N_Mat, P_Pri) pools, and Immobilisation which operates in the reverse direction. The N and P fluxes through these local-cycling pathways are determined by the need to preserve constrained stoichiometric ratios of C, N and P in the different litter and soil pools.

• A further product of the microbial activity is Gaseous N Loss, which we treat as a proportional "transaction cost" on mineralisation, immobilisation and N flows between litter and SOM pools.

• N Fixation by legumes, Atmospheric N Deposition and N Fertilisation are external pathways into the N_Mat pool, and P Fertilisation is an external input to the P_Pri pool. N Leaching and P Leaching are external pathways out of these pools.

• Exchange with Soil-Bound P accounts for the buffering of plant-available P (P_Pri) by exchange with more inert mineral P pools (P_Sec, P_Occ).

• Several external pathways identified formally in Equations (2.2) to (2.4) are not considered further in the present versions of BiosEvolve or BiosEquil. The movement of sediment and attached nutrients by Water Transport is treated elsewhere in the National Land and Water Resources Audit (Prosser et al. 2001). Wind Transport and (especially) Fire Fluxes are potentially significant but could not be treated with the time and resources available. Atmospheric P Deposition is probably too small to warrant treatment. Weathering of P is neglected because it is too slow to have significant influence at management time scales. All these pathways could be included in the present framework by appropriate extensions.

3 Mass Balance Equations

In this section, the total mass balances for water, C, N and P (Equations (2.1) to (2.4)) are partitioned into mass balance equations for the component pools shown in Figure 1.

3.1 Soil Water

Consider a total soil water store with a control volume extending from the soil surface to the plant rooting depth, in which the water store is \( W \). The fluxes moving water into and out of this store are defined by the balance equation
\[
\frac{dW}{dt} = \left[ F_{\text{W(Rain)}} + F_{\text{W(Irrig)}} - F_{\text{W(Elter)}} \right] - F_{\text{W(EVeg)}} - F_{\text{W(ESoil)}} - F_{\text{W(Runoff)}} - F_{\text{W(Leach)}} \\
= F_{\text{W(EffRain)}} - F_{\text{W(EVeg)}} - F_{\text{W(ESoil)}} - F_{\text{W(Runoff)}} - F_{\text{W(Leach)}}
\] (3.1)

Water fluxes are denoted \( F_{\text{W(Path)}} \) where \( (\text{Path}) \) is a water flux pathway: \( \text{(Rain)} = \) net precipitation including snow; \( \text{(Irrig)} = \) irrigation; \( \text{(Elter)} = \) evaporation of intercepted water; \( \text{(EVeg)} = \) vegetation transpiration; \( \text{(ESoil)} = \) soil evaporation; \( \text{(Runoff)} = \) surface runoff; \( \text{(Leach)} = \) leaching or deep drainage through the lower boundary of the soil water control volume.

The effective precipitation \( [F_{\text{W(EffRain)}} = F_{\text{W(Rain)}} + F_{\text{W(Irrig)}} - F_{\text{W(Elter)}}] \) is the precipitation reaching the soil surface accounting for rainfall, irrigation and canopy interception loss.

Formally, the water store \( W \) has units [kg water m\(^{-2}\)], and water fluxes \( F_{\text{W(Path)}} \) have dimension [kg water m\(^{-2}\) s\(^{-1}\)]. However, it is more convenient to use units for \( W \) of metres (or millimetres) of liquid water, and units for \( F_{\text{W(Path)}} \) of [m (liquid water) year\(^{-1}\)] or [mm (liquid water) year\(^{-1}\)]. Here \( W[m] = W[kg\text{ water m}^{-2}] / \rho_w \), where \( \rho_w \) is the density of liquid water [kg water m\(^{-3}\)], and likewise for \( F_{\text{W(Path)}} \).

\textit{BioSequilibrium} uses a single water store governed by Equation (3.1). In \textit{BioEvolve}, the water store is divided into two unsaturated-zone soil pools \( (W_1 \text{ and } W_2) \), corresponding to the stores in layers defined by the A and B soil horizons and a pool for shallow groundwater \( (W_g, \text{ the water table height above a datum}) \). The rate equations for these pools are

\[
\begin{align*}
\frac{dW_1}{dt} &= F_{\text{W(Per)}}01 - F_{\text{W(Per)}}12 - F_{\text{W(EVeg)}}1 - F_{\text{W(ESoil)}} \\
\frac{dW_2}{dt} &= F_{\text{W(Per)}}12 - F_{\text{W(Per)}}2g - F_{\text{W(EVeg)}}2 \\
\frac{dW_g}{dt} &= F_{\text{W(Per)}}2g - F_{\text{W(Base)}} / \sigma_p
\end{align*}
\] (3.2)

where \( F_{\text{W(Per)}}01 \), \( F_{\text{W(Per)}}12 \) and \( F_{\text{W(Per)}}2g \) are respectively the vertical percolation or drainage fluxes from the surface into layer 1, from layer 1 to layer 2, and from layer 2 to the groundwater; \( F_{\text{W(Base)}} \) is the flux out of the groundwater store due to base flow or exfiltration into streams; and \( \sigma_p \) is the porosity of the material in which the groundwater is located.

The relationships between Equations (3.1) and (3.2) are:

- The contributions to \( F_{\text{W(EVeg)}} \) from root water uptake in layers 1 and 2 are \( F_{\text{W(EVeg)}}1 \) and \( F_{\text{W(EVeg)}}2 \), respectively, so that \( F_{\text{W(EVeg)}} = F_{\text{W(EVeg)}}1 + F_{\text{W(EVeg)}}2 \).
- The infiltration flux through the soil surface is \( F_{\text{W(Per)}}01 = F_{\text{W(EffRain)}} - F_{\text{W(Runoff)}} \).
- The leaching flux from the soil column to the groundwater store is \( F_{\text{W(Per)}}2g = F_{\text{W(Leach)}} \).
- In Equation (3.2), the equations for \( W_1 \) and \( W_2 \) sum to Equation (3.1).
3.2 Carbon, Nitrogen and Phosphorus: Balance Equations for Functional Pools

**Plant Pools:** We first write the overall balances of C, N and P in the sum of all plant pools \((Pla = Lea + Woo + Roo)\). From Figure 1, these are:

\[
\begin{align*}
\frac{dC_{Pla}}{dt} & = F_{C(NPP)} - F_{C(Pla:Lit)} - F_{C(Pla:Disturb)} \\
\frac{dN_{Pla}}{dt} & = F_{N(Mnl:Pla)} - F_{N(Pla:Lit)} - F_{N(Pla:Disturb)} \\
\frac{dP_{Pla}}{dt} & = F_{P(Pri:Pla)} - F_{P(Pla:Lit)} - F_{P(Pla:Disturb)}
\end{align*}
\]

where \(F_{C(NPP)}\) is the air-to-plant C flux by NPP; \(F_{N(Mnl:Pla)}\) and \(F_{P(Pri:Pla)}\) are the fluxes of N and P from the plant-available mineral pools to the plant by root uptake; \(F_{X(Pla:Lit)}\) is the flux of \(X\) (= C, N or P) from the plant pool to the litter pool by the death of plant material; and \(F_{X(Pla:Disturb)}\) is the flux of \(X\) from the plant pool to external pools via disturbance.

There are three main disturbance fluxes: *herbivory* by both native and introduced grazing animals; *fire*; and *offtake* of plant material as product in harvest. We do not attempt a detailed treatment of disturbance, but instead regard all these fluxes as losses of material from the soil-plant system, to sinks outside the landscape control volume (in the atmosphere or in stored product). This neglects the fact that many disturbance fluxes involve returns of material to other, non-plant landscape pools in Figure 1: for instance, inputs to passive C from fire via char, and inputs to mineral N and P pools from animal excreta. Such returns would be included explicitly in a more detailed treatment of disturbance.

Now we turn to the balance equations for the components of the plant pools \((Lea, Woo, Roo1, Roo2)\). From Figures 1, 2 and 3, these are:

\[
\begin{align*}
\frac{dC_{Lea}}{dt} & = a_{Lea} F_{C(NPP)} - F_{C(Lea:Res)} - F_{C(Lea:Disturb)} \\
& = a_{Lea} F_{C(NPP)} - k_{Lea} C_{Lea} - h_{Lea} C_{Lea} \\
\frac{dN_{Lea}}{dt} & = a_{Lea} F_{C(NPP)} - F_{N(Lea:Res)} - F_{N(Lea:Disturb)} \\
& = a_{Lea} F_{C(NPP)} - \frac{k_{Lea} C_{Lea}}{r_{CN(Lea)}} - \frac{h_{Lea} C_{Lea}}{r_{CN(DeadLea)}} \\
\frac{dP_{Lea}}{dt} & = a_{Lea} F_{C(NPP)} - F_{P(Lea:Res)} - F_{P(Lea:Disturb)} \\
& = a_{Lea} F_{C(NPP)} - \frac{k_{Lea} C_{Lea}}{r_{CP(Lea)}} - \frac{h_{Lea} C_{Lea}}{r_{CP(DeadLea)}}
\end{align*}
\]

(likewise for Woo, Roo1, Roo2)
where $a_{Aaa}$ are allocation ratios for the partition of NPP between leaf, wood and root (satisfying $a_{Lea} + a_{Woo} + a_{Roo1} + a_{Roo2} = 1$); $r_{CN(Aaa)}$ and $r_{CP(Aaa)}$ are respectively the C:N and C:P mass ratios in the live plant store $Aaa$ (one of $Lea$, $Woo$, $Roo1$, $Roo2$); $r_{CN(DeadAaa)}$ and $r_{CP(DeadAaa)}$ are the C:N and C:P ratios in the dead material (litter) formed as material in the live plant store $Aaa$ dies and enters the litter pools via the residue pool; $r_{CN(DisturbAaa)}$ and $r_{CP(DisturbAaa)}$ are the C:N and C:P ratios in the plant material removed by disturbance (herbivory, fire, offtake); $k_{Pla}$ is the rate constant for mortality (the transfer of live plant material to litter); and $h_{Pla}$ is the rate constant for disturbance (summed over all disturbance processes). Both $k_{Pla}$ and $h_{Pla}$ have the dimension $[\text{time}^{-1}]$.

The first term on the right hand side of each of Equations (3.6) to (3.8) accounts for plant production, the second for conversion of living plant material to litter, and the third for removal of plant material by disturbance. The lower line in each equation gives the phenomenological equations which specify the fluxes in the upper line in terms of stores and parameters. The phenomenological equations for the disturbance fluxes treat these as continuous processes (though the rate $h_{Aaa}$ can vary with time) rather than instantaneous disturbance events. Carbon uptake is assumed to be associated with N and P uptake by specified C:N and C:P ratios in plant material.

When Equations (3.3) to (3.8) represent time averages over an interval long enough to describe a statistically steady state, the left hand sides approach zero ($dC_{Pla}/dt \to 0$, $dN_{Pla}/dt \to 0$, $dP_{Pla}/dt \to 0$). In the case of the plant component C balances, Equation (3.6), it then follows that $a_{Aaa}FC = k_{C}Aaa + h_{C}Aaa$, where all quantities are long-time averages. In the case of the plant component N and P balances, Equations (3.7) and (3.8), it follows that over a long time average, $r_{CN(Aaa)} = r_{CN(DeadAaa)} = r_{CN(DisturbAaa)}$ and likewise for $r_{CP}$ (this result is easily seen for the case of no disturbance, $h_{Aaa} = 0$, and follows more generally by allowing $h_{Aaa}$ to vary arbitrarily). Hence, for the rest of this work, we do not distinguish among $r_{CN(Aaa)}$, $r_{CN(DeadAaa)}$ and $r_{CN(HarvAaa)}$, writing all of them as $r_{CN(Aaa)}$. The treatment of $r_{CP}$ is similar.

The quantities $r_{CN(Aaa)}$, $r_{CP(Aaa)}$, $a_{Aaa}$, $k_{Aaa}$ and $h_{Aaa}$ (with $Aaa = Lea, Woo, Roo1$ or $Roo2$) are externally specified.

**Litter and Soil Organic Pools:** The balance equations for the litter and soil pools have identical forms for C, N and P, and therefore are written generically for an entity $X (= C, N$ or $P)$. Following Figures 2 and 3, the balance equations for the litter ($Res$, $Met$, $Str$) pools are:

\[
\frac{dX_{Res}}{dt} = F_{X(Pla:Res)} - F_{X(Res:Out)} \tag{3.9}
\]

\[
\frac{dX_{Met}}{dt} = F_{X(Res:Met)} - F_{X(Met:Out)} \tag{3.10}
\]

\[
\frac{dX_{Str}}{dt} = F_{X(Res:Str)} - F_{X(St:Out)} \tag{3.11}
\]
The equations for the SOM (Act, Hum, Pas) pools are:

\[
\begin{align*}
\frac{dX_{\text{Act}}}{dt} &= F_{X(\text{Met: Act})} + F_{X(\text{Str: Act})} + F_{X(\text{Hum: Act})} + F_{X(\text{Pas: Act})} - F_{X(\text{Act: Out})} \\
\frac{dX_{\text{Hum}}}{dt} &= F_{X(\text{Act: Hum})} + F_{X(\text{Str: Hum})} - F_{X(\text{Hum: Out})} \\
\frac{dX_{\text{Pas}}}{dt} &= F_{X(\text{Act: Pas})} + F_{X(\text{Hum: Pas})} - F_{X(\text{Pas: Out})}
\end{align*}
\] (3.12, 3.13, 3.14)

where \( F_{X(Aaa:Out)} \) is the flux of \( X \) out of pool \( Aaa \) to all destinations combined, and \( F_{X(Aaa:Bbb)} \) is the flux of \( X \) from pool \( Aaa \) to pool \( Bbb \) at the point of entry into the destination pool \( Bbb \). This stipulation is important because some transformations involve losses or gains en route, such as respiratory loss of C, loss of N and P from SOM by mineralisation or gaseous loss, and gain of N and P to SOM by immobilisation from mineral pools.

In Equation (3.9), the fluxes from the plant pools (collectively \( Pla \)) to the litter pools, through the residue pool \( Res \), are

\[
\begin{align*}
F_{C(\text{Pla:Lit})} &= F_{C(\text{Pla:Res})} = k_{\text{Lea}}C_{\text{Lea}} + k_{\text{Woo}}C_{\text{Woo}} + k_{\text{Roo1}}C_{\text{Roo1}} + k_{\text{Roo2}}C_{\text{Roo2}} \\
F_{N(\text{Pla:Lit})} &= F_{N(\text{Pla:Res})} = \frac{k_{\text{Lea}}C_{\text{Lea}}}{r_{\text{CN}(\text{DeadLea})}} + \frac{k_{\text{Woo}}C_{\text{Woo}}}{r_{\text{CN}(\text{DeadWoo})}} + \frac{k_{\text{Roo1}}C_{\text{Roo1}}}{r_{\text{CN}(\text{DeadRoo})}} + \frac{k_{\text{Roo2}}C_{\text{Roo2}}}{r_{\text{CN}(\text{DeadRoo})}} \\
F_{P(\text{Pla:Lit})} &= F_{P(\text{Pla:Res})} = \frac{k_{\text{Lea}}C_{\text{Lea}}}{r_{\text{CP}(\text{DeadLea})}} + \frac{k_{\text{Woo}}C_{\text{Woo}}}{r_{\text{CP}(\text{DeadWoo})}} + \frac{k_{\text{Roo1}}C_{\text{Roo1}}}{r_{\text{CP}(\text{DeadRoo})}} + \frac{k_{\text{Roo2}}C_{\text{Roo2}}}{r_{\text{CP}(\text{DeadRoo})}}
\end{align*}
\] (3.15)

These are the sums of the plant-to-residue turnover terms in Equations (3.6), (3.7) and (3.8).

**Mineral Pools:** The mineral N pool is influenced by (1) local-cycling fluxes between mineral N and the plant, litter and SOM pools, and (2) external fluxes. The balance equation is

\[
\frac{dN_{\text{Mnl}}}{dt} = F_{N(\text{TotalNetMin})} - F_{N(\text{Mnl:Pla})} + F_{N(\text{Fix})} + F_{N(\text{Dep})} + F_{N(\text{Fert})} - F_{N(\text{GasLoss})} - F_{N(\text{Leach})}
\] (3.16)

Of the local-cycling fluxes, \( F_{N(\text{TotalNetMin})} \) is the total net mineralisation flux of N (the difference between gross mineralisation and gross immobilisation for all local-cycling pathways), and \( F_{N(\text{Mnl:Pla})} \) is the N flux from the mineral pool taken into plant tissue during growth. The external fluxes, which have descriptive notations, are defined in Section 6.4. All fluxes are positive into the soil control volume.

For soil P, there are three pools (\( P_{\text{Pri}}, P_{\text{Sec}}, P_{\text{Occ}} \)). The primary pool interacts with other plant, litter and soil P pools through local cycling and external fluxes as for the \( N_{\text{Mnl}} \) pool. The
secondary and occluded P pool buffer this interaction through exchange with the primary pool. The governing rate equations are:

\[
\frac{dP_{\text{Pri}}}{dt} = F_{P(\text{TotalNetMin})} - F_{P(\text{Pri:PLa})} + F_{P(\text{Sec:Pri})} - F_{P(\text{Pri:Sec})} + F_{P(\text{Fert})} - F_{P(\text{Leach})}
\]

\[
\text{-------------------local cycling-----------------} \quad |\text{-external fluxes-}|
\]

\[
\frac{dP_{\text{Sec}}}{dt} = F_{P(\text{Pri:Sec})} - F_{P(\text{Sec:Pri})} - F_{P(\text{Sec:Occ})}
\]

\[
\frac{dP_{\text{Occ}}}{dt} = F_{P(\text{Sec:Occ})}
\]

4 Net Primary Production

4.1 Background

Historically, NPP has been determined either by very simple models or by very complex models; see Raupach et al. (2002) for a review, from which the following summary is drawn.

The basis of many simple models is the idea of a light use efficiency, proposed for agricultural crops by Monteith (1977) and Kumar and Monteith (1981). They suggested that

\[
\text{NPP} = s\varepsilon L\Phi_{\text{PAR}},
\]

where \(\varepsilon L\) is the light use efficiency, \(\Phi_{\text{PAR}}\) is the canopy-level flux of absorbed photosynthetically active radiation (PAR), and \(s\) is a "stress function" between 0 and 1 which accounts for limitations in resources other than light, primarily water and nutrients. While a theoretical value for the maximum light use efficiency \(\varepsilon L\) can be derived from the energetics of photosynthesis (Prince and Goward 1995), the actual efficiency in practice (the product \(s\varepsilon L\)) is only a fraction of this value, because of water and nutrient limitations. This class of model is almost completely empirical.

On the other hand, complex models are based on mechanistic descriptions of the processes of plant autotrophic respiration and photosynthesis at leaf level (Wong et al. 1979; Farquhar et al. 1980; Ball et al. 1987; Leuning 1990, 1995; de Pury and Farquhar 1997; Wang and Leuning 1998). These are then scaled up (Raupach et al. 2002) to provide a description at the level of a whole plant canopy. Models of this type represent a mechanistic link between the energy, water and carbon budgets. This approach was introduced into the terrestrial component of global climate models by Collatz et al. (1991), Sellers et al. (1992, 1994) and Denning et al. (1996). However, a significant difficulty is the very large number of parameters required by the model, for which in many cases little empirical guidance is available.

In this work we have used an intermediate-complexity model in which a simple, semi-mechanistic expression for NPP is constructed directly at the scale of a whole vegetation canopy. Knowledge of leaf-scale processes is invoked to identify a form for this expression with few enough parameters to be commensurate with available large-scale data. The intention is to capture the main mechanistic controls on NPP dynamics without introducing unwarranted complexity (for instance through the use of multiple canopy layers with an associated large number of empirical coefficients).
NPP is modelled in three stages, described respectively in Sections 4.2 to 4.4:

- We accommodate autotrophic respiration by expressing NPP as a fraction of photosynthetic assimilation or Gross Primary Production (GPP);
- We formulate an expression for the NPP limited only by light and water ($F_C^+$);
- We formulate an expression for the actual NPP ($F_C$) resulting from nutrient limitation in addition to light and water limitation, using a mixture of biophysical and scaling arguments.

### 4.2 Assimilation and Autotrophic Respiration

NPP is the net carbon flux from the atmosphere to a vegetated surface resulting from the difference between assimilation and autotrophic respiration:

$$F_C = F_{C(NPP)} = F_{C(Assim)} - F_{C(AutoRespiration)}$$  \hspace{1cm} (4.1)

where $F_{C(Assim)}$ and $F_{C(AutoRespiration)}$ are the carbon fluxes due to assimilation and autotrophic respiration, respectively. The NPP, formally $F_{C(NPP)}$, is henceforth written just as $F_C$ for brevity, unless confusion could arise.

Following Landsberg and Waring (1997), we assume that, over time scales of a year or longer, NPP is a fixed fraction $r_{NG}$ (the net/gross productivity ratio) of GPP or net assimilation $F_{C(Assim)}$. Hence:

$$F_C = F_{C(NPP)} = r_{NG} F_{C(Assim)}$$  \hspace{1cm} (4.2)

where $r_{NG} = 0.45$. The key simplification in Equation (4.2) is not the value of $r_{NG}$ (which folds with other coefficients introduced below to form a single multiplicative parameter), but rather the assumption that the responses of GPP and autotrophic respiration to both plant carbon stores and environmental variables are proportional. Such proportionality is substantiated by both experimental evidence for a variety of plant types (Gifford 1995, Gifford et al. 1996) and by theoretical arguments (Loomis and Amthor 1996, Dewar et al. 1999) though the values of $r_{NG}$ depend somewhat on plant type. At the whole-ecosystem scale relevant to this work, the value $r_{NG} = 0.45$ is consistent with evidence presented by Landsberg and Waring (1997) and with remote-sensing studies (Goetz et al. 1999).

### 4.3 Light and Water Limited NPP

The light and water limited NPP, $F_C^+$, is the NPP with freely available nutrients. It is modelled using the following principles.

- Light availability is determined by the flux of photosynthetically active radiation (PAR) absorbed by the canopy, and water availability by the flux of water transpired by the canopy (the term $F_{WEVeg}$ in Equation (3.1)). The long term averages of both these fluxes are well constrained by climate and leaf area. The PAR flux is determined by the intercepted solar irradiance (the product of incident irradiance and the fraction of PAR absorbed by the canopy). The transpired water flux is determined by rainfall in dry (water-limited) environments, and by net irradiance in moist environments where evaporation is limited by energy supply from irradiance. Hence a model for the long-term average of $F_C^+$ can be constructed using the driver variables of radiation and rainfall.
• $F_C^+$ is expressible as the product of two factors: (a) the concentration gradient between the CO$_2$ at leaf surfaces in the canopy and the carbon in the products of photosynthesis, and (b) a conductance for movement of C down this gradient, formed from stomatal and plant biochemical resistances in series.

• The mathematical form of the bulk canopy model for $F_C^+$ is a simplified version of the form used for the same processes at the scale of a single leaf. Undetermined coefficients in the canopy-scale model have leaf-scale counterparts but must be treated as empirical at the canopy scale.

Using these principles, the model for $F_C^+$ is developed in the following steps. The notation and units in the model for $F_C^+$ (Section 4.3) are kept in accord with plant physiological conventions, with conversion to units appropriate elsewhere once $F_C^+$ has been found.

**Step 1:** The net assimilation $F_{C(Assim)}$ is written independently in terms of two conductance-gradient products:

$$A = F_{C(Assim)} = G_{sC} (C_s - C_i)$$

$$A = G_{pC} (C_i - \Gamma^*)$$

Here $A$ is the conventional plant physiological notation for the net carbon assimilation $F_{C(Assim)}$ [mol C m$^{-2}$ s$^{-1}$] (positive from air to surface); $C_s$ and $C_i$ are respectively the CO$_2$ concentrations at leaf surfaces and in intercellular cavities [mol C mol air$^{-1}$]; $\Gamma^*$ is the CO$_2$ compensation point [mol C mol air$^{-1}$]; and $G_{sC}$ and $G_{pC}$ are respectively the bulk (canopy-scale) conductances for transfer of CO$_2$ through stomata and biochemical transfer of C from the intercellular cavity to photosynthetic product [mol air m$^{-2}$ s$^{-1}$]. Equation (4.3) describes CO$_2$ transfer through stomata, and Equation (4.4) describes plant biochemical uptake of C by photosynthesis from air in the intercellular spaces.

Of several possibilities, the following empirical expression is used to define $\Gamma^*$:

$$10^6 \Gamma^* = 37 \left[ 1.37^{(T_s-25)/10} \right]$$

where $T_s$ is the leaf surface temperature in deg C. This expression is due to von Caemmerer (2000). Other empirical forms for $\Gamma^*$ are given by Brooks and Farquhar (1985), Jordan and Ogren (1984), and Collatz et al. (1991) as used by Prince and Goward (1995).

**Step 2:** The intercellular concentration $C_i$ is algebraically eliminated, giving

$$A = \frac{C_s - \Gamma^*}{R_{sC} + R_{pC}}$$

where $R_{sC} = 1/G_{sC}$ and $R_{pC} = 1/G_{pC}$ are the resistances corresponding to the conductances $G_{sC}$ and $G_{pC}$.

**Step 3:** The bulk stomatal resistance $R_{sC}$ is evaluated in terms of the corresponding resistance for water transfer, $R_{sW} = 1/G_{sW}.$ Equation (4.3) for stomatal CO$_2$ transfer has a counterpart for water transfer (positive from surface to air):
\[ E_V = F_{W(EVeg)} = G_{sW} (Q_i - Q_s) \]  (4.7)

where \(E_V\) is shorthand for the canopy transpiration \(F_{W(EVeg)}\) [mol water m\(^{-2}\) s\(^{-1}\)]; \(Q_s\) and \(Q_i\) are respectively the water vapour concentrations at leaf surfaces and in intercellular cavities [mol water mol air\(^{-1}\)]; and \(G_{sW} = 1/R_{sW}\) is the bulk (canopy-scale) conductance for transfer of water vapour through stomata [mol air m\(^{-2}\) s\(^{-1}\)]. Because the bulk stomatal pathways for water vapour and CO\(_2\) transfer are the same, the conductances \(G_{sW}\) (for water) and \(G_{sC}\) (for CO\(_2\)) are related simply by \(G_{sW} = 1.6G_{sC}\) (where the factor 1.6 represents the difference between the molecular diffusivities of water vapour and CO\(_2\) in air). Further, the water vapour concentration difference \(Q_i - Q_s\) is closely approximated by the saturation deficit at leaf surfaces, \(D_s = Q_{sat}(T_s) - Q_s\) (where \(Q_{sat}(T_s)\) is the saturated water vapour concentration at the leaf surface temperature \(T_s\)). The resulting expression for \(R_{sC}\) in terms of water vapour gradients and fluxes is:

\[ R_{sC} = 1.6D_s / E_V \]  (4.8)

Both \(D_s\) and \(E_V\) can be estimated from climatological data (see below), thus yielding \(R_{sC}\).

**Step 4:** A formulation is written for the bulk resistance \(R_{pC}\) for biochemical transfer to photosynthetic product, based on simplifications of leaf-scale photosynthesis models. Here, we use the following simple choice:

\[ \frac{1}{R_{pC}} = G_{pC} = \frac{\alpha_V \Phi_V}{C_s - \Gamma} \]  (4.9)

where \(\alpha_V\) is the canopy-level quantum yield [mol C (mol PAR\(^{-1}\)], and \(\Phi_V\) is the PAR flux absorbed by the vegetation canopy [mol PAR m\(^{-2}\) s\(^{-1}\)]. This is given by Beer’s Law:

\[ \Phi_V = (1 - \exp(-c_{PAR} \Lambda)) r_{PARSolar} a_s \Phi_{S↓} \]  (4.10)

where \(r_{PARSolar}\) is the ratio of PAR to solar irradiance (taken as \(r_{PARSolar} = 2.0\) mol PAR MJ\(^{-1}\)), \(a_s\) is the canopy albedo (not distinguished from the whole-surface albedo), \(\Phi_{S↓}\) is the incoming global shortwave irradiance, \(\Lambda\) is the leaf area index, and \(c_{PAR}\) is the extinction coefficient for PAR in the canopy.

Equation (4.9) treats \(G_{pC}\) as determined by the product of the absorbed PAR flux \(\Phi_V\) and quantum yield \(\alpha_V\) (that is, by light). For dimensional reasons the product \(\alpha_V \Phi_V\) must be divided by a CO\(_2\) concentration, here \(C_s - \Gamma\). As shown in the box below, this choice is made so that the resulting simplified model (Equation (4.12) below) is a linearisation of the nonlinear C3 leaf photosynthesis model of Farquhar et al. (1980):

\[ \frac{1}{R_{pC}} = G_{pC} = \frac{\beta_l}{C_l + \gamma_l} \]  (4.11)

where \(\beta_l\) and \(\gamma_l\) are dimensional quantities taking different values in Rubisco-limited and electron-transport-limited conditions, and the actual leaf assimilation is the lesser of the two options thus defined; see for instance Lambers et al. (1998). While Equation (4.9) is a reasonable initial choice, it may not be the best simplification of Equation (4.11). This is an
area of the model that will be the subject of further work. However, such refinement is not expected to have a significant quantitative impact on the results of the NPP model, because of calibration processes described in Section 9.

**Step 5:** The value of \( A = F_{C(\text{Assim})} \) is found by substituting the values of \( R_{sC} \) and \( R_{pC} \) into Equation (4.6), and using Equations (4.8) and (4.9). This gives

\[
A = \frac{C_s - \Gamma^*}{1.6D_s E_y} + \frac{C_s - \Gamma^*}{\alpha_i \Phi_y} \tag{4.12}
\]

\[
F^*_C = r_{NG} A = \frac{r_{NG} (C_s - \Gamma^*)}{1.6D_s E_y} + \frac{C_s - \Gamma^*}{\alpha_i \Phi_y} \tag{4.13}
\]

Equation (4.13) is the solution for the light and water limited NPP \((F_C^+)\).

**Use of nonlinear photosynthesis model:** If Equation (4.11) is used to define \( R_{pC} \), then \( A \) is given by the quadratic equation:

\[
A^2 - A \left[ \beta_1 + G_{sc} \left( C_s + \gamma_1 \right) \right] + \beta_1 G_{sc} \left( C_s - \Gamma^* \right) = 0 \tag{4.14}
\]

with the solution:

\[
A = \frac{2A_i}{1 + \left( 1 - \frac{4A_i^2 R_{sc}}{\beta_1 \left( C_s - \Gamma^* \right)} \right)^{1/2}} \tag{4.15}
\]

with \( A_i = \frac{C_s - \Gamma^*}{R_{sc} + C_s + \gamma_1} \) and \( R_{sc} = \frac{1}{G_{sc}} = \frac{1.6D_s}{E_y} \)

This solution is a nonlinear version of Equation (4.12). However, it is not used directly here because of the added complications of parameterising \( \beta_1 \) and \( \gamma_1 \) at large scales.

### 4.4 NPP with Nutrient Limitation

The actual NPP \((F_C)\) is found from the light and water limited NPP \((F_C^+)\) by considering the additional effect of mineral nutrient (N and P) limitation on plant growth. In this subsection it is convenient to introduce some shortened notation:

- \( E_y = E_{W(E_{vg})} \) is the plant water uptake in transpiration [kg water m\(^{-2}\) s\(^{-1}\)] (as before);
- \( W = W_1 + W_2 \) is the total soil water store in the root zone [kg water m\(^{-2}\)];
• N and P are the stores of mineral N and primary P in the soil root zone, so that
  \( N = N_{Mnl1} + N_{Mnl2} \) and \( P = P_{Pri1} + P_{Pri2} \) (in kg N m\(^{-2}\) and kg P m\(^{-2}\), respectively);

• \( \nu \) and \( \rho \) are respectively the flux-weighted average whole-plant N:C and P:C ratios,
  including leaves, wood and roots, defined in Equation (4.16) below;

The expression for \( F_C \) is found by the following steps.

**Step 1:** From Equations (3.7) and (3.8), the fluxes of mineral N and P into the plant are:

\[
F_{N(Mnl:Pla)} = \left( \frac{a_{Lea}}{r_{CN(Lea)}} + \frac{a_{Woo}}{r_{CN(Woo)}} + \frac{a_{Roo1} + a_{Roo2}}{r_{CN(Roo)}} \right) F_C = \nu F_C
\]

\[
F_{P(Pri:Pla)} = \left( \frac{a_{Lea}}{r_{CP(Lea)}} + \frac{a_{Woo}}{r_{CP(Woo)}} + \frac{a_{Roo1} + a_{Roo2}}{r_{CP(Roo)}} \right) F_C = \rho F_C
\]

(4.16)

where \( \nu \) and \( \rho \) (the N:C and P:C ratios in whole-plant growth) are defined by the flux-
weighted averages of \( 1/r_{CN} \) and \( 1/r_{CP} \) in the various pools according to Equation (4.16). These
expressions follow from the balances of N and P in the conducting pathways between roots
and growing tissues, assuming no storage along these pathways.

**Step 2:** It is assumed that when nutrients are limiting (but not otherwise), the fluxes \( F_{N(Mnl:Pla)} \)
and \( F_{P(Pri:Pla)} \) scale with the nutrient stores (N and P respectively) and the time scale \( W/E_V \)
characterising the rate of water use by vegetation. Since a flux has the dimension
(store)/(time scale), this implies that \( F_{N(Mnl:Pla)} \) and \( F_{P(Pri:Pla)} \) are of order \( NE_V/W \) and \( PE_V/W \),
respectively. Hence:

\[
F_{N(Mnl:Pla)} = c_N E_V N \frac{E_V}{W}; \quad F_{P(Pri:Pla)} = c_P E_V P \frac{E_V}{W}
\]

(4.17)

where \( c_N \) and \( c_P \) are "uptake coefficients" of order 1, describing the efficiency with which
available N and P in the soil are taken up into the plant.

**Step 3:** Over short time intervals (say around a day), plant growth requires a supply of C, N
and P in ratios which are biochemically constrained to lie within narrow ranges specified by \( \nu \)
and \( \rho \). If the supply of N and P in the soil root zone is adequate, then short-term growth
proceeds at the light and water limited rate, but if N or P is limiting then growth can proceed
only at a rate determined by the flux of mineral N or P into the plant from the soil. This
implies that over short time scales:

\[
f_C = \min \left( f_C^+, \frac{f_{N(Mnl:Pla)}}{\nu}, \frac{f_{P(Pri:Pla)}}{\rho} \right) = \min \left( f_C^+, \frac{c_N E_V N}{\nu W}, \frac{c_P E_V P}{\rho W} \right)
\]

(4.18)

where short-term variables (varying over times of a day or less) are distinguished from their
time-averaged counterparts by lower-case letters, so that \( f_C, f_C^+ \), \( E_V, n, p \) and \( W \) are the short-
term, time-dependent values of the long-term averaged variables \( F_C, F_C^+, E_V, N, P \) and \( W \). In
the second equality, the short-term counterpart of Equation (4.17) has been used.
Figure 6 shows the behaviour of the system implied by Equation (4.18), in a three-dimensional space with independent variables \((n,p)\) and dependent variable \(f_C\). The solution for \(f_C\) falls on one of three planes: the two sloping planes \(f_C = (c_N eV n)/(\nu w)\) (N limited) and \(f_C = (c_P eV p)/(\rho w)\) (P limited), and the horizontal plane \(f_C = f_C^+\) (light or water limited). Which of these planes yields the solution is determined by the minimum in Equation (4.18), with the current values of the independent variables \(n, p\) and \(f_C^+\). The outcome is a "flat-topped roof" with contours as shown in Figure 7a.

**Step 4:** To obtain an equivalent expression of the form \(F_C = \text{func}(f_C^+, N, P)\) for the time-averaged NPP in nutrient-limited conditions, it is necessary to average Equation (4.18) over a period long enough to encompass statistical variations in the short-term independent variables \(f_C^+, n\) and \(p\). The averaging is over an ensemble in which the planes \(f_C = (c_N eV n)/(\nu w)\) and \(f_C = (c_P eV p)/(\rho w)\) have a variety of slopes \([c_N eV)/(\nu w)\) and \([c_P eV)/(\rho w)\] as \(e\) and \(w\) change in response to weather, and likewise the horizontal plane \(f_C = f_C^+\) has a variety of locations as \(f_C^+\) changes. The averaged solution satisfies the following constraints:

1. The relationship \(F_C = \text{func}(f_C^+, N, P)\) is expected to be smooth and monotonic, because time-averaging blurs the sharp-edged character of the minimum solution (Figure 7a) into a set of smooth contours (Figure 7b).

2. At large \(N\) and \(P\) (when all nutrients are freely available), \(F_C \to F_C^+\).

3. As either \(N\) or \(P\) become negligible, \(F_C \to 0\).

4. In order of magnitude, the slopes of the solution at small \(N\) and at small \(P\) are \(\partial F_C/\partial N \sim E_v/(\nu W)\) at small \(N\), and \(\partial F_C/\partial P \sim E_v/(\rho W)\) at small \(P\) (from Equation (4.17)).

The following simple form for \(F_C = \text{func}(f_C^+, N, P)\) satisfies all these constraints:

\[
F_C = s_N(N) s_P(P) F_C^+
\]

\[(4.19)\]

where \(s_N(N)\) and \(s_P(P)\) are multiplicative "stress functions" or "nutrient response functions" between 0 and 1; \(b_N\) and \(b_P\) are dimensionless "response coefficients" of order 1, parameterising the long-term average efficiency with which plant growth responds to plant-available N and P; and the quantities \(N^+\) and \(P^+\) are scales for the mineral N and P stores (with dimension kg N m\(^{-2}\) and kg P m\(^{-2}\)). These scales specify the stores at which N and P limitations (respectively) affect time-averaged plant growth. They are defined by

\[
N^+ = \nu F_C^+ W / E_v; \quad P^+ = \rho F_C^+ W / E_v
\]

\[(4.20)\]

This definition ensures that constraint (4) is satisfied, because it ensures that \(\partial F_C/\partial N\) is of order \((N/N^+)F_C^+ \sim E_v/(\nu W)\) in the limit \(N \to 0\), and likewise for \(P\).

Equations (4.19) and (4.20) do not define a unique function \(F_C(N,P)\) which satisfies constraints (1) to (4), but these constraints are strong enough that any function satisfying them is likely to produce similar results. The choice above is an algebraically simple one.
5 Steady State Solutions for NPP and Mineral Nutrients

5.1 Simplified Equation System

At the heart of *BiosEquil* are steady-state solutions to a simplified coupled equation system determining the nutrient-limited NPP $F_C$ (taking the light and water limited NPP $F_C^L$ to be specified) and the plant-available mineral nutrient stores $N$ and $P$.

The starting point is the conservation equations for the total plant-available nitrogen ($N_{Avl}$) and plant-available phosphorus ($P_{Avl}$) defined by Equations (2.8) and (2.9). From Figure 1 and Section 3, we write these equations in the steady state and parameterise the flux terms:

\[
0 = \frac{dN_{Avl}}{dt} = \left( F_{N(Pla:Lit)} - F_{N(Mnl:Pla)} + F_{N(Pla:Dep)} + F_{N(Fert)} - F_{N(GasLoss)} - F_{N(Leach)} \right) = \left( (1-r_{Disturb})vF_C - c_N E_v N/W \right) + \left( r_{Fix} vF_C + F_{N(Dep)} + F_{N(Fert)} \right) - \left( r_{GasLoss} vF_C - k_{Leach} N \right)
\]

\[
0 = \frac{dP_{Avl}}{dt} = \left( F_{P(Pla:Lit)} - F_{P(Pri:Pla)} + F_{P(Fert)} - F_{P(Leach)} \right) = \left( (1-r_{Disturb})pF_C - c_P E_v P/W \right) + \left( F_{P(Fert)} \right) - \left( k_{Leach} P \right)
\]

In each equation, the first line in each sum of fluxes includes the local cycling fluxes, the second line the input external fluxes, and the third line the output external fluxes. As in Section 4.4, $N$ and $P$ are the stores of the plant-available nutrients (mineral N and primary P), $N = N_{Mnl1} + N_{Mnl2}$ and $P = P_{Pri1} + P_{Pri2}$; and $v$ and $p$ are the average whole-plant N:C and P:C ratios. The parameterisation for each flux (identified in the left-hand bracketed sum) is given by the term in the corresponding position in the right-hand (parameterised) sum.

The parameterisations are based on phenomenological equations given in detail in Section 6. Briefly, they are (for N only, since the case of P is similar):

- $F_{N(Pla:Lit)}$: In steady-state conditions, the N flux leaving the plant pool is equal to the N flux entering it, $vF_C$ (the N flux in the local plant cycle). From Equation (3.4) and Figure 1, this exit N flux from the plant pool consists of two parts, a fraction $(1-r_{Disturb})vF_C$ entering the litter pool and a fraction $r_{Disturb}vF_C$ accounting for loss of N from the plant pool by disturbance (herbivory, fire, and offtake of plant material as product in harvest). Here $r_{Disturb}$ is a number between 0 and 1. The N flux to disturbance is treated as a loss to the plant-soil system, ultimately returning N to the atmosphere. In the case of herbivory, the N removed from the plant pool is mainly excreted and thus in reality is transferred to the organic and mineral N pools. However, this N is in a form subject to rapid gaseous loss, and we assume simplistically that it is all returned to the atmosphere.

- $F_{N(Mnl:Pla)}$: From Equation (4.17), this flux is parameterised as $c_N E_v N/W$, a formulation advanced in Section 4 for nutrient limited conditions. However, it is applied here for general steady-state conditions. This assumption is further discussed in Section 5.5.
• \(F_{N(\text{Fix})}\): As discussed in Section 6.4, N fixation is parameterised as \(r_{\text{Fix}}\nu FC\), where \(r_{\text{Fix}}\) is the fraction of the plant N requirement for growth supplied by legume fixation, typically around 0.1 but 1 or greater for crop and pasture legumes.

• \(F_{N(\text{Dep})}, F_{N(\text{Fort})}\): These fluxes are specified external inputs; see Section 8.2.

• \(F_{N(\text{GasLoss})}\): This is parameterised as \(r_{\text{GasLoss}}\nu FC\), where \(r_{\text{GasLoss}}\) is about 0.02; see Section 6.4 for details.

• \(F_{N(\text{Leach})}\): This is parameterised as \(k_{\text{Leach}}N\), where the leaching rate constant \(k_{\text{Leach}} = \frac{FW(\text{Leach})}{W}\); see Sections 6.4 and 7.4.

The parameterisation of \(F_{N(\text{Fix})}\) and \(F_{N(\text{GasLoss})}\) in terms of the NPP \((FC)\) is based on the idea that these external fluxes scale with overall carbon-nitrogen turnover, for which the most basic measure is \(FC\).

It is useful to write the balance equations (5.1) and (5.2) and the nutrient limited NPP equation (4.19) in a dimensionless form, by defining the dimensionless dependent variables (denoted in this section by small letters):

\[
f = F_{C}/F_{C}^+ , \quad n = N/N^+ , \quad p = P/P^+
\]

where \(F_{C}^+\) is the light and water limited NPP from Equation (4.13), and \(N^+\) and \(P^+\) are the mineral N and P scales defined by Equation (4.20). In terms of these dimensionless variables, Equations (4.19), (5.1) and (5.2) become

\[
f = s_{N} s_{p} \quad \text{with} \quad s_{N} = \left(\frac{n}{n + b_{N}}\right) , \quad s_{p} = \left(\frac{p}{p + b_{p}}\right)
\]

\[
0 = (1 + y_{N}) f - c_{N} n + x_{N} - \kappa n
\]

\[
0 = (1 + y_{p}) f - c_{p} p + x_{p} - \kappa p
\]

where the external nutrient fluxes (see Equations (3.16) and (3.17)) are characterised by the following dimensionless variables:

\[
x_{N} = \left(\frac{F_{N(\text{Fort})}}{F_{N(\text{Dep})}}\right)\left(\nu F_{C}^+\right) , \quad x_{p} = \frac{F_{p(\text{Fort})}}{\rho F_{C}^+}
\]

\[
y_{N} = -r_{\text{Disturb}} + r_{\text{Fix}} - r_{\text{GasLoss}} , \quad y_{p} = -r_{\text{Disturb}}
\]

\[
\kappa = k_{\text{Leach}} W/E_{V}
\]

The variables \(x_{N}\) and \(x_{p}\) express the N and P input fluxes from fertilisation and deposition; \(y_{N}\) and \(y_{p}\) express the disturbance, fixation and gaseous loss fluxes; and \(\kappa\) is the ratio of the rate constants for depletion of soil moisture by leaching (\(k_{\text{Leach}}\)) and by transpiration (\(E_{V}/W\)), a measure of the significance of the nutrient leaching flux. Equation (5.7) defines dimensionless variables which measure the significance of external nutrient fluxes relative to the maximum local-cycling nutrient uptake flux (that is, the flux associated with the light and water limited NPP). The external fluxes vanish when \(x_{N} = x_{p} = y_{N} = y_{p} = \kappa = 0\).
5.2 Analytic Solutions

The algebraic solutions of Equations (5.5) and (5.6) for the steady-state \( n \) and \( p \) are (in both dimensionless and dimensional forms):

\[
n = \frac{(1+y_N)f+x_N}{c_N + \kappa}, \quad N = \frac{F_{N(Fert)} + F_{N(Dep)} + v(1-r_{Disturb} + r_{Fix} - r_{GasLoss})F_C}{c_N E_Y/W + k_{Leach}} \tag{5.8}
\]

\[
p = \frac{(1+y_P)f+x_P}{c_P + \kappa}, \quad P = \frac{F_{P(Fert)} + p(1-r_{Disturb})F_C}{c_P E_Y/W + k_{Leach}} \tag{5.9}
\]

Equations (5.8) and (5.9) are not a closed solution because the dimensionless NPP \( f \) depends on \( n \) and \( p \) through the stress functions \( s_N \) and \( s_P \). The full, closed solution is found by solving Equations (5.4), (5.5) and (5.6) together for \( f, n \) and \( p \). Eliminating \( n \) and \( p \), a closed but implicit solution is obtained for \( f \):

\[
f = \left( \frac{x_N + (1+y_N)f}{x_N + (1+y_N)f + b_N c_N + b_N \kappa} \right) \left( \frac{x_P + (1+y_P)f}{x_P + (1+y_P)f + b_P c_P + b_P \kappa} \right) \tag{5.10}
\]

Given values for the external fluxes \((x_N, x_P, y_N, y_P, \kappa)\) and the coefficients \((b_N, b_P, c_N \text{ and } c_P)\), Equation (5.10) can be solved for \( f \). Thence, using Equations (5.8) and (5.9), \( n \) and \( p \) are determined. Formally Equation (5.10) is a cubic and an analytic solution is available, but it is simpler numerically to iterate for \( f \) from the starting condition \( f = 1 \). Convergence is rapid.

5.3 Constraints on Parameters

A significant constraint on the coefficients \( b_N, b_P, c_N \text{ and } c_P \) is obtained by considering the limit in which the external nutrient fluxes are negligible compared with the local-cycling fluxes, the case \( x_N = x_P = y_N = y_P = \kappa = 0 \). In this case Equation (5.10) simplifies to

\[
f = \frac{f^2}{(f + b_N c_N)(f + b_P c_P)} \tag{5.11}
\]

This is a cubic with three solutions, one being the trivial solution \( f = 0 \). To obtain the other two solutions, we restrict (for simplicity) to \( b_N = b_P = b, c_N = c_P = c \). This simplification implies that, in terms of the dimensionless variables defined by Equation (5.3), uptake and response to N and P have similar dynamics. Then Equation (5.11) becomes

\[
f^2 + (2bc - 1)f + (bc)^2 = 0 \tag{5.12}
\]

which has the pair of solutions

\[
f = \frac{1 - 2bc \pm \sqrt{1 - 4bc}}{2} \tag{5.13}
\]

Of these roots the larger is the physically realistic one, since it is the one to which an iterative process converges, that is, the dynamically stable root. Equations (5.12) and (5.13) imply that
the nutrient limited NPP \( (f) \) is a function of the product of the uptake and response coefficients \((bc)\), a result consistent with the intuitively reasonable assertions that \(f\) is an increasing function of each coefficient and \(f\) approaches 0 as either \(b\) or \(c\) approaches 0.

From Equations (5.8), (5.9) and (5.4), the solutions for \(n\) and \(p\) and the nutrient stress factors in this case are

\[
 n = p = \frac{f}{c}; \quad s_N = s_p = \frac{f}{f + bc}
\]

Equation (5.13) also imposes a powerful constraint on the coefficients \(b\) and \(c\). For real solutions to exist, these coefficients must satisfy

\[
 0 \leq bc \leq \frac{1}{4}
\]

The constraint is even tighter than is apparent from Equation (5.15), because the possible nutrient response of the landscape-scale NPP is

\[
\frac{\text{maximum possible NPP with unlimited nutrients}}{\text{equilibrium NPP}} = \frac{F_C^*}{F_C} = \frac{1}{f}
\]

Nutrient responses in Australian landscapes are typically observed to be significant (a factor of two or more). To be consistent with a nutrient response of this order, the equilibrium \(f\) must be 0.5 or less. Figure 8 shows the solution \(f\) from Equation (5.13) plotted against the product \(bc\). The values of \(bc\) consistent with such a value for \(f\) fall in a well-confined range, approximately between 0.18 and 0.25. The NPP is sensitive only to the product \(bc\), so the split between \(b\) and \(c\) is not as important (though it does influence the leakage fluxes and the nutrient stores). We used \(b = c = 0.45\), \(bc = 0.202\).

### 5.4 Estimating the Complete N Budget Including Disturbance Fluxes

The above analysis can be used, with a major caution spelt out below, to obtain estimates of all terms in the nutrient budgets including the disturbance terms. We concentrate on the case of N. The starting point is the conservation equation for the total plant N pool, Equation (3.4):

\[
0 = \frac{dN_{Pla}}{dt} = F_{N(Mnl:Pla)} - F_{N(Pla:Lit)} - F_{N(Pla:Disurb)}
\]

\[
= \frac{c_s E_{s,N}}{W} - (1 - r_{Disurb})vF_C - r_{Disurb}vF_C\]

\[
= \frac{c_s E_{s,N}}{W} - vF_C
\]

\[
(5.17)
\]

where the parameterisations on the right hand side are consistent with Equation (5.1). In particular, the sum of the fluxes from plant to litter and plant to disturbance is the N flux in the local plant cycle, \(vF_C\). Subtracting Equation (5.17) from Equation (5.1) gives the disturbance flux as

\[
F_{N(Pla:Disurb)} = r_{Disurb}vF_C = F_{N(Dep)} + F_{N(Fert)} + (r_{Fix} - r_{GasLoss})vF_C - k_{Leach}N
\]

\[
(5.18)
\]
All terms on the right hand side of this equation are independently determined, when values are specified for \( r_{\text{Fix}} \), \( r_{\text{GasLoss}} \), \( k_{\text{Leach}} \) and the external input fluxes \( F_{N(\text{Dep})} \) and \( F_{N(\text{Fert})} \), and solutions for \( F_C \) and \( N \) are available from the dimensionless dependent variables \( f \) and \( n \) given by Equations (5.10) and (5.8). Thus the N loss from disturbance by herbivory, fire and product offtake, \( r_{\text{Disturb}}F_C \), can be calculated.

Strictly the calculation should be iterative because the solutions for \( f \) and \( n \) from Equations (5.10) and (5.8) depend on \( r_{\text{Disturb}} \) through the dimensionless variable \( y_N \) defined in Equation (5.7). The iterative procedure is:

1. Make the initial estimate \( r_{\text{Disturb}} = 0 \).
2. Solve for \( f \) and \( n \), and thence \( F_C \) and \( N \), using Equations (5.10) and (5.8).
3. Estimate \( r_{\text{Disturb}} \) and the N loss by disturbance, \( F_{N(\text{Pla,Disturb})} \), using Equation (5.18).

Steps 2 and 3 could be repeated iteratively to convergence, but the first iteration gives a satisfactory approximation because \( r_{\text{Disturb}} \) is usually much less than 1. We used the first iteration estimate only. This method has been applied to estimate continental N disturbance fluxes both without European-style agricultural nutrient inputs (fertilisers, legume N inputs) and with agricultural inputs; see Section 4.3 of Report 1 and Section 9.4 of this report.

### 5.5 Caution and Discussion

The disturbance calculations, and also the calculations of the mineral N and P stores and the external fluxes dependent on them, are subject to a major caution for the following reason. In the above analysis, the uptake coefficients \( c_N \) and \( c_P \) have been assumed to be constant. However, as indicated when these coefficients were introduced in Equation (4.17), this assumption is only justifiable in nutrient-limited conditions (that is, when \( n \) and \( p \) approach 0). In general, \( c_N \) and \( c_P \) vary as nutrient uptake efficiency changes with nutrient supply. The precise nature of this variation can be seen from the plant N balance equation in the steady state, Equation (5.17), and its counterpart for P. In dimensionless form, these are

\[
0 = c_N n - f, \quad 0 = c_P p - f \tag{5.19}
\]

so that (generalising Equation (5.14) which was derived for a special case):

\[
c_N = \frac{f}{n} = \frac{s_p(p)}{n + b_n}, \quad c_P = \frac{f}{p} = \frac{s_n(n)}{p + b_p} \tag{5.20}
\]

Thus, \( c_N = c_N(n, p) \) and \( c_P = c_P(n, p) \), with \( c_N \) approaching a constant value in N-limited conditions \((n \rightarrow 0 \text{ with } p \text{ remaining non-zero})\) and similarly for \( c_P \).

This dependence does not affect the argument in Section 5.3 determining constraints on the product \( bc \). The main implication is that the parts of the above analysis which depend on a specific value for \( c \) (as opposed to \( bc \)) must be interpreted with caution. These include the values of the mineral nutrient stores \((n \text{ and } p)\), or their dimensional counterparts \( N = N_{\text{mnl1}} + N_{\text{mnl2}} \) and \( P = P_{\text{Pri1}} + P_{\text{Pri2}} \); and the external nutrient fluxes dependent on these stores (mainly leakage, from \( F_{N(\text{Leach})} = k_{\text{Leach}}N \) and likewise for \( P \), and disturbance, from Equation (5.18)). Our estimates for these quantities are valid in a restricted range of \((f, n, p)\) space within which \( c \) is approximately constant, and become progressively weaker approximations as conditions move across larger regions of \((f, n, p)\) space.
Despite this caution, we are confident that the predicted spatial patterns of the above quantities are realistic, and that the main trends in the predictions are credible; see Section 9.4 for further discussion.

The overall analysis in this section can be seen as a quantification of the "resource balance" hypothesis (Field 1983; Bloom et al. 1985; Field et al. 1995) or the related "balanced activity" hypothesis (Davidson 1969; Hilbert and Reynolds 1991), which asserts that ecosystems tend towards an equilibrium in which NPP is co-limited by acquired light, water and nutrients. This is a result of natural selection, as plants maximise net benefit for growth and reproduction by adjusting structure and function (carbon and nutrient allocation, water use dynamics) in response to ambient resource availability. It follows that all acquired resources are equally limiting on average, in an ecosystem in ecological equilibrium with its resource environment. When the environment is changed (for example by nutrient inputs), there is a rapid change in resource use patterns, resulting in changes in the C, N and P balances reflected (for instance) in changed disturbance fluxes through Equation (5.20).

6 Fluxes of C, N and P through Litter and Soil Pools

This section outlines the equations determining the organic stores of C, N and P, both in litter ($\text{Lit} = \text{Res} + \text{Met} + \text{Str}$) and in soil organic matter ($\text{SOM} = \text{Act} + \text{Hum} + \text{Pas}$), and the relevant inter-pool fluxes. These pools and fluxes are shown in detail in Figures 2 and 3. The phenomenological equations for the fluxes are based on those used in the Century model for biogeochemical cycling (Parton et al. 1987, 1988, 1993).

6.1 Output Fluxes of C, N and P from Litter and Soil Pools

The material in each litter and soil pool ($\text{Res}$, $\text{Met}$, $\text{Str}$, $\text{Act}$, $\text{Hum}$, $\text{Pas}$) decays at a specified rate, representing the total output flux out of each of these pools. The output N and P fluxes are related to the C flux through the C:N and C:P ratios of the material in the pool. For each pool, the rate constant is the product of a maximum value $k_{\text{Aaa}}$ (for pool $\text{Aaa}$) and multiplicative stress functions $s_W(W)$ and $s_T(T)$ (between 0 and 1) accounting for the effects of soil moisture ($W$) and temperature ($T$). Hence, the decay or total output fluxes are

$$
\begin{align*}
F_{C(\text{Aaa};\text{Out})} &= C_{\text{Aaa}} k_{\text{Aaa}} s_W(W) s_T(T) \\
F_{N(\text{Aaa};\text{Out})} &= F_{C(\text{Aaa};\text{Out})}/r_{\text{C:N}_{\text{Aaa}}} \\
F_{P(\text{Aaa};\text{Out})} &= F_{P(\text{Aaa};\text{Out})}/r_{\text{C:P}_{\text{Aaa}}}
\end{align*}
$$

(6.1)

Values for the C:N ratios $r_{\text{C:N}_{\text{Aaa}}}$, C:P ratios $r_{\text{C:P}_{\text{Aaa}}}$, and rate constants $k_{\text{Aaa}}$ are given later. The stress functions $s_W(W)$ and $s_T(T)$ take the forms

$$
\begin{align*}
s_W(W) &= \min[(4/3)W/W_{\text{sat}}, 1] 
\end{align*}
$$

(6.2)
where \( W_{sat} \) is the saturated soil water store, so that \( W/W_{sat} \) is the relative water content. The temperature stress function is a fit to Figure 2 of Parton et al. (1993).

### 6.2 C Fluxes Into Litter and Soil Pools

The C fluxes into the litter (\( Met, Str \)) and soil (\( Act, Hum, Pas \)) pools are found by partitioning the fluxes out of upstream pools, with the following partitioning factors (Figure 2):

- The C flux out of the plant residue pool \( Res \) is partitioned between the \( Str \) and \( Met \) litter pools in the ratio \((1−γ) : γ\);
- The C flux out of \( Str \) is partitioned between \( Act \) and \( Hum \) in the ratio \((1−α) : α\);
- The C flux out of \( Act \) is partitioned between \( Hum \) and \( Pas \) in the ratio \((1−δ) : δ\);
- The C flux out of \( Hum \) is partitioned between \( Act \) and \( Pas \) in the ratio \((1−β) : β\);
- In the eight transformation pathways \( Met\rightarrow Act, Str\rightarrow Act, Str\rightarrow Hum, Act\rightarrow Hum, Act\rightarrow Pas, Hum\rightarrow Act, Hum\rightarrow Pas \) and \( Pas\rightarrow Act \), a fraction \( θ \) of the C flux is oxidised by microbial respiration and lost to the atmosphere, leaving a fraction \((1−θ)\) to reach the downstream pool. The sum of these losses is the soil heterotrophic respiration of CO2. Four different values of the partitioning factor (\( \theta_1, \theta_2, \theta_3, \theta_4 \)) are used to describe the different pathways, as shown in Figure 2.

The result of these assumptions is the following specification for the ten C fluxes entering the litter (\( Met, Str \)) and soil (\( Act, Hum, Pas \)) pools:

\[
F_{C(Aaa:Bbb)} = p_{(Aaa:Bbb)} q_{(Aaa:Bbb)} F_{C(Aaa:Out)}
\]  

(6.4)

Here \( Aaa \) is the source pool for the flux, and \( Bbb \) the destination pool. The factors \( p_{(Aaa:Bbb)} \) describe partitioning of the C flow from \( Aaa \) to \( Bbb \), and the factors \( q_{(Aaa:Bbb)} \) describe respiration loss along the pathway from \( Aaa \) to \( Bbb \). These factors are given by
\[
\begin{align*}
\begin{bmatrix}
    p_{\text{Res:Met}} & = & \gamma \\
p_{\text{Res:Str}} & = & 1 - \gamma \\
p_{\text{Met:Act}} & = & 1 \\
p_{\text{Str:Act}} & = & 1 - \alpha \\
p_{\text{Str:Hum}} & = & \alpha \\
p_{\text{Act:Hum}} & = & 1 - \delta \\
p_{\text{Act:Pas}} & = & \delta \\
p_{\text{Hum:Act}} & = & 1 - \beta \\
p_{\text{Hum:Pas}} & = & \beta \\
p_{\text{Pas:Act}} & = & 1
\end{bmatrix}
\quad \text{and} \quad
\begin{bmatrix}
    q_{\text{Res:Met}} & = & 1 \\
q_{\text{Res:Str}} & = & 1 \\
q_{\text{Met:Act}} & = & 1 - \theta_1 \\
q_{\text{Str:Act}} & = & 1 - \theta_1 \\
q_{\text{Str:Hum}} & = & 1 - \theta_3 \\
q_{\text{Act:Hum}} & = & 1 - \theta_4 \\
q_{\text{Act:Pas}} & = & 1 - \theta_4 \\
q_{\text{Hum:Act}} & = & 1 - \theta_1 \\
q_{\text{Hum:Pas}} & = & 1 - \theta_1 \\
q_{\text{Pas:Act}} & = & 1 - \theta_1
\end{bmatrix}
\end{align*}
\] (6.5)

The total heterotrophic respiration flux from the litter and soil pools to the atmosphere is

\[
F_{C(\text{Met:Atm})} + F_{C(\text{Str:Atm})} + F_{C(\text{Act:Atm})} + F_{C(\text{Hum:Atm})} + F_{C(\text{Pas:Atm})} = \theta_1 F_{C(\text{Met:Out})} + (\alpha \theta_3 + (1 - \alpha) \theta_1) F_{C(\text{Str:Out})} + \theta_4 F_{C(\text{Act:Out})} + \theta_4 F_{C(\text{Hum:Out})} + \theta_4 F_{C(\text{Pas:Out})}
\] (6.6)

6.3 N and P Fluxes into Litter and Soil Pools

The transfer of N and P into the litter (Met, Str) and soil (Act, Hum, Pas) pools is mediated by the flows of organic matter among the pools, described by the C fluxes. However, the N and P transfers are also constrained stoichiometrically by the C:N and C:P ratios of the destination pools, which take prescribed values. Each transformation is accompanied by mineralisation (organic to mineral) or immobilisation (mineral to organic) processes, to the extent necessary to ensure joint mass conservation of C, N and P. Hence, the flux of N or P from pool Aaa to pool Bbb is accompanied by a flux of N and P to or from the mineral pools N\text{Min} and P\text{Min}. In the case of N, the mineralisation or immobilisation flux is

\[
\begin{align*}
F_{N(\text{Res:Met})}\text{NetMin} & = \gamma F_{N(\text{Res:Out})} - F_{C(\text{Res:Met})} / r_{CN(\text{Met})} \\
F_{N(\text{Res:Str})}\text{NetMin} & = (1 - \gamma) F_{N(\text{Res:Out})} - F_{C(\text{Res:Str})} / r_{CN(\text{Str})} \\
F_{N(\text{Met:Act})}\text{NetMin} & = F_{N(\text{Met:Out})} - F_{C(\text{Met:Act})} / r_{CN(\text{Act})} \\
F_{N(\text{Str:Act})}\text{NetMin} & = (1 - \alpha) F_{N(\text{Str:Out})} - F_{C(\text{Str:Act})} / r_{CN(\text{Act})} \\
F_{N(\text{Str:Hum})}\text{NetMin} & = \alpha F_{N(\text{Str:Out})} - F_{C(\text{Str:Hum})} / r_{CN(\text{Hum})} \\
F_{N(\text{Act:Hum})}\text{NetMin} & = (1 - \delta) F_{N(\text{Act:Out})} - F_{C(\text{Act:Hum})} / r_{CN(\text{Hum})} \\
F_{N(\text{Act:Pas})}\text{NetMin} & = \delta F_{N(\text{Act:Out})} - F_{C(\text{Act:Pas})} / r_{CN(\text{Pas})} \\
F_{N(\text{Hum:Act})}\text{NetMin} & = (1 - \beta) F_{N(\text{Hum:Out})} - F_{C(\text{Hum:Act})} / r_{CN(\text{Act})} \\
F_{N(\text{Hum:Pas})}\text{NetMin} & = \beta F_{N(\text{Hum:Out})} - F_{C(\text{Hum:Pas})} / r_{CN(\text{Pas})} \\
F_{N(\text{Pas:Act})}\text{NetMin} & = F_{N(\text{Pas:Out})} - F_{C(\text{Pas:Act})} / r_{CN(\text{Act})}
\end{align*}
\] (6.7)
where \( F_{N(Aaa:Out)} \) is defined by Equation (6.1), and \( F_{N(Aaa:Bbb)} \) is defined at the point of entry into \( Bbb \), and thus includes the contribution from the mineralisation or immobilisation associated with transfer from \( Aaa \) to \( Bbb \). The choice between net mineralisation and net immobilisation is made by the sign of the right hand side (RHS) in each of Equations (6.7). The RHS for transfer from \( Aaa \) to \( Bbb \) is the difference between a supply term proportional to \( F_{N(Aaa:Out)} \) and a demand term \( F_{C(Aaa:Bbb)} r_{CN(Bbb)} \). If RHS > 0, then supply exceeds demand: the excess supply feeds a net mineralisation flux. If RHS < 0, then demand exceeds supply: the extra demand is made up by a net immobilisation flux expressed as a negative net mineralisation flux.

It is also necessary to ensure that there is a supply limitation on immobilisation from the mineral N or labile P pool if that pool is nearly empty, because unconstrained immobilisation could otherwise cause \( N_{Mnl} \) or \( P_{Pri} \) to become negative. This can be achieved by recasting Equation (6.1) (for N and P output fluxes) and Equation (6.7) (for mineralisation or immobilisation) generically as

\[
F_{X(Aaa:Bbb)} = \frac{P_{(Aaa:Bbb)} F_{C(Aaa:Out)}}{r_{CX(Aaa)}} - F_{X(Aaa:Bbb) NetMin} \\
F_{X(Aaa:Bbb) NetMin} = P_{(Aaa:Bbb)} F_{C(Aaa:Out)} \left( \frac{1}{r_{CX(Aaa)}} - \frac{1}{r_{CX(Bbb)}} \right) L_{Imm} \\
L_{Imm} = \begin{cases} 0 & \text{if } F_{X(Aaa:Bbb) NetMin} < 0 \text{ and } X_{Min} = 0 \\ 1 & \text{otherwise} \end{cases}
\]

(6.8)

where \( F_{X(Aaa:Bbb) NetMin} \) is the net mineralisation occurring in conjunction with the N or P flux from pool \( Aaa \) to pool \( Bbb \); \( P_{(Aaa:Bbb)} \) is the partitioning factor defined by Equation (6.5); and \( L_{Imm} \) is a limiting factor equal to either 1 or 0 which prevents an immobilisation flux occurring from the mineral pool (\( N_{Mnl} \) or \( P_{Pri} \)) if that pool is empty. If there is no constraint on immobilisation due to supply limitation of mineral N or P, then \( L_{Imm} = 1 \) and Equation (6.8) reduces to

\[
F_{X(Aaa:Bbb)} = \frac{P_{(Aaa:Bbb)} F_{C(Aaa:Out)}}{r_{CX(Bbb)}}
\]

(6.9)

In this case the N or P flux from \( Aaa \) into \( Bbb \) is determined by the C:N or C:P ratio of the destination pool \( Bbb \), and the corresponding C flux excluding respiration loss, \( P_{(Aaa:Bbb)} F_{C(Aaa:Out)} \) (since respiration depletes C but not N or P).

### 6.4 Fluxes of Mineral N and P

The mineral N and P fluxes in the conservation equations (3.16) and (3.17) are divided into local cycling fluxes and external fluxes. These are specified as follows.

**Local Cycling Fluxes of N and P:** The total net mineralisation is the sum of the flux terms \( F_{X(Aaa:Bbb) NetMin} \) from Equation (6.8), for the ten pathways \( Aaa:Bbb = \text{Res:Met, Res:Str, Met:Act, Str:Act, Str:Hum, Act:Hum, Act:Pas, Hum:Act, Hum:Pas and Pas:Act} \). This net flux enters the pool \( N_{Mnl} \) or \( P_{Pri} \) in the cases of N and P, respectively. Hence:
The plant uptake fluxes $F_{N(Mnl:Pla)}$ and $F_{P(Pla:Pla)}$ are given by Equations (4.17) and (4.18) in *BiosEquil* and *BiosEvolve*, respectively.

**External N Fluxes:** In Equation (3.16), five external fluxes act on the mineral N pool, associated with fixation, deposition, fertilisation, gaseous loss and leaching. These are modelled as follows:

- **Fixation of N**, $F_{N(Fix)}$, is modelled by specifying a fraction $r_{Fix}$, the fraction of the N requirement by plants in their growth that is supplied by symbiotic legume fixation. From Equation (4.17), the N requirement of plants in growth is $F_{N(Mnl:Pla)} = \nu FC$ (where $\nu$ is the average N:C ratio in whole-plant growth and $FC$ is the NPP). Hence we write

$$F_{N(Fix)} = r_{Fix} \nu FC$$

The fraction $r_{Fix}$ is given different values according to the propensity of the vegetation for legume fixation (see Table 1). A generic value $r_{Fix} = 0.1$ is adopted for most vegetation, but values of 1.0 and 1.5 are used for pulse crops and pasture legumes, respectively, consistent with values assumed in NLWRA Project 5.4d on farm nutrient balances (M. Unkovich and D. Reuter, personal communication). For simplicity, all fixed N is assumed to enter the mineral ($N_{Mnl}$) pool, though the real distribution of fixed N among organic and inorganic pools is much more complex.

- **Atmospheric deposition of N**, $F_{N(Dep)}$, occurs by dry gaseous deposition, dry particulate deposition via dust, and wet deposition of N dissolved in rainfall. Only the last of these is modelled explicitly, taking $F_{N(Dep)} = FW_{Rain} [N]_{Rain}$, where $FW_{Rain}$ is the rainfall $[kg \text{ water m}^{-2} \text{ s}^{-1}]$ and $[N]_{Rain}$ is the dissolved nitrogen concentration in rainfall $[kg \ N \ (kg \text{ water}^{-1})]$. A spatially and temporally uniform value of $[N]_{Rain}$ was assumed in the present work, though this is a gross simplification of reality. Surveys of available measurements (e.g. Bridgman 1989; Ayers and Gillett 1988; Ayers and Granek 1997) suggest that a value $[N]_{Rain} = 10^{-7} \ kg \ N \ (kg \text{ water}^{-1})$ is representative (with a scatter of around 50%) of data in areas away from sources of urban or industrial pollution. On the grounds that towns and industrial centres are sparse on the Australian continent, this value has been used everywhere. Nitrogen deposition near urban centres will therefore be underestimated. However, the general pattern of continental $F_{N(Dep)}$ should be reproduced because of its strong dependence on total rainfall. Another source of underestimation of $F_{N(Dep)}$ is the neglect of dry deposition of N. However, because $F_{N(Dep)}$ is a small contributor to the $N_{Mnl}$ balance (Report 1, Figure 25), these deficiencies are not likely to have a major influence on overall results.

- **Fertiliser addition of N**, $F_{N(Fert)}$, is a specified external flux determined by a spatial input data set; see Section 8.2 for details.

- **Gaseous loss of N**, $F_{N(GasLoss)}$, is modelled as a fraction $r_{GasLoss}$ of the net mineralisation flux if this flux is positive:

$$F_{N(GasLoss)} = \max\left(r_{GasLoss} F_{N(TotalNetMin)}, 0\right)$$

(6.12)
This model is a gross oversimplification of the complex biogeochemistry of nitrogen and its gaseous loss, but it captures the essential feature that gaseous loss is a transaction cost associated with mineralisation or immobilisation of N due to microbial biochemistry. The restriction to positive $F_N(TotalNetMin)$ prevents unrealistic gaseous N uptake. In BiosEquil it is assumed that $F_N(TotalNetMin)$ can be approximated by $vF_C$, so that $F_N(GasLoss) = r_{GasLoss}vF_C$, and that the fraction $r_{GasLoss} = 0.02$ (see Table 1).

- **Leaching of dissolved N, $F_N(Leach)$**, is modelled as

\[
F_N(Leach) = \frac{N_{Mnl2}F_W(Leach)}{W_2}
\]

equivalent to

\[
F_N(Leach) = F_W(Leach) \left[ \frac{[N]_{Soil2}}{N_{Mnl2}} \right] \text{ with } \frac{N_{Mnl2}}{W_2}
\]

and to

\[
F_N(Leach) = k_{Leach}N_{Mnl2} \text{ with } k_{Leach} = F_W(Leach)/W_2
\]

The latter two expressions for $F_N(Leach)$ are equivalent. In the first, $F_N(Leach)$ is expressed as the product of the water leaching flux and concentration of mineral N dissolved in the soil water in the lower soil layer (from which leaching occurs). This concentration is estimated as the ratio of the mineral N and water stores in that soil layer, both in units of kg m$^{-2}$. In the second expression, $F_N(Leach)$ is expressed as the product of the mineral N store in the lower soil layer and a leaching rate constant equal to that for water from the deep soil layer, $k_{Leach} = F_W(Leach)/W_2$.

A simple rule-based approach is used to estimate $k_{Leach}$ and $F_W(Leach)$ in BiosEquil, in lieu of a mechanistic approach used in BiosEvolve; see Section 7.4 for details.

**External P Fluxes**: In Equation (3.17), only two external fluxes act on the mineral P pools, associated with fertilisation and leaching. However, in addition, exchanges occur between the $P_{Pri}$, $P_{Sec}$ and $P_{Occ}$ pools. These fluxes are modelled as follows:

- **Fertiliser addition of P, $F_P(Fert)$**, is a specified external flux to the $P_{Pri}$ pool, determined by a spatial input data set; see Section 8.2 for details.

- **The leaching flux of P is $F_P(Leach) = P_{Pri2}(F_W(Leach)/W_2)$**, as for the N leaching flux, Equation (6.13). It acts only on the $P_{Pri}$ pool, as this is the only water-soluble P pool.

- **The P fluxes between the $P_{Pri}$, $P_{Sec}$ and $P_{Occ}$ pools** are specified by adsorption and desorption coefficients, so that

\[
F_{P(Pri;Sec)} = k_{P(Pri;Sec);Ads} P_{Pri},
F_{P(Sec;Pri)} = k_{P(Sec;Pri);Des} P_{Sec},
F_{P(Sec;Occ)} = k_{P(Sec;Occ);Ads} P_{Sec}
\]

These coefficients are not equal, since the exchange between the primary and secondary P pools exhibits hysteresis (desorption from secondary to primary is slower than adsorption from primary to secondary). The exchange between secondary and occluded pools is entirely one-way, so the occluded pool is a sink for P. Table 1 gives values for these rate constants derived from one author’s experience (DJB). Note that in this work we take $k_{P(Sec;Occ)} = 0$, so the occluded pool does not influence the P dynamics.
7 Water Fluxes

The phenomenological equations for the fluxes in the water balance, Equation (3.1), are different in *BiosEquil* and *BiosEvolve*, because of the very different time resolutions of the two models. In this report only the *BiosEquil* formulation is described.

In *BiosEquil* an algebraic model is required for the long-term average water balance, Equation (3.1), in the steady state where the average storage change \( \frac{dW}{dt} \) is negligible compared with the fluxes in the balance. The principles of the model are that (1) long-term average total evaporation is determined by water supply (rainfall) in dry environments and by energy supply (radiation) in wet environments; (2) regional energy-limited evaporation is equal to Priestley-Taylor evaporation; (3) a single-parameter hyperbolic function interpolates between dry (rainfall-limited) and wet (energy-limited) total evaporation rates; and (4) total evaporation is the sum of plant transpiration and soil evaporation, with a partition dependent on leaf area index.

7.1 Potential Evaporation

When a sufficiently large region (around 10 km or more in extent) is well supplied with water, the total evaporation is determined only by the available radiant energy and is equal to the Priestley-Taylor evaporation rate \( F_{W(PT)} \). Thus, Priestley-Taylor evaporation is taken to be the measure of potential evaporation at regional scales. This was originally proposed by Priestley and Taylor (1972) and has recently been supported (Raupach 2000, 2001) by analysing the quasi-equilibrium between the surface energy balance and entrainment of dry air into the Convective Boundary Layer (CBL) above the surface from the overlying troposphere. The Priestley-Taylor evaporation rate is defined by

\[
\begin{align*}
\lambda F_{W(q)} &= \Phi_{E(q)} = \frac{\varepsilon_a \Phi_A}{\varepsilon_a + 1} \\
\lambda F_{W(PT)} &= \Phi_{E(PT)} = c_{PT} \Phi_{E(q)}
\end{align*}
\]

where:

- \( \Phi_A, \Phi_{E(q)} \) and \( \Phi_{E(PT)} \) are respectively the available energy flux, the thermodynamic equilibrium latent heat flux and the Priestley-Taylor latent heat flux, all in [W m\(^{-2}\)]. The evaporation rate \( F_W \) corresponding to a latent heat flux \( \Phi_E \) is \( F_W = \Phi_E / \lambda \), where \( \lambda \) is the latent heat of vaporisation of water.

- \( c_{PT} \) is the Priestley-Taylor coefficient, taken as \( c_{PT} = 1.26 \) (Priestley and Taylor 1972; Raupach 2000).

- \( \varepsilon_a = (\lambda/c_p)dQ_{sat}/dT \) is the dimensionless slope of the curve of saturation specific humidity \( Q_{sat}(T) \) against temperature \( T \) (with \( \lambda \) the latent heat of vaporisation of water and \( c_p \) the isobaric specific heat of air), evaluated at the air temperature \( T_a \). The quantity \( \varepsilon_a \) is the ratio of latent to sensible heat uptake as a parcel of saturated air is warmed while maintaining saturation; it is a rapidly increasing function of temperature, so that \( \varepsilon_a = (1.28, 2.25, 3.78, 6.11) \) at \( T_a = (10, 20, 30, 40) \)°C, and \( \varepsilon_a/(\varepsilon_a + 1) = (0.56, 0.69, 0.80, 0.86) \) at the same temperatures. The equilibrium evaporative fraction \( \Phi_{E(q)}/\Phi_A \) is defined by the ratio \( \varepsilon_a/(\varepsilon_a + 1) \) at the air (CBL potential) temperature (Raupach 2001).
The available energy flux is taken as equal to the net irradiance, neglecting contributions from ground heat flux because the averaging time is long. Thus:

$$\Phi_A = \left[ (1 - a_s) \Phi_{S\downarrow} + e_s \left( \Phi_{L\downarrow} - \sigma T_s^4 \right) \right]$$

(7.2)

where $\Phi_{S\downarrow}$ and $\Phi_{L\downarrow}$ are the incoming global shortwave and longwave irradiances; $a_s$ is the surface albedo, $e_s$ the surface emissivity and $T_s$ the surface temperature; and $\sigma$ is the Stefan-Boltzmann constant ($5.67 \times 10^{-8}$ W m$^{-2}$ K$^{-4}$). Since $T_s$ is not determined explicitly, slightly different expressions are used in practice to account for the difference between $T_a$ and $T_s$ (Raupach 2001):

$$\Phi_A^* = \left[ (1 - a_s) \Phi_{S\downarrow} + e_s \left( \Phi_{L\downarrow} - \sigma T_a^4 \right) \right]$$

$$\Phi_{E(q)} = \frac{p_a \varepsilon_a \Phi_A^*}{p_a \varepsilon_a + 1}$$

$$\Phi_{E(PT)} = c_{PT} \Phi_{E(q)} = \frac{p_a \varepsilon_a \Phi_A^*}{p_a \varepsilon_a + 1}$$

(7.3)

with $p_a = \frac{g_a}{g_a + g_r}$ and $g_r = \frac{4e_s \sigma T_a^3}{\rho c_p}$

Here $\Phi_A^*$ is the isothermal available energy flux, and $g_a$ and $g_r$ are respectively the aerodynamic and radiative conductances. The latter is evaluated from Equation (7.3) and the former is prescribed. The formula used in practice for the potential (Priestley-Taylor) evaporation [$\Phi_{E(PT)} = \lambda F_{W(PT)}$] is given on the third line of Equation (7.3).

### 7.2 Actual Evaporation and Transpiration

The steady-state water balance is simplified to

$$\frac{dW}{dt} = 0 = P - E - R$$

(7.4)

where (comparing with Equation (3.1)) $P = F_{W(\text{EffRain})}$ is the total effective rainfall; $R = F_{W(\text{Runoff})} + F_{W(\text{Leach})}$, is the total runoff including both surface and subsurface flow; and $E = F_{W(\text{EVeg})} + F_{W(\text{ESoil})} = E_V + E_S$ is the total evaporation (with $E_V = F_{W(\text{EVeg})}$ being the transpiration and $E_S = F_{W(\text{ESoil})}$ the soil evaporation). It is then assumed that

$$E \rightarrow P, \quad R \rightarrow 0 \quad \text{as} \quad P/E_{PT} \rightarrow 0$$

(7.5)

$$E \rightarrow E_{PT}, \quad R \rightarrow P - E_{PT} \quad \text{as} \quad P/E_{PT} \rightarrow \infty$$

(7.6)

where $E_{PT} = F_{W(PT)}$ is the Priestley-Taylor evaporation from Equation (7.3). Equation (7.5) says that there is negligible runoff when the "precipitation index" $P/E_{PT}$ is very small (rainfall much less than potential evaporation); Equation (7.6) says that evaporation is limited by the potential value when $P/E_{PT}$ is large.
The dimensionless evaporation \( e = E/E_{PT} \) and runoff \( r = R/E_{PT} \) can now be expressed as single-parameter functions of the dimensionless precipitation \( p = P/E_{PT} \), such that the limits in Equations (7.5) and (7.6) are satisfied. (The notation \( e, r \) and \( p \) for these dimensionless variables is restricted to this subsection). Suitable single-parameter functions are:

\[
\begin{align*}
  e &= \left( \frac{p^a}{1 + p^a} \right)^{1/a} ; \\
  r &= 1 - \left( \frac{p^a}{1 + p^a} \right)^{1/a} \\
\end{align*}
\]

(7.7)

where \( a \) is a parameter determining how closely the function \( e(p) \) follows the "broken-stick" form \( e = p \) when \( p < 1 \) and \( e = 1 \) when \( p > 1 \), as shown in Figure 9 (discussed further in Section 9.1). Large values of \( a \) follow the “broken-stick” form tightly. Small values imply more gentle curvature, and consequently lower values for \( E/P \) and higher runoff \( (R/P) \).

Finally, the total evaporation \( E \) is partitioned into transpiration \( (E_T) \) and soil evaporation \( (E_S) \) components, using an empirical expression similar in form to Beer’s Law for light extinction (Equation (4.10)):

\[
\begin{align*}
  E &= E_T + E_S \\
  E_T &= (1 - \exp(-c_{ESoil}\Lambda))E \\
  E_S &= \exp(-c_{ESoil}\Lambda)E \\
\end{align*}
\]

(7.8)

where \( \Lambda \) is the single-sided leaf area index of the canopy and \( c_{ESoil} \) is an extinction coefficient describing the attenuation of soil evaporation as canopy cover increases.

In applying these algorithms in BiosEquil, the effective rainfall \( P_{EffRain} \) was calculated from climate data on rainfall and land use data on irrigation (Section 8.2). Interception losses (Equation (3.1)) were ignored.

7.3 Soil Moisture

In BiosEvolve, the soil moisture in two layers \( (W_1 \) and \( W_2) \) is determined by solving a set of time-dependent water balance equations, Equation (3.2).

In BiosEquil, a much simpler expedient is used to find the long-term average soil moisture \( W \) (summed over all soil layers): we approximate \( W \) as

\[
W/W_{sat} = E/E_{PT}
\]

(7.9)

where \( W_{sat} \) is the saturation soil moisture store and \( E_{PT} \) is the potential (Priestley-Taylor) evaporation. Though crude, this approximation is conservative (it does not produce wild values) and is sufficient for the present purpose because \( W \) essentially affects only the external nutrient (leakage) fluxes in BiosEquil. The adequacy of this approximation is the subject of continuing work.
7.4 Drainage

Drainage in *BiosEvolve* is calculated using a two-layer, daily-time-step compartment or “bucket” model with Green-Ampt surface infiltration and moisture-content-dependent drainage rates out of each layer, accounting for vertical (inter-layer) variation of soil hydraulic properties. The details will be described elsewhere.

In *BiosEquil*, the long-term average drainage is calculated with a simple rule-based algorithm based on the experience of one of the authors (JMK). The drainage flux is parameterised as

\[
F_{W(\text{Drain})} = m_{\text{Cult}} r_{\text{Drain}} P
\]

with

\[
r_{\text{Drain}} = r_{\text{DrainSand}} \left(1 - f_{\text{Clay}} \right) + r_{\text{DrainClay}} f_{\text{Clay}}
\]

and

\[
m_{\text{Cult}} = \left(1 - f_{\text{Crop}} \right) + f_{\text{Crop}} m_{\text{Crop}}
\]

(7.10)

where \(P = F_{W(\text{EffRain})}\) is the total effective rainfall, \(r_{\text{Drain}}\) is the fraction of effective rainfall leaving the soil root zone as drainage, and \(m_{\text{Cult}}\) is a multiplier accounting for the effects of cultivation. The soil was assumed to be cultivated for any cropping land use. The fraction \(r_{\text{Drain}}\) is small (around 0.01) and is specified as a weighted mean of preset values \((r_{\text{DrainClay}}\) and \(r_{\text{DrainSand}}\)) for clay and non-clay soils, determined by the clay fraction \(f_{\text{Clay}}\). The cultivation multiplier \(m_{\text{Cult}}\) is 1 in the absence of cultivation, takes a preset value \(m_{\text{Crop}}\) in the presence of cultivation, and is weighted between these two values according to the cropped fraction of land area \(f_{\text{Crop}}\). The values used for these parameters are given in Table 1.

It is convenient to specify a drainage rate constant \(k_{\text{Leach}}\), such that

\[
F_{W(\text{Drain})} = k_{\text{Leach}} W
\]

(7.11)

This is the rate constant for the depletion of the soil water store by drainage. It is used in specifying the drainage fluxes of nitrogen and phosphorus (Sections 5 and 6).

The long-term average drainage thus calculated depends only upon rainfall, soil type (sand or clay) and land use (cultivation). This is a gross simplification since drainage clearly depends on many other factors including vegetation type and management, topographic position and so on. Actual drainage will also vary more among soil types than indicated by a simple clay/non-clay classification. These drainage estimates are for the purpose of estimating regional-scale leaching fluxes, and should be treated with appropriate caution.

8 Spatial Input Data and Model Operation

8.1 Operating Environment

*BiosEvolve* and *BiosEquil* were coded as a set of modules in standard Fortran 95, using the Compaq Visual Fortran development environment. To run continentally at 0.05° resolution the models require a high-end PC workstation with about 1 gigabyte of RAM, principally to accommodate the large number of stores kept in memory during a run. In the versions of the programs used for NLWRA Project 5.4a, major arrays were allocated at compile time. In
versions developed since then, they are allocated at run time using dimensions read from a control file.

*Bios* parameters are defined primarily through one control file. For *BiosEquil*, the contents of this file are shown in Table 1. The parameters provided include:

- single values for spatially invariant parameters, and default single values for spatial parameters for which spatial information could not be obtained during this project (Table 1: parameters 1-29 and 71-96)
- constant values of forcing variables, used only for testing purposes in single-column mode, with spatial dimension 1 (Table 1: parameters 36-58)
- flags for turning functions and output types on and off (Table 1: parameters 30-35, 97-98)
- indexes of map file names containing spatially distributed parameters (Table 2)
- lookup tables for the distribution of spatially varying parameters (Table 2)

Note that most of these parameters are operational (switches and other settings) or well known physical constants. There are only a few “sensitive” parameters, which were determined as outlined in Section 9.

*BiosEvolve* and *BiosEquil* use the same parameter and forcing data, except that forcing variables for *BiosEquil* are the mean monthly or annual averages of the daily time series used by *BiosEvolve* (1980 to 1999). A second control file allows *BiosEquil* to cycle through and generate equilibrium solutions for a variety of environmental and management scenarios (see Report 1).

### 8.2 Spatial Input Data

All spatial data used as inputs to the *Bios* models required some modification to bring them into full spatial and temporal correspondence with the model requirements. The modifications required for *BiosEquil* are described here.

**Land mask:** The spatial domain is a land mask of the Australian continent comprising 278190 land cells (0.05° resolution) within an area bounded by 10°S, 45°S and 112°W, 155°W. The continental land mask is an Arcview grid conversion of the standard NATMAP 1:2.5 million coastline of Australia (TOPO-2.5M).

All spatial input data have been resampled to match this land mask, such that data nominally represent cells with even 0.05° boundaries, with coastlines matched exactly to the landmask coastline. To do this, missing coastal cells were filled by nearest-neighbour methods and extra-coastal cells removed.

For processing, all spatially distributed input and output is packed to or unpacked from 278190-element vectors.

**Region Masks:** Region masks for 12 ANRA Drainage Divisions and 245 ANRA Drainage Basins (NLWRA 2001) were constructed by Arcview grid conversion of polygon coverages supplied by NLWRA. The ANRA masks were used to generate regionally-averaged outputs.

**Vegetation Cover:** Vegetation cover at each grid cell is specified by two leaf area indices, one for the woody component (annually averaged) and one for grassy vegetation (12 monthly averages) based on empirical relationships between LAI and fractional cover. These were supplied as 0.05° grids from a companion project (Lu *et al.* 2001) using time series analysis of
Normalised Difference Vegetation Index (NDVI) data from the Pathfinder AVHRR dataset for the period 1981 to 1994.

**Climate Forcings:** Daily gridded data at 0.05° resolution for rainfall, solar radiation, temperature and humidity for the period 1980-1999 were supplied by the Queensland Department of Natural Resources (QDNR) (Jeffrey *et al.* 2001). These data were centred rather than bounded on even 0.05° latitudes and longitudes, so they were regridded with a 0.025° shift by area-weighted averaging of the four adjacent cells. For *BiosEquil*, 20-year monthly averages were calculated from these data.

**Fertilisation, Fixation and Offtake:** N and P fertiliser inputs, N inputs from sown legumes, and N and P offtakes from plant and animal farm produce were supplied by Reuter (2001) as annual values per class of crop per SLA for the years 1989-1994. Crop classes used by Reuter were permanent cropping, horticulture, and fertilised pasture. To distribute these data to 0.05°, an Arcview grid conversion was performed on a Statistical Local Area (SLA) polygon coverage, resulting in a region mask of 771 SLAs at 0.05°. Bureau of Resource Sciences (BRS) landuse data for 1996-97 (NLWRA 2000) were reclassified to the Reuter scheme and aggregated from 0.01° to create proportion maps of the three crop classes at 0.05°. For *BiosEquil*, annual SLA totals were averaged in time and distributed according to landuse proportion and SLA evenly across those months broadly identified as the fertilising, fixing, or offtake seasons. Annual average amounts per SLA were conserved in all cases.

**Irrigation:** Irrigated area fraction for each 0.05° cell was determined by aggregating the 0.01° BRS irrigation mask (NLWRA 2000) specifying each 0.01° cell as subject to irrigation or not. Monthly irrigation amounts were estimated from the climatology by assuming that irrigation occurs to the extent necessary to raise the transpiration of the irrigated vegetation to the potential (Priestley-Taylor) evaporation rate.

**Soil Properties:** A 0.05° gridded map of soil type (strictly of Principal Profile Form, PPF) was generated from the Digital Atlas of Australian Soils polygon coverage (NRIC 1991) by Arcview grid conversion. Each cell was assigned the dominant PPF by area from a set of 725 possible forms. A lookup table of the soil physical properties for each PPF was generated from revised interpretations of the 725 forms (McKenzie *et al.* 2000). The lookup table and PPF map were used at run time to generate soil property arrays, separately for an upper and a lower soil layer, of layer depth, bulk density, silt and clay fractions and saturated volumetric moisture content. With the exception of the last, these properties are given directly by the lookup table of McKenzie *et al.* (2000). The saturated volumetric moisture content, $M_s$, is calculated as

$$M_s = 0.93 \left(1 - \frac{\rho_{\text{Bulk}}}{\rho_{\text{Quartz}}} \right)$$

(Williams *et al.* 1992) where $\rho_{\text{Bulk}}$ and $\rho_{\text{Quartz}}$ are the bulk soil density and the density of quartz (2650 kg m$^{-3}$).

For *BiosEvolve*, two other soil properties are needed. The saturated hydraulic conductivity $K_s$ is taken directly from McKenzie *et al.* (2000). The actual hydraulic conductivity, $K(M)$, varies with volumetric moisture content, $M$, according to
\[
\frac{K}{K_c} = \left(\frac{M}{M_c}\right)^B
\]

\[
B = -2/B' + 3
\]

\[
B' = -0.295 + 0.0442(\text{STR}) + 0.132 \ln(\rho_{\text{Bulk}}) - 0.0278(\rho_{\text{Bulk}}) + 0.0787 \ln(\text{TEX})
\]

(8.2)

from Williams et al. (1992). The lookup key in McKenzie et al. (2000) gives the structure (STR) as classes 1 to 5, the bulk density (\(\rho_{\text{Bulk}}\)) and the texture class (TEX) for each of the upper and lower soil horizons. We take STR = 1 for structure classes 1 and 2, and STR = 2 for classes 3 to 5.

9 Model Calibration, Testing and Sample Results

9.1 Water Fluxes in BiosEquil

This subsection describes calibration, testing and a few highlight results from the water balance calculations in BiosEquil, based on the water balance equations given in Section 3.1 and the phenomenological equations for water fluxes given in Section 7. Further results are given in Report 1, Section 4.1. A summary of all parameter values appears in Table 1.

**Calibration:** The only adjustable parameters in the BiosEquil water balance model are the Priestley-Taylor coefficient \(c_{PT}\) (Equation (7.1)), the power \(a\) specifying the curvature in the relationship between \(E\) and \(P\) (Equation (7.7)) and the coefficient \(c_{ESoil}\) in the expression for the fraction of total evaporation due to the soil (Equation (7.8)). These were set as follows:

- The Priestley-Taylor coefficient \(c_{PT}\) was not treated as an adjustable parameter; we used the well-known value \(c_{PT} = 1.26\) (Priestley and Taylor 1972; Raupach 2000).
- The parameter \(a\) was set by comparing the predictions of Equation (7.7) and data for long-time-averaged evaporation in forested, mixed and pasture catchments, collected by one of the present authors (LZ). Figure 9 shows this comparison. The agreement is good for such a simple model, with values of \(a\) between 1.5 and 2.5 depending on vegetation type, with lower values associated with more grassy catchments. The sensitivity of the continental-scale predictions to \(a\) is low. For simplicity we used the uniform value \(a = 2.5\).
- The parameter \(c_{ESoil}\) was set uniformly to 3, after investigating its effect on the prediction of \(\frac{<E_S>}{<E>}\) (where the angle bracket denotes a continental spatial average). This value for \(c_{ESoil}\) gave \(\frac{<E_S>}{<E>} = 0.45\) (that is, 45% of the total continental evaporation takes place from the soil and 55% by transpiration, neglecting a small interception component). Smaller values of \(c_{ESoil}\) gave values of \(\frac{<E_S>}{<E>}\) which we believed to be unrealistically high, while substantially higher values of \(c_{ESoil}\) are not supportable on physical grounds.

**Testing and Sample Results:** Figure 10 shows a comparison of the predicted runoff \(R\) from Equations (7.4) and (7.7), compared with data from 245 ANRA catchments covering the whole continent (NLWRA 2001). There is significant scatter as is expected from the simple, steady-state, low-parameter parameter approach adopted in BiosEquil, but the overall agreement is good enough to give confidence in the predictions of \(E\). It should be noted that
Figure 10 is a severe test, especially in low-runoff catchments where \( R = P - E \) is a small fraction of both \( P \) and \( E \).

As a sample continental-scale prediction, Figure 11 (same as Figure 6 from Report 1) shows mean annual and mean monthly total evaporation; see Report 1, Section 4.1, for discussion and further results.

### 9.2 Net Primary Production

This subsection describes calibration, testing and a few results from the NPP calculations in BiosEquil, based on Section 4. Further results are given in Report 1, Section 4.2.

**Calibration:** The algorithm for the light and water limited NPP (\( FC^+ \)), Equation (4.13), contains only one free parameter, the linearised canopy-level quantum yield \( \alpha_1 \) (noting that we take the temperature dependence of the CO2 compensation point \( \Gamma^* \) to be defined \textit{a priori} by Equation (4.5)). The actual NPP (\( FC \)) is determined from the light and water limited NPP (\( FC^+ \)) mainly by the product of coefficients \( bc \), through Equation (5.10), with a small additional effect from external nutrient fluxes. We have argued in Section 5.3 that \( bc \) is tightly constrained by the structure of the equations and the requirement that solutions exist, and do not depart from the value \( bc = 0.2 \) inferred from this argument.

We set \( \alpha \) by calibration against point NPP data from the VAST 1.0 dataset (Barrett 2001). This is a collection of point measurements of NPP (based on plant growth and litterfall data), above-ground biomass carbon and soil carbon, drawn from literature values for several hundred sites across the Australian continent. All sites were selected to be representative of "natural" or nominally undisturbed conditions. The different variables (NPP, biomass C, soil C) are not typically available at coincident points.

Figure 12a shows the sample locations for the 184 NPP point measurements used in the present comparison. These points span practically the full range of climate and vegetation types on the Australian continent, but it is important to note that the sampling is not unbiased. For example, the mean rainfall at these 184 locations is 1.17 m y\(^{-1}\), in comparison with a whole-continent mean rainfall for Australia of 0.465 m y\(^{-1}\). Hence, the VAST data for NPP are biased toward the wetter, generally more productive parts of the continent. Nevertheless, the VAST dataset is an invaluable resource.

For each NPP location in the VAST dataset, the NPP predicted by BiosEquil (with parameter values from Table 1 and climate data appropriate to that point) is plotted against the observed NPP in Figure 13. The same data are plotted on linear axes in the left panel, and logarithmic axes in the right panel. The value of \( \alpha \) was chosen to optimise this fit, and once assigned, its value was subsequently held fixed.

The overall agreement is good, with a correlation coefficient of 0.7 (linear axes). The only bias immediately observable in Figure 9 is a slight tendency for the model to underpredict the highest observed values of NPP. The maximum NPP predicted by the model is about 1 kgC m\(^{-2}\) y\(^{-1}\), whereas higher values are observed on a few sites, with values as high as 1.4 kgC m\(^{-2}\) y\(^{-1}\) observed at 3 (out of 184) sites.

**Testing and sample Results:** Figure 14 shows a comparison against observations of the predicted dependence of the NPP on the surface saturation deficit \( D_s \), through the appearance of \( D_s \) in Equation (4.13). For this purpose, values of \( D_s \) were inferred from the meteorological
data at each of the 184 test sites, with a correction to allow for the difference between $D_s$ (at the surface) and the saturation deficit at a typical meteorological observation height of 2 m, based on theory given by Raupach (2001).

Figure 14 shows that the strong dependence of NPP on saturation deficit predicted by Equation (4.13) is confirmed by observations. In both predictions and data, the NPP varies by around a factor of 5 through the observed range of saturation deficit values. The physiological reason for this result is the effect of saturation deficit on water use efficiency (WUE).

Defining WUE as $\frac{F_{\text{Assim}}}{F_{\text{Wet}}(\text{Veg})} = A/E_V$, and using Equations (4.3) to (4.8), we have

$$WUE = \frac{A}{E_V} = \left( \frac{1}{1.6} \right) \frac{C_s - C_i}{Q_i - Q_s} = \left( \frac{1}{1.6} \right) C_s \left( 1 - \frac{C_i}{C_s} \right) D_s \quad (9.1)$$

where $1.6 = G_s / G_{sc}$ as in Section 4.3, and $D_s = Q_i - Q_s$ if the intercellular cavities (humidity $Q_i$) are assumed saturated at leaf-surface temperature. Now, $C_s / C_i$ is a conservative quantity at about 0.65 for C3 plants, and $C_i$ does not vary strongly in space or time over the scales of interest here. Therefore, the most variable quantity influencing WUE in Equation (8.1) is $D_s$. This is a basic physiological constraint on water use efficiency and thence on plant growth in water-limited environments.

As a sample continental-scale prediction, Figure 15 (same as Figure 12 in Report 1) shows the mean annual net primary production with present agricultural and nutrient inputs; see Report 1, Section 4.2, for discussion and further results.

### 9.3 Carbon and Nutrient Stores

This subsection describes calibration, testing and a few results from calculations of the carbon stores in biomass, litter and soil in BiosEquil, based on Sections 3.2 and 5. Further results are given in Report 1, Section 4.2.

**Calibration:** There are several parameters in the model for C stores, including allocation coefficients ($a_{\text{AaA}}$, Equations (3.4) to (3.6)); rate constants ($k_{\text{AaA}}$, Equations (3.4) to (3.6)); partition factors ($p_{\text{AaA:Bbb}}$, Equation (5.5)); and respiration loss fractions in litter and soil transfers ($q_{\text{AaA:Bbb}}$, Equation (5.5)). Of these, the partition factors and respiration rate constants were set to values used in the Century model (Parton et al. 1993) and not adjusted thereafter. We adopted this course, recognising that these values might not be optimal for Australian conditions, in order to keep the number of adjustable parameters small. The allocation coefficients for biomass, litter and soil C pools were assigned initial values from related modelling work (Barrett and Xu 2002).

The rate constants were assigned by comparing the steady-state predictions from BiosEquil against observations of C stores from the VAST 1.0 dataset (see Section 9.2). Figure 16 shows the comparison of the predictions of BiosEquil with VAST observations at up to 577 sites, for biomass C ($= C_{\text{Lea}} + C_{\text{Woo}} + C_{\text{Roo1}} + C_{\text{Roo2}}$), litter C ($= C_{\text{Res}} + C_{\text{Met}} + C_{\text{Str}}$) and soil C ($= C_{\text{Act}} + C_{\text{Hum}} + C_{\text{Pas}}$). A correction based on allocation ratios was applied to the biomass data to account for the fact that the observations refer only to above-ground biomass whereas the comparison is for total biomass including both above-ground and below-ground pools. The only coefficients adjusted in this comparison were the turnover rate constants for the plant, litter and soil pools, keeping the ratios among sub-pools (for instance, leaf, wood and root) to
values consistent with Table 1. Thus, three degrees of freedom in the parameterisation were
allowed in optimising the fit in Figure 16.

Though the scatter is large, there is good overall agreement between the predictions and all
measurement sets in Figure 16 (biomass, litter, soil). Given the disparate sources of the data, a
high degree of scatter is expected.

Further parameters in the nutrient model are the N:C and P:C ratios in the various stores.
Values for these ratios were assigned a priori, mainly from one author’s experience (DJB).

9.4 Mineral N Balance

A final important result is the prediction for the plant-available nitrogen balance (Equation
(5.1)), especially its disturbance term. This was estimated using the method outlined in
Section 5.4, which involves no adjustable parameters beyond those mentioned for water
fluxes and NPP (Sections 9.1 and 9.2) and the choice of the coefficient \( c \) (determined from the
product \( bc = 0.2 \) by assuming \( b = c \)).

Figure 17 (same as Figure 25 in Report 1) shows the predictions for all terms in the steady-
state balance of plant-available N, averaged across the 12 ANRA Drainage Divisions. The
predictions are shown for present agricultural inputs of nutrients from fertiliser application
and crop and pasture legumes, and also without agricultural inputs. It is significant that small
negative disturbance fluxes are predicted in the absence of agricultural nutrient inputs, which
would be expected of ecosystems which have evolved to use scarce nutrients efficiently. The
disturbance loss fluxes in the presence of agricultural nutrient inputs are substantially higher,
balanced mainly by increased N fixation.

10 Summary and Conclusions

This report is a detailed statement of the algorithms used in the BiosEquil and BiosEvolve
models, developed in 2000-2001 for the prediction of the balances (stores and fluxes) of
water, carbon, nitrogen and phosphorus over large land regions. The work was undertaken
under Project 5.4a of the National Land and Water Resources Audit, “Landscape Nutrient
Flux and Water Balance”. The application of the model, the input data sources and the main
results are described in Report 1 [Landscape Balances of Water, Carbon, Nitrogen and
Phosphorus: (1) Project Description and Results (Raupach et al. 2001, CLW Technical
Report 40/01)]. The primary results are outlined in Report 1 and recapitulated in the executive
summary of this report.

In summary, broad features of the model formulations are as follows (drawn from Report 1).
More subtle aspects, including issues of parameter calibration, are discussed in Section 9.

**Dynamical-system description of landscape biogeochemistry:** We have developed a formal
structure (Section 2 and Appendix A) based on two kinds of equation: (1) conservation or
mass balance equations of the generic form

\[
\text{Change of store with time} = \sum [\text{Fluxes entering store}] - \sum [\text{Fluxes leaving store}]
\] (10.1)
and (2) *phenomenological equations* which specify the fluxes appearing in the mass balance equations, of the form

\[
\text{Flux} = \text{Function} (\text{Stores}; \text{Forcing Variables}; \text{Parameters})
\]  

(10.2)

Here, *Stores* include all water, C, N and P stores represented in the model; *Forcing Variables* include both meteorological drivers (rainfall, solar radiation, temperature, humidity) and land management drivers (nutrient inputs from fertilisers and legumes, product offtake in harvest, water inputs from irrigation); and *Parameters* are of three kinds: process parameters (such as light use efficiency or maximum photosynthetic capacity); properties of the soil or landform (such as soil depth or layer structure, and the hydraulic and thermal properties of soil layers); and properties of the vegetation and land surface (such as height, leaf area index or albedo). The phenomenological equations are scale dependent, and are chosen here to describe landscape function at large scales (cell size about 5 km).

**Spatial Scales, Temporal Scales and the Statistical Steady State:** A dynamic, time-dependent model (*BiosEvolve*) and a statistically steady-state model (*BiosEquil*) have been developed. Both use a spatial resolution of 0.05° (about 5 km) and a spatial domain encompassing the Australian continent. The results presented in Report 1 are from *BiosEquil*, which accordingly is the main focus of this report. Some aspects of *BiosEvolve* are also described for comparison.

The time step of *BiosEvolve* is 1 day. *BiosEquil* has no time step, as it determines long-term average values of the stores and fluxes in the water, C, N and P balances. Provided that the forcing variables (meteorological and land management) are statistically steady, the solutions to a simplified algebraic equation system (Sum[Fluxes] = 0) describe the average state of the system after the temporal fluctuations are smoothed out. To find this average state algebraically by this route, the phenomenological equations (2) must apply to the time-averaged quantities. In *BiosEquil*, a mean annual cycle with monthly time steps is retained in calculating evaporation, transpiration and NPP (that is, these quantities are seasonally varying with the same pattern each year). All other stores and fluxes are calculated as long-term averages.

**Water fluxes (evaporation, transpiration and drainage):** In *BiosEvolve*, the treatment of the water balance involves explicit temporal resolution of all water fluxes in two soil layers. In the statistically steady-state model *BiosEquil*, the following much simpler formulations are used for the time-averaged water fluxes:

- Long-term average total evaporation is determined by water supply (rainfall) in dry environments and by energy supply (radiation) in wet environments.
- Potential evaporation, the maximum attainable in wet environments, is identified as energy-limited evaporation and quantified as the Priestley-Taylor evaporation (1.26 times the available energy from net radiation).
- A single-parameter hyperbolic function interpolates between dry (rainfall-limited) and wet (energy-limited) total evaporation rates.
- The total evaporation is the sum of plant transpiration and soil evaporation. The partition between plant and soil is determined by the leaf area index alone.
• A single water store is considered, encompassing the entire soil root zone. Its time-averaged relative water content is approximated as the ratio of actual total evaporation (including plant and soil contributions) to potential (Priestley-Taylor) evaporation.

• A rule-based method is used to estimate deep drainage, involving assignment of a drainage fraction on the basis of soil texture, with modification to account for cultivation. The actual time-averaged drainage is the product of this fraction and the time-averaged effective rainfall.

• The formulation for total evaporation has been tested against a set of data from small catchments. Also, the water balance formulation has been tested at continental scale by comparing predicted mean runoff with the mean runoff for 245 ANRA (Australian Natural Resources Atlas) Drainage Basins (NLWRA 2001).

Net Primary Productivity (NPP): The treatments in BiosEquil and BiosEvolve are identical. GPP (Gross Primary Productivity, the carbon flux into plants by photosynthetic assimilation) and NPP (Net Primary Productivity, equal to GPP less plant or autotrophic respiration) are modelled as follows:

• Autotrophic respiration is modelled by expressing NPP as a fixed fraction (0.45) of GPP;

• An expression is found for the NPP limited only by light and water ($F_{C+}$). This is determined jointly by transpiration, via a water use efficiency, and from incident radiation via a light use efficiency (an approach which recognises that the primary limit on NPP in Australia is water availability).

• The NPP limited by light and water ($F_{C+}$) is then used to find the actual NPP ($F_C$) resulting from nutrient limitation in addition to light and water limitation, by applying a combination of biophysical and scaling arguments.

• The NPP formulation has been calibrated and tested against a set of 184 point data from the VAST dataset (Barrett 2001).

• A key property of the NPP formulation is that the NPP is predicted to have a strong dependence on saturation deficit (dryness of the air), through the effect of saturation deficit on water use efficiency: that is, an increase in saturation deficit implies a lower water use efficiency, which implies a lower NPP (all else being equal). Data confirm that this dependence is real.

Steady-state solutions for NPP and mineral nutrients: At the heart of BiosEquil are steady-state solutions to a simplified coupled equation system determining the nutrient-limited NPP $F_C$ (taking the light and water limited NPP $F_{C+}$ to be specified) and the plant-available mineral nutrient stores $N$ and $P$. The essential features of the approach are (1) balances of plant and plant-available (litter, soil organic and mineral) nutrients; (2) simple phenomenological equations for both the local-cycling and external fluxes in these balances, based on scaling arguments; (3) strong constraints on the coefficients in these phenomenological equations, from the form of the solutions. The result is a closed analytic solution for $F_C$, $N$ and $P$, including an estimate of the nutrient flux due to disturbance (herbivory, fire, offtake). This is calculated from a perturbation to the nutrient budget with local cycling only (where nutrient uptake to vegetation balances nutrient return to the available pool via litterfall), by estimating disturbance as the nutrient flux required to balance other external fluxes.

Carbon and nutrient fluxes in litter and soil: Again the treatments in BiosEquil and BiosEvolve are identical, as follows:
• Carbon fluxes out of stores are governed by rate constants dependent on temperature and soil moisture.
• Nutrient (N, P) fluxes follow carbon fluxes in stoichiometric ratios determined by destination (not source) stores.
• The stores and flows of C, N and P in litter and soil are modelled following the Century model of litter and soil biogeochemistry (Parton et al. 1987, 1988, 1993).
• The predictions for biomass, litter and soil carbon have been tested against several hundred point data from the VAST dataset.

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**Appendix A: Mathematical Foundations**

**Dynamic Models**

This Appendix makes a very general statement of the mathematical structure of the model, following Raupach et al. (2002). Let $\mathbf{X}(t) = \{X_r(t)\}$ be the set of all water, C, N and P stores represented in the model, dependent on time $t$. The index $r$ encompasses all pools in all grid cells in the model domain (which may be a single landscape element, a region, the Australian continent, or the land surfaces of the earth). The set $\mathbf{X}(t)$ defines the state variables of the model. The behaviour of $\mathbf{X}(t)$ is controlled by a set of fluxes of water, C, N and P into and out of each store, through a set of mass conservation equations which can be written generically (for an arbitrary store $r$) as

$$
\frac{\partial X_r(t)}{\partial t} = F_{r1}(t) + F_{r2}(t) + \ldots = \sum_s F_{rs}(t)
$$

(A.1)

where $F_{rs}(t)$ is the flux entering store $r$ by process $s$ (a positive or negative number, respectively, according to whether process $s$ causes an increase or a decrease in store $r$). Let $\mathbf{F}(t) = \{F_{rs}(t)\}$ denote the set of all fluxes.

In general, the fluxes $\mathbf{F}(t)$ are dependent on three kinds of variable: first, the set of stores or state variables $\mathbf{X}(t)$. Second, the fluxes depend on a set of time-dependent external forcing variables including meteorological variables (such as rainfall, temperature, solar radiation and humidity), and variables specifying land management (such as fertiliser application rate and irrigation rate). The set of these external forcing variables is denoted $\mathbf{M}(t)$. Third, the fluxes depend on a set of time-independent parameters, collectively denoted $\mathbf{P}$. These are of three kinds: process parameters, $\mathbf{P}_{\text{process}}$ (such as light use efficiency or maximum photosynthetic capacity); properties of the soil or landform, $\mathbf{P}_{\text{soil}}$ (such as soil depth or layer structure, and the hydraulic and thermal properties of soil layers); and properties of the vegetation, $\mathbf{P}_{\text{veg}}$ (such as height, leaf area index or albedo). Hence, the fluxes are generically specified by a set of equations of the form

$$
F_{rs}(t) = F_{rs}\left(\mathbf{X}(t), \mathbf{M}(t), \mathbf{P}\right) = F_{rs}\left(\mathbf{X}(t), \mathbf{M}(t), \mathbf{P}_{\text{process}}, \mathbf{P}_{\text{soil}}, \mathbf{P}_{\text{veg}}\right)
$$

(A.2)

These equations represent the set of process descriptions in the model, and can be called "phenomenological equations" (by analogy with non-equilibrium thermodynamics).

Equations (A.1) and (A.2) formalise the water, C, N and P cycles on a landscape as a dynamical system, governed by a coupled set of differential and algebraic equations which together specify the evolution of the stores $\mathbf{X}(t)$ and the fluxes $\mathbf{F}(t)$ in response to specified external forcing variables $\mathbf{M}(t)$ and parameters $\mathbf{P}$. To determine $\mathbf{X}(t)$ and $\mathbf{F}(t)$ it is necessary to solve a set of differential equations in time, to find the dynamic or temporally evolving behaviour of the system.

There are some fundamental differences between equations (A.1) and (A.2):
The conservation equations (A.1) are differential (a set of coupled first-order differential equations in time), whereas the phenomenological equations (A.2) are algebraic, involving no time derivatives.

The conservation equations (A.1) are linear in the stores $X$ and fluxes $F$, whereas the phenomenological equations (A.2) are generally nonlinear in $X$, $M$ and $P$.

The phenomenological equations (A.2) are semi-empirical statements which in general depend on the scale of application (that is, the space and time intervals over which $X$, $F$, $M$ and $P$ are averaged or discretised in the model). In contrast, the conservation equations (A.1) are true at any scale (that is, with $X$ and $F$ averaged over any defined space and time intervals).

**Statistical Steady-State Models**

In its most general form, finding the full temporal behaviour of the system is a complicated and data-intensive problem to solve. Hence it is useful to consider a much simpler problem, that of finding the statistically steady state. This is helpful for four reasons: first, it provides the best initial condition for a full, time-dependent solution. Second, it is useful in its own right as a measure of the long-term average behaviour of the system under defined external forcing, specified by long-term average values of the climate and land management variables $M$. Third, this solution can be used to test a dynamic model, which (with constant forcing) converges in the long term to the steady state solution. Fourth, the difference between two statistically steady state solutions with different long-term average external forcing variables (say $M_1$ and $M_2$) provides a measure of the long-term system response to a change in forcing from $M_1$ to $M_2$. Examples of changes which can be analysed in this way include long-term climate change and long-term changes in inputs or offtakes of nutrients.

The steady-state solution arises when the storage changes $\partial X_r/\partial t$ in Equation (A.1) are negligible in comparison with the fluxes, so that Equation (A.1) reduces to

$$\sum_s F_{rs} (X, M, P) = 0$$

(A.3)

This set of $r$ equations, together with the phenomenological equations (A.2), forms a closed set of algebraic equations for the time-independent, steady-state stores $X$ and fluxes $F$. Usually this can be solved much more easily than the fully time-dependent model.

The statistically steady state solution arises when the external variables $M(t)$ are statistically steady in time, through they may fluctuate randomly in response to weather, interannual climate variability or variations in land management. In this case, $M(t)$, $X(t)$ and $F(t)$ are stationary random processes. Equations (A.2) and (A.3) still apply, on the understanding that $X$, $F$ and $M$ are all time averaged over a sufficiently long period (say $T$) that the storage change $[X_r(T) - X_r(0)]/T$ can be ignored relative to the time-averaged fluxes $F_{rs}$. Raupach et al. (2002) derive this limit formally.

**Scaling and Averaging**

The stores $X(t) = \{X_r(t)\}$ and fluxes $F(t) = \{F_{rs}(t)\}$ are averaged in space over the control volumes defined in Section 2, and in time over a period $T$ which is a single time step (1 day) in the case of BiosEvolve and a long period (many years) in the case of BiosEquil. It is
important to identify the nature and consequences of this averaging, because much of the information used to specify the phenomenological equations (A.2) comes from process studies at smaller space and time scales. The problem of translating this information up to the scale of the model is the "upscaling" or "aggregation" problem. The brief discussion in this subsection identifies several strategies used to tackle this problem in different parts of BiosEvolve and BiosEquil, following Raupach et al. (2002).

Suppose that \( x_r \) and \( f_{rs} \) are respectively the locally variable stores and fluxes from which \( X_r \) and \( F_{rs} \) are produced by space or time averaging, so that (for fluxes)

\[
F_{rs}(t) = \frac{1}{A} \int_A f_{rs}(r, t) \, dr \quad \text{(spatial averaging over horizontal area } A) \tag{A.4}
\]

\[
F_{rs}(t) = \frac{1}{T} \int_0^T f_{rs}(t + s) \, ds \quad \text{(temporal averaging over time } T) \tag{A.5}
\]

and similarly for the relationships between \( x_r(t) \) and \( X_r(t) \). Lower-case and upper-case letters distinguish "fine-scale" and "coarse-scale" variables, where these terms respectively denote sub-grid-scale, unresolved variables and resolved or grid-scale variables in the model. At fine scale, the counterparts of the conservation equations (A.1) are

\[
\frac{\partial x_r}{\partial t} = f_{r1} + f_{r2} + \ldots = \sum_s f_{rs}(t) \tag{A.5}
\]

Because of the linearity of the conservation equations and the averaging operation defined by Equation (A.4), there is a precise, term-by-term correspondence between Equations (A.1) and (A.5). However, the situation is more complex for the phenomenological equations (A.2). Their fine-scale counterpart is

\[
f_{rs}(t) = f_{rs}(x(t), m(t), p) \tag{A.6}
\]

where \( m \) and \( p \) are respectively the fine-scale forcing variables and parameters in the phenomenological equations. The "upscaling" or "aggregation" problem is to determine \( F_{rs}(X,M,P) \) at coarse scale, given (often incomplete) information about \( f_{rs}(x,m,p) \) at fine scale. It is a nontrivial problem for three reasons: first, nonlinearity. The phenomenological equations are nonlinear in general, so the functional forms \( f_{rs}(x,m,p) \) at fine scale and \( F_{rs}(X,M,P) \) at coarse scale are not the same. Second, lack of information: there is often not enough information to infer \( F_{rs}(X,M,P) \) from \( f_{rs}(x,m,p) \) without extra assumptions or empirical information. The lack of information may arise from unmeasured statistical variability in the fine-scale forcing variables \( m \) or parameters \( p \) (for example, soil heterogeneity), or from the chaotic behaviour of small-scale processes (for example, turbulence). Third, emergence: new large-scale phenomena, not explicit in the fine-scale \( f_{rs}(x,m,p) \), may appear in the coarse-scale \( F_{rs}(X,M,P) \) because of large-scale, nonlinear interactions between system components.

There are several ways of dealing with the aggregation problem, all of which are used in BiosEvolve and BiosEquil according to circumstance. The options can be set out as a sequence of binary choices (Raupach et al. 2002):

1. One may form an aggregated model \( F_{rs}(X,M,P) \), or use a distributed set of disaggregated models \( f_{rs}(x,m,p) \). In the latter option, the fine-scale model is evaluated over the spatial or
temporal domain of the integrals in Equation (A.4), and the integrations done explicitly. This requires explicit knowledge of the fine-scale forcing variables m or parameters p. In BiosEquil, this approach is used to annual-average fluxes by integrating explicitly over the seasonal variability resolved as 12 monthly-mean climatologies.

2. Suppose that the former option (an aggregated model) is taken in choice 1. Then, the functional forms of the aggregated phenomenological equations \( F_{rs} = F_{rs}(X,M,P) \) may either be the same as or different from the forms of the fine-scale equations \( f_{rs} = f_{rs}(x,m,p) \). If different forms are used, then the fine-scale and coarse-scale equations rest on different empirical foundations, and the fine-scale and coarse-scale parameters (p and P, respectively) have different physical meanings. Fine-scale information about p is of no direct help in finding either P or the form of the phenomenological equations at coarse scales, and a new coarse-scale model must be developed ab initio, without recourse to fine-scale models except possibly for empirical calibration. This option is used to develop the simplified water balance description in BiosEquil.

3. Suppose that the former option (identical forms for fine-scale and coarse-scale equations) is taken in choice 2. Then, the coarse-scale parameters P may be determined either directly from the fine-scale parameters p as "effective parameters", or by "statistical estimation". The latter option involves evaluation of the coarse-scale \( F_{rs} \) in Equation (A.4) by integration over statistical distributions of the independent variables x, m and p in the fine-scale model \( f_{rs} = f_{rs}(x,m,p) \). The "effective-parameter" option is used in the assimilation description in BiosEvolve and BiosEquil, and the "statistical estimation" option in the descriptions of nutrient uptake and response in BiosEquil.
References


## Tables and Figures

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Table 1: Table of parameters used in program BiosEquil07g to produce the results on the CDROM BiosRelease02. This table is extracted from file BiosEquil07gData.ctl.
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<td>TempMax</td>
<td>Monthly maximum daily surface air temperature (°C) for the period 1980-1999.</td>
<td>Jeffrey et al. 2001</td>
<td></td>
</tr>
<tr>
<td>Rain</td>
<td>Monthly rainfall (mm) for the period 1980-1999.</td>
<td>Jeffrey et al. 2001</td>
<td></td>
</tr>
<tr>
<td>rLAI (wood)</td>
<td>Annual woody component of leaf area index for the period 1981-1994 (dimensionless).</td>
<td>Lu et al. 2001</td>
<td></td>
</tr>
</tbody>
</table>
| FNFert            | Annual N input as fertiliser to all crop types (kg m⁻² y⁻¹), read from separate files for permanent croppi
|                   | horticulture, and fertilised pasture.                                       | Reuter 2001         | F_N(Fert)      |
| FPFert            | Annual P input as fertiliser to all crop types (kg m⁻² y⁻¹), read from separate files for permanent croppi
|                   | horticulture, and fertilised pasture.                                       | Reuter 2001         | F_P(Fert)      |
| FNOfftake         | Annual N offtake from all crop types (kg m⁻² y⁻¹), read from separate files for permanent croppin
|                   | horticulture, and fertilised pasture.                                       | Reuter 2001         |                |
| FPOfftake         | Annual P offtake from all crop types (kg m⁻² y⁻¹), read from separate files for permanent croppin
|                   | horticulture, and fertilised pasture.                                       | Reuter 2001         |                |
| FracCrop          | Cell area fraction planted to permanent cropping, used for the calculation of leached N flux. | NLWRA 2000         |                |
| FracPulseCrop     | Cell area fraction planted to pulse crops, for the calculation of N fixation. | NLWRA 2000         |                |
| FracPasLegume     | Cell area fraction planted to legume pasture, for the calculation of N fixation. | NLWRA 2000         |                |
| FracIrrig         | Fraction of cell area irrigated                                             | NLWRA 2000          |                |
| HillEro           | Hillslope waterborne erosion (kgSoil m⁻² y⁻¹)                               | Prosser et al. 2001 |                |
| SoilType          | Index code (1 to 725) for ‘principal profile forms’ given in the Digital Atlas of Australian Soils | NRIC 1991          |                |

**Soil parameters for 2 layers assigned from lookup table indexed to soil type map**

<table>
<thead>
<tr>
<th>Name in Code</th>
<th>Description</th>
<th>Reference</th>
<th>Symbol in Text</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth1/2</td>
<td>Depth (m) of the soil layer</td>
<td>McKenzie et al. 2000</td>
<td></td>
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<tr>
<td>Wvol1/2sat</td>
<td>Saturated volumetric water content (m³ m⁻³)</td>
<td>McKenzie et al. 2000</td>
<td>M_s</td>
</tr>
<tr>
<td>ClayFrac1/2</td>
<td>Clay fraction in soil layer</td>
<td>McKenzie et al. 2000</td>
<td></td>
</tr>
<tr>
<td>SiltFrac1/2</td>
<td>Silt fraction in soil layer</td>
<td>McKenzie et al. 2000</td>
<td></td>
</tr>
<tr>
<td>BulkDens1/2</td>
<td>Bulk density (kg m⁻³)</td>
<td>McKenzie et al. 2000</td>
<td></td>
</tr>
</tbody>
</table>

Table 2: Spatially distributed parameters (0.05° resolution) in *BiosEquil*
Figure 1: Major pools and pathways in the linked water, C, N and P cycles through the atmosphere, plants and soil. NPP is the sum of photosynthesis and plant (not litter and soil) respiration.
Figure 2: Aggregate pools and pathways of carbon for modelling purposes. Within the broad classes of plant, litter and soil organic matter (SOM), functionally distinctive pools are: Lea (living leaf); Woo (living wood); Roo (living root); Res (a plant residue pool which collects all detritus resulting from death of living material in the plant pools); Met (the metabolic, fast-turnover litter pool); Str (the structural, slow-turnover litter pool); Act (the active or microbial pool for SOM); Hum (the slow or humic SOM pool); Pas (the pool for passive or inert SOM, with a very long turnover time). Carbon is returned to the atmosphere at various points by heterotrophic respiration.
Figure 3: Aggregate pools and pathways of nitrogen and phosphorus for modelling purposes. In addition to those given for carbon, pools include: $Mnl$ (mineral N in all oxidation states); $Pri$ (the primary, plant-available or soluble phosphorus pool); $Sec$ (secondary insoluble P); $Occ$ (occluded insoluble P). Microbial activity is accompanied by mineralisation which transfers N and P from the organic to the mineral ($N_{Mnl}, P_{Pri}$) pools, and immobilisation which operates in the reverse direction.
Figure 4: Pathways into and out of the major pools of mineral N and P.
Figure 5: Mineral phosphorus pools defined according to different levels of plant availability or chemical reactivity. Chemical extraction methods used to determine P in laboratory soil tests (reagents given in red) do not completely align with the primary, secondary and occluded pools.
Figure 6: Schematic diagram showing the determination of the short-term NPP $f_C$ as a function of independent variables ($n, p$), the short-term stores of mineral N and plant-available P. The solution for $f_C$ is the minimum of solutions from the two sloping planes $f_C = c_ne_n/(\nu \omega)$ and $f_C = c_pe_p/(\rho \omega)$, and the horizontal plane $f_C = f_C^+$. 

Figure 7: Contours of NPP as a function of stores of mineral N and plant-available P. Left side: short-term relationship. Right side: long-term relationship obtained by averaging the short-term relationship over an ensemble of values of the forcing variables $f_C$, $e$ and $w$. 
Figure 8: The solution for $f = FC/F_C^+$ as a function of $bc$, from Equation (5.13) (only the larger, physically realistic root is shown).
Figure 9: Comparison between predictions of the model in *BiosEquil* for time-average evaporation and data for forested, mixed and pasture catchments collected by one of the present authors (LZ). The model predicts the normalised evaporation $E/E_{PT}$ as a function of normalised precipitation $P/E_{PT}$, where $E_{PT}$ is the potential evaporation defined as the Priestley-Taylor evaporation (specified from energy supply only). The curves are for three values of the parameter $a$ in the model, which determines the curvature of the prediction (a small $a$ value implies gentle curvature; as $a$ approaches infinity, the curve approaches the "broken-arrow" form $E/E_{PT} = P/E_{PT}$ for $P/E_{PT} < 1$, and $E/E_{PT} = 1$ for $P/E_{PT} > 1$). The three values are $a = 2.48$ (forest), 1.64 (mixed) and 1.50 (pasture).

Figure 10: Comparison between steady-state runoff predictions from *BiosEquil* and observed mean annual runoff in 245 ANRA drainage basins on the Australian continent. Outlier is the Goulburn catchment, for which quoted observed runoff substantially exceeds annual rainfall.
Figure 11: Total evaporation (canopy transpiration plus soil evaporation): mean annual (left panel) and mean monthly (right panel).
Figure 12: data points for tests of NPP (left) and biomass, litter and soil C predictions (right). Data from the VAST 1.0 dataset (Barrett 2001).
Figure 13: Comparison between steady-state NPP predicted by *BiosEquil* and observations at 184 sites in the Vast 1.0 dataset (Barrett 2001). Left panel: linear axes; right panel: logarithmic axes.

Figure 14: The dependence of NPP on saturation deficit (the difference between saturated and actual specific humidity) at the surface, as observed in the Vast 1.0 dataset (blue) and predicted by *BiosEquil* (red).
Figure 15: Mean annual Net Primary Productivity ($F_C$) with current climate and current agricultural inputs.
Figure 16: Comparison between carbon pools predicted by BiosEquil and observations at 577 sites in the Vast 1.0 dataset, not necessarily the same as sites for NPP observations (Figure 4a). All axes in kgC/m². Left panels: biomass C (leaf, wood and root pools); centre panels: litter C (metabolic and structural pools); right panels: soil C (active, humic and passive pools). Top row: linear axes; bottom row: logarithmic axes.
Figure 17: Comparison of spatially averaged flux terms in the steady-state mineral N budget for 12 drainage divisions with and without European-style agriculture. N flux terms are fertilisation (+), atmospheric deposition (+), fixation (+), gaseous loss (-), leaching (-), and disturbance (-).