Modelling Water and Carbon Canopy Fluxes

by

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Declaration of Authorship

I, RHYS JAMES WHITLEY, declare that this thesis titled, ‘MODELLING WATER AND CARBON CANOPY FLUXES’ and the work presented in it are my own. I confirm that:

- This work was done wholly or mainly while in candidature for a research degree at this University.
- Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated.
- Where I have consulted the published work of others, this is always clearly attributed.
- Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work.
- I have acknowledged all main sources of help.
- Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself.

Signed:

Date:
The thing the ecologically illiterate don’t realize about an ecosystem is that it’s a system. A system! A system maintains a certain fluid stability that can be destroyed by a misstep in just one niche. A system has order, a flowing from point to point. If something dams the flow, order collapses. The untrained miss the collapse until too late. That’s why the highest function of ecology is the understanding of consequences.

Kynes in "Appendix I: The Ecology of Dune"

Excerpt from Dune by Frank Herbet
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<tr>
<td>ANN</td>
<td>Artificial Neural Network</td>
</tr>
<tr>
<td>APAR</td>
<td>Absorbed Photosynthetically Active Radiation</td>
</tr>
<tr>
<td>BA</td>
<td>Basal Area</td>
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<tr>
<td>CUE</td>
<td>Carbon Use Efficiency</td>
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<tr>
<td>EC</td>
<td>Eddy Covariance</td>
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<tr>
<td>ET</td>
<td>Evapotranspiration</td>
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<tr>
<td>GA</td>
<td>Genetic Algorithm</td>
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<tr>
<td>GENOUCE</td>
<td>GENetic Optimisation Using Derivatives</td>
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<tr>
<td>GPP</td>
<td>Gross Primary Productivity</td>
</tr>
<tr>
<td>LAI</td>
<td>Leaf Area Index</td>
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<td>LUE</td>
<td>Light Use Efficiency</td>
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<tr>
<td>LWP</td>
<td>Leaf Water Potential</td>
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<td>ME</td>
<td>Model Efficiency</td>
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<tr>
<td>MJS</td>
<td>Modified Jarvis-Stewart model</td>
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<tr>
<td>MNDR</td>
<td>Multivariate-Nonlinear-Dummy Regression</td>
</tr>
<tr>
<td>NPP</td>
<td>Net Primary Productivity</td>
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<tr>
<td>NSW</td>
<td>New South Wales</td>
</tr>
<tr>
<td>PAR</td>
<td>Photosynthetically Active Radiation</td>
</tr>
<tr>
<td>PEP</td>
<td>Phosphoenolpyruvate</td>
</tr>
<tr>
<td>PSD</td>
<td>Particle Size Distribution</td>
</tr>
<tr>
<td>RMSE</td>
<td>Root Mean Square Error</td>
</tr>
<tr>
<td>RuBisCO</td>
<td>Ribulose Bisphosphate Carboxylase-Oxygenase</td>
</tr>
<tr>
<td>RuP₂</td>
<td>Ribulose Bisphosphate</td>
</tr>
<tr>
<td>Abbreviation</td>
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<td>--------------</td>
<td>----------------------------------------</td>
</tr>
<tr>
<td>SA</td>
<td>Site-Average model</td>
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<tr>
<td>SOFM</td>
<td>Self Organising Feature Map</td>
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<td>SOLO</td>
<td>Self Organising Linear Optimisation</td>
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<tr>
<td>SPA</td>
<td>Soil Plant Atmosphere model</td>
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<td>SPAC</td>
<td>Soil Plant Atmosphere Continuum</td>
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<td>SS</td>
<td>Site-Specific model</td>
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<tr>
<td>SWC</td>
<td>Soil Water Content</td>
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<td>SWP</td>
<td>Soil Water Potential</td>
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<tr>
<td>VPD</td>
<td>Vapour Pressure Deficit</td>
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<tr>
<td>WUE</td>
<td>Water Use Efficiency</td>
</tr>
<tr>
<td>WA</td>
<td>Western Australia</td>
</tr>
</tbody>
</table>
Physical Constants

Relative diffusivity of water vapour to CO$_2$ in air $a_c$ 1.56 unitless
Specific heat capacity of the air $c_p$ 1.013 MJ kg$^{-1}$ °C$^{-1}$
Gravitational constant $g$ 9.807 m$^2$ s$^{-1}$
Molecular mass of air $M_a$ 28.96440 g mol$^{-1}$
Molecular mass of water $M_w$ 18.01528 g mol$^{-1}$
Atmospheric Pressure $P_a$ 101300.0 Pa
Universal gas constant $\mathcal{R}$ 8.1344 J K$^{-1}$ mol$^{-1}$
Emissivity of the earth’s surface $\epsilon$ 0.96 unitless
CO$_2$ compensation point @ 25°C $\Gamma^*$ 36.5 μmol mol$^{-1}$
Psychometric constant $\gamma$ 0.066 kPa °C$^{-1}$
von Kármán constant $\kappa$ 0.41 unitless
Latent heat of vaporisation of water $\lambda$ 2.3845 MJ kg$^{-1}$
$\pi$ 3.14159265 unitless
Density of air $\rho_a$ 1.204 kg m$^{-3}$
Density of water $\rho_w$ 998.2 kg m$^{-3}$
Stephen-Boltzmann constant $\sigma$ $5.6703 \times 10^{-8}$ W m$^{-2}$ K$^{-4}$
Symbols

\( A_{cat} \) Catchment area \( m^2 \)
\( A_c \) RuBisCO activity-limited assimilation \( \mu mol \ m^{-2} \ s^{-1} \)
\( A_d \) Rate of CO\(_2\) diffusion \( \mu mol \ m^{-2} \ s^{-1} \)
\( A_g \) Gross assimilation \( \mu mol \ m^{-2} \ s^{-1} \)
\( A_j \) Light-limited assimilation \( \mu mol \ m^{-2} \ s^{-1} \)
\( A_n \) Net assimilation \( \mu mol \ m^{-2} \ s^{-1} \)
\( C\% \) Percentage of clay (PSD) \%
\( C_a \) Ambient CO\(_2\) concentration \( \mu mol \ mol^{-1} \)
\( C_i \) Intercellular CO\(_2\) concentration \( \mu mol \ mol^{-1} \)
\( C_{leaf} \) Leaf capacitance \( \text{mmol m}^{-2} \text{ MPa}^{-1} \)
\( C_m \) CO\(_2\) concentration in the mesophyll cells \( \mu mol \ mol^{-1} \)
\( C_s \) CO\(_2\) concentration in the bundle sheath cells \( \mu mol \ mol^{-1} \)
\( D_v \) Vapour pressure deficit \( \text{kPa} \)
\( D_{vmax} \) Daily maximum vapour pressure deficit \( \text{kPa} \)
\( D_{peak} \) Position of peak vapour pressure deficit \( \text{kPa} \)
\( D_0 \) Lohammer constant for \( D_v \) \( \text{kPa} \)
\( d_{0p} \) Zero plane displacement height \( \text{m} \)
\( d_{root} \) Depth of roots \( \text{m} \)
\( d_{soil} \) Depth of soil \( \text{m} \)
\( E_0 \) Potential evaporation \( \text{mm hr}^{-1} \)
\( E_c \) Canopy transpiration \( \text{mm hr}^{-1} \)
\( E_{cmax} \) Maximum canopy transpiration \( \text{mm hr}^{-1} \)
\( E_s \) Soil evaporation \( \text{mm hr}^{-1} \)
$E_t$  Tree transpiration  
$E_T$  Evapotranspiration  
$g_a$  Aerodynamic conductance  
$g_b$  Boundary layer conductance  
$g_{bs}$  Bundle sheath conductance  
$g_c$  Canopy conductance  
$g_{cmax}$  Maximum canopy conductance  
$g_{plant}$  Whole plant hydraulic conductance  
$g_s$  Stomatal conductance to H$_2$O  
$g_{sc}$  Stomatal conductance to CO$_2$  
$g_{s0}$  Residual stomatal conductance  
$g_{smax}$  Maximum stomatal conductance  
$g_{smin}$  Minimum stomatal conductance  
$g_t$  Total conductance to H$_2$O  
$H_s$  Relative humidity  
$h$  Height of canopy  
$J_e$  Potential rate for electron transport  
$J_{max}$  Maximum rate for electron transport  
$J_w$  Flow of water to the xylem  
$K$  Soil hydraulic conductivity  
$K_c$  Enzyme catalytic activity for CO$_2$  
$K_o$  Enzyme catalytic activity for O$_2$  
$K_m$  Combined enzyme catalytic activity  
$K_p$  Enzyme catalytic activity for PEP  
$k_{D_1}$  vapour pressure deficit shape parameter 1  
$k_{D_2}$  vapour pressure deficit shape parameter 2  
$k_T$  $C_4$ first order rate constant for PEP carboxylase  
$k_R$  Solar radiation constant  
$L$  Rate of CO$_2$ leakage from the bundle sheath to the mesophyll cells  
$L_{SA}$  Specific leaf area
Symbols

\( M_{cj} \quad \text{C}_4 \text{CO}_2 \text{ flux determined by } A_c \text{ and } A_j \quad \mu \text{mol m}^{-2} \text{s}^{-1} \)
\( m_{\text{root}} \quad \text{Root biomass} \quad \text{kg m}^{-3} \)
\( N_f \quad \text{Total leaf nitrogen content} \quad \text{g m}^{-2} \)
\( N_{LA} \quad \text{Nitrogen per leaf area} \quad \text{g m}^{-2} \)
\( O_i \quad \text{Intercellular O}_2 \text{ concentration} \quad \mu \text{mol mol}^{-1} \)
\( O_s \quad \text{O}_2 \text{ concentration in the mesophyll cells} \quad \mu \text{mol mol}^{-1} \)
\( O_{si} \quad \text{O}_2 \text{ concentration in the bundle sheath cells} \quad \mu \text{mol mol}^{-1} \)
\( Q_p \quad \text{Quantum flux density (PAR)} \quad \mu \text{mol m}^{-2} \text{s}^{-1} \)
\( R_{a,b} \quad \text{Total above and below-ground resistance} \quad \text{MPa m}^2 \text{s mol}^{-1} \)
\( R_d \quad \text{Dark respiration} \quad \mu \text{mol m}^{-2} \text{s}^{-1} \)
\( R_m \quad \text{Mitochondrial respiration} \quad \mu \text{mol m}^{-2} \text{s}^{-1} \)
\( R_n \quad \text{Net radiation} \quad \text{W m}^{-2} \)
\( R_s \quad \text{Solar radiation} \quad \text{W m}^{-2} \)
\( R_{\text{plant}} \quad \text{Plant resistance} \quad \text{MPa m}^2 \text{s mol}^{-1} \)
\( R_{\text{root}} \quad \text{Root resistance} \quad \text{MPa m}^2 \text{s mol}^{-1} \)
\( R_{\text{soil}} \quad \text{Soil resistance} \quad \text{MPa m}^2 \text{s mol}^{-1} \)
\( r_b \quad \text{Boundary layer resistance} \quad \text{s m}^{-1} \)
\( r_{\text{root}} \quad \text{Fine root radius} \quad \text{m} \)
\( r_s \quad \text{Stomatal resistance} \quad \text{s m}^{-1} \)
\( S\% \quad \text{Percentage of sand (PSD)} \quad \% \)
\( S_A \quad \text{Sapwood area} \quad \text{m}^2 \text{ ha}^{-1} \)
\( T_a \quad \text{Ambient air temperature} \quad ^\circ\text{C} \)
\( T_{\text{amax}} \quad \text{Daily maximum air temperature} \quad ^\circ\text{C} \)
\( T_{l} \quad \text{Leaf temperature} \quad ^\circ\text{C} \)
\( U_z \quad \text{Windspeed} \quad \text{m s}^{-1} \)
\( V_{cmax} \quad \text{Maximum rate for RuBisCO carboxylation} \quad \mu \text{mol m}^{-2} \text{s}^{-1} \)
\( V_o \quad \text{Rate for RuBisCO oxygenation} \quad \mu \text{mol m}^{-2} \text{s}^{-1} \)
\( V_p \quad \text{Rate for PEP carboxylation} \quad \mu \text{mol m}^{-2} \text{s}^{-1} \)
\( V_{pr} \quad \text{PEP regeneration rate} \quad \mu \text{mol m}^{-2} \text{s}^{-1} \)
\( V_{pmax} \quad \text{Maximum rate for PEP carboxylation} \quad \mu \text{mol m}^{-2} \text{s}^{-1} \)
\( x_{\text{root}} \quad \text{Mean distance between roots} \quad \text{m} \)
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<thead>
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<th>Description</th>
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<td>$z_h$</td>
<td>Height of humidity measurement</td>
<td>m</td>
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<td>$z_m$</td>
<td>Height of wind measurement</td>
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<tr>
<td>$z_{oh}$</td>
<td>Roughness length governing heat transfer</td>
<td>m</td>
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<td>$z_{om}$</td>
<td>Roughness length governing momentum transfer</td>
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<tr>
<td>$\alpha_j$</td>
<td>Quantum yield of whole chain electron transport</td>
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<tr>
<td>$\alpha_{rf}$</td>
<td>Combined constant: Quantum yield and absorbed photons used by the C$_4$ reaction process</td>
<td>mol mol$^{-1}$</td>
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<tr>
<td>$\beta_e$</td>
<td>Proportionality of error</td>
<td>unitless</td>
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<td>$\beta_{co}$</td>
<td>Co-limitation between light, RuBisCO and CO$_2$ limited flux</td>
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<td>Slope between vapour pressure and temperature</td>
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<td>Soil water potential</td>
<td>MPa</td>
</tr>
<tr>
<td>$\Psi_l$</td>
<td>Leaf water potential</td>
<td>MPa</td>
</tr>
<tr>
<td>$\Psi_{lpd}$</td>
<td>Pre-dawn leaf water potential</td>
<td>MPa</td>
</tr>
<tr>
<td>$\Psi_{lmin}$</td>
<td>Minimum leaf water potential</td>
<td>MPa</td>
</tr>
<tr>
<td>$\theta_c$</td>
<td>Critical point for transpiration</td>
<td>m$^3$ m$^{-3}$</td>
</tr>
<tr>
<td>$\theta_f$</td>
<td>Field capacity of the soil</td>
<td>m$^3$ m$^{-3}$</td>
</tr>
<tr>
<td>$\theta_j$</td>
<td>Shape coefficient for non-rectangular hyperbola</td>
<td>unitless</td>
</tr>
<tr>
<td>$\theta_{tr}$</td>
<td>Transition between light-limited and RuBisCO limited CO$_2$ flux</td>
<td>unitless</td>
</tr>
<tr>
<td>$\theta_s$</td>
<td>Soil water content</td>
<td>m$^3$ m$^{-3}$</td>
</tr>
<tr>
<td>$\theta_{sat}$</td>
<td>Saturated water content of the soil</td>
<td>m$^3$ m$^{-3}$</td>
</tr>
<tr>
<td>$\theta_w$</td>
<td>Wilting point for transpiration</td>
<td>m$^3$ m$^{-3}$</td>
</tr>
</tbody>
</table>
Modelling the water and carbon fluxes from forest canopies provides useful insight into the dynamics of the exchange of water vapour for atmospheric CO$_2$ and the processes that govern this exchange. The work presented in this thesis aimed to answer four questions related to modelling of canopy gas-exchange. The first two questions involved the development of a simple empirical model of canopy water-use to see whether i) water fluxes from a canopy could be estimated without the need for canopy conductance and ii) could such a model be applied across multiple sites without the need for site-specific calibration? The remaining two questions involved the modification and improvement of a highly mechanistic and complex soil-plant-atmosphere (SPA) continuum model, which was done in order to iii) replicate canopy gas-exchange for a Australian tropical savanna and iv) to improve the simulated leaf gas-exchange process of a SPA model.

A simple empirical model of canopy water-use ($E_c$), a modified Jarvis-Stewart (MJS) model, was developed in order to circumvent the problem of requiring surface conductance as an input in order to calculate transpiration. This was accomplished by modelling an empirical relationship of the multivariate response of $E_c$ to solar radiation ($R_s$), vapour pressure deficit ($D_v$) and soil moisture content ($\theta_s$). The MJS model was shown to provide favourable short- and mid-term (annual) estimates of $E_c$ that only required three more readily available abiotic inputs ($R_s$, $D_v$ and $\theta_s$) and a small set of site-calibrated model parameters. Predictions of $E_c$ determined from the MJS model were able to replicate the observed data and compared favourably with the established Penman-Monteith (PM) equation and a statistical benchmark created using an artificial neural network (ANN).

In addition to this, the applicability of the MJS model was tested for five disparate Australian woodland sites, where model parameters were calibrated for each individual site and simultaneously for all sites. The result was that while MJS model was able to give a good representation of the measured data using site-specific parameters, using a parameter set that describes an average response of $E_c$ to the environment performed equally well. This was despite each site being comprised of different tree species and occurring over different soil profiles. This showed that the MJS model is partially insensitive to variation in the values of the model parameters and that the number of inputs into the MJS can be
further reduced. The conclusion was that this model is broadly applicable for many sites in temperate Australia and one that can be used as a tool in the management of water resources.

While the MJS model provided a useful management tool, in order to investigate the dynamics of water and carbon gas-exchange from forest canopies, the more complex SPA model of Williams et al. (1996a) was used. While the SPA model has been applied in ecosystems globally with much success, the lack of C₄ photosynthesis has limited its application to savanna ecosystems. Modification of the SPA model was therefore undertaken in order to improve its applicability to savannas through incorporation of C₄ photosynthesis. This was an important improvement as savannas are dominated by C₄ grasses, which contribute significantly to ecosystem water and carbon fluxes. This modification allowed the SPA model to be parameterised to a savanna site in northern Australia, which was simulated over 5 years to replicate measurements of carbon and water fluxes derived from eddy-covariance. The SPA model allowed C₃ and C₄ water and carbon fluxes to be separated and this showed that the C₄ grasses contribute significantly to total savanna productivity (48%), but a much smaller amount to total water-use (23%). Additionally, it was determined the seasonal variation in leaf area index was driving the seasonality in productivity and water-use and the savanna site was determined to be energy-limited (limited by its light interception).

The modification and application of the SPA model to a savanna site highlighted important issues in the way leaf gas-exchange is represented in the model. An investigation into the leaf gas-exchange process handled by SPA showed that there was an imbalance between assimilation and transpiration, as a result of simulated stomatal conductance being increased to unreasonably high levels in order to maximise carbon gain. In order to correct this problem, the modelled gas-exchange was modified to follow the *optimality hypothesis* of Cowan and Farquhar (1977), such that carbon gain is maximised while water lost from the leaf is simultaneously minimised. This improvement was tested in a purely theoretical exercise, where leaf gas-exchange (default and improved schemes) was simulated over a drought. The result of this simulation was that the improved scheme produced a reduction in canopy water-use, while carbon gain remained high and comparable with that of the default scheme.