Responses to Reviewer Comments

Anonymous Referee #1

Comment 1.1

The simulation results suggest that resource limitation is the driving force behind the tree grass dynamics of northern Australia. This finding is in agreement with a number of recent Australian reviews and studies and adds to the international discussion on savanna function. It would be interesting to consider the driving processes in this model (parameter sensitivity) and impact of various assumptions on the simulation outcomes. This could also allude to where the Australian setting differs from international savannas and how the global model could be achieved.

Response 1.1

We have included the following modification in the discussion: “Our findings support the view that Australian savannah tree cover is primarily controlled by availability of soil resources rather than disturbance. Simulated tree cover emerges from the balance between production – controlled by resource availability – and turnover, controlled both by resource availability and the frequency and intensity of disturbance. In our simulations for Australia, a high proportion of biomass loss was attributable to resource-limited. Of the total biomass lost to mortality, 68% was attributable to resource-limitation at the wet northern end of the NATT, increasing to 84% at the arid southern end. The remaining minority of biomass turnover was attributable to disturbance loss, largely from fire. However, the approach of HAVANA-POP remains valid for regions in which savannah vegetation structure is controlled by the disturbance regime.”

Comment 1.2

P16320 line 7. (and page 16318 Line 18). It is not clear in the text (without reading detail of Table 1) how the depth of the two layers was defined. Was the 20cm top layer cut-off defined from the soil description obtained from the soil maps, or is it related to the expected rooting depth of the native C4 tropical grasses? As grasses only have access to the top layer, an increase in this layer depth will affect grass growth. Likewise, the 4m depth of lower layer seems deeper than most soil descriptions from northern Australia (Soils Atlas) and this value will significantly influence tree biomass and population dynamics. Please state the basis for the depth cut-off as these are critical values and vary.
considerable in the literature with grasses reported from 20 cm to > 1 m. How would changing the depth of the bottom layer between 1 and 6 m influence the tree population and biomass? These soil properties need to be justified in order to validate the output of the simulations.

Response 1.2

We agree that the model is sensitive to these depth parameters. We have clarified that these have been sourced from the literature by inserting the following text in Section 2.1:

"The two state variables of the water balance model are soil water stores \( W_1, W_2 \) [m-water] corresponding to upper and lower soil layers, the boundary between them corresponding to the approximate vertical extent of the grass root profile (Janos et al. 2008), and the total depth that of the tree roots (Hutley et al. 2000)."

Further, we have included the appropriate references for the soil depths in Table 1.

Comment 1.3

P16324 line 13. It is not clear whether multiple tree and grass species were simulated or only the tree/grass functional groups. A description of the type species could be provided.

Response 1.3

We have clarified that species were not distinguished by inserting the following text in Section 2.2:

"A single set of parameters was adopted for all trees and all grasses respectively: species were not distinguished."

Comment 1.4
Page 16330 line 25. I do not understand how the regular exposure of the vegetation to fire results in curing of C4 grasses. Surely, exposure to fire will result in combustion of grasses and low soil water is the cause of C4 grass curing.

Response 1.4.

We agree that this wording was wrong and we have omitted the phrase altogether.

Technical corrections

Comment 1.5

Page 16324 line 5. “by proportion a” should this be alpha as per equation?

Response 1.5

Done

Comment 1.6

Page 16330 line 22. Woodlands rather than wood-lands as per grasslands and shrublands.

Response 1.6
Page 16331 line 22. Is DINGO presented elsewhere that can be cited? The following paragraphs could then be condensed.

Response 1.7

No: at the time of writing there was no citable reference for DINGO. DINGO developer, Jason Beringer, is a co-author on this paper.

Comment 1.8

Page 16333 line 15. (see Table 1 for calibrated parameters)

Response 1.8

The following sentence has been inserted "The parameters subject to calibration are shown in Table 1."

Comment 1.9

Page 16339 line 10. Please define LSM.
Response 1.9

Now done at first usage.

Comment 1.10

Page 16348 Table 1. Lines for Ga, kE,w and KL,g could have source on single line to reduce size.

Response 1.10

Done

Comment 1.11

Page 16352 Figure 2. Consider adding "flux site abbreviations..." to caption as per Figure 3.

Response 1.11

Done

Comment 1.12
Page 16354 Figure 5. Is there an extra space between y and -1?

Response 1.12

An issue of figure rendering: to be fixed in final figure submission.

Comment 1.13

Page 16354 Figure 5. Replace square brackets with round brackets for Williams et al 1996 for consistency.

Response 1.13

Done
Comment 2.1

The manuscript is well-written and the ideas clearly presented. The title and introduction suggest that the manuscript will provide a more detailed understanding of treegrass partitioning in savanna regions, but the rather standard implementation of carbon allocation scheme and the presentation of the results as more as a benchmarking exercise results in the manuscript being somewhat overall technical. To address the technical issue, would it be possible to run a 'no-fire' scenario. For example, it would be useful to know how much of the tree-grass partitioning along the transect is due to the correct dynamic allocation scheme versus simply being driven by the diagnostic fire information.

Response 2.1

Although we haven’t performed a "no-fire" simulation, we used our results to quantify the relative roles of fire vs resource limitation on biomass turnover, and found that the effect of fire is relatively small and is not largely responsible for tree-grass partitioning along the transect. This has been emphasized in a modification to the discussion:

“Our findings support the view that Australian savannah tree cover is primarily controlled by availability of soil resources rather than disturbance. Simulated tree cover emerges from the balance between production – controlled by resource availability – and turnover, controlled both by resource availability and the frequency and intensity of disturbance. In our simulations for Australia, a high proportion of biomass loss was attributable to resource-limitation. Of the total biomass lost to mortality, 68% was attributable to resource-limitation at the wet northern end of the NATT, increasing to 84% at the arid southern end. The remaining minority of biomass turnover was attributable to disturbance loss, largely from fire.”

Comment 2.2

Secondly, the model is set up to evaluate co-existed for just one woody and one grass functional type – I wasn’t clear whether the parameters are global, or whether they vary along the transect. Is it possible to add a sensitivity test or vary the traits along the gradient to also illustrate their importance? Because the implementation of the NSC is rather novel, I would like to see some more
Comment 2.2

Response 2.2

The parameters are global and do not vary along the transect (see Response 1.3 above), although the known dependence of specific leaf area with mean annual precipitation is incorporated (Equation 1.38). It is an interesting idea to vary parameters along the transect, but it is out of scope for this paper. Moreover, in the interests of parsimony it is desirable for parameters to be globally applicable.

Comment 2.3

Response 2.3

We have clarified that the absolute size of the NSC pool is unknown, when we first describe it in Section 2: “Dynamics of vegetation carbon stores are governed by growth and turnover rates. Growth is constrained to be equal to net primary production (NPP, equal to gross primary production minus autotrophic respiration) in the long term, but is temporally dependent on the size of an implicit NSC store, soil water availability and the deviation of the structural carbon store from an internally computed carbon carrying capacity, above which growth stops and NPP is stored away as NSC. No assumption is made as to the absolute size of the NSC store; rather it is the cumulative deviation due to the imbalance between NPP and growth that is maintained as a state variable of the model.”

Detail in the Results that presents the size of the NSC pool, the size of the NSC pool relative to the leaf/root/stem pools, and some discussion of how realistic this might be (i.e., what happens when the NSC pool becomes too large, if this occurs)? Also, why is the NSC pool not treated as a state variable, i.e., in Section 2.2.

Because the implementation of the NSC is rather novel, I would like to see some more detail in the Results that presents the size of the NSC pool, the size of the NSC pool relative to the leaf/root/stem pools, and some discussion of how realistic this might be (i.e., what happens when the NSC pool becomes too large, if this occurs)? Also, why is the NSC pool not treated as a state variable, i.e., in Section 2.2.
Further, we have included NSC in the state variables listed in Section 2.2: “The state variables of the vegetation model are carbon pools in leaves and fine roots of trees and grass, and the woody carbon pool (stem plus coarse roots) in trees, and the cumulative difference between NPP and growth, which equates to the deviations of NSC for trees and grasses from an (unknown) baseline value.”

The change in NSC storage is shown in Figure 6b(i).

We avoid instances of the NSC pool becoming "too large" by constraining growth and NPP to be equal in the long term (Equation 1.21)

Comment 2.4

Regarding the water budget, i) does the saturated volumetric water content consider the difference between field capacity and wilting point (perhaps add to Table 1), ii) is the soil evaporative layer considered to be equal the upper soil layer?

Response 2.4

(i) No: the saturated volumetric water content parameter is not associated with wilting point or field capacity.

(ii) The formulation for soil evaporation is given in Equation 1.12: it depends on the moisture content of the upper soil layer.

Comment 2.5

The timesteps could be more clearly presented for GPP, NPP, and allocation.
Response 2.5

We have inserted the following text in Section 2: “The time-step is one day.”

Comment 2.6

Is there a reproductive cost on GPP?

Response 2.6

No, although this could be added to the growth respiration cost (Equation 1.22).

Comment 2.7

In the Section 4, I wasn’t able to follow which parameters were calibrated – a short list would be helpful.

Response 2.7

Please See Table 1. In Section 4, we have added the following text: “The parameters subject to calibration are shown in Table 1.”
Comment 3.1

Pg 16317, lines 3 and 4. The term "resource uptake surfaces" is not clear; I understand this as a modelling term, not something that species respond to.

Response 3.1

We explain what is meant by resource uptake surfaces:

"Species respond by producing resource uptake surfaces quickly to optimise uptake of the most limiting resource—leaves to capture light when soil water is abundant, fine roots to increase water uptake as supplies deplete"

Comment 3.2

Pg 16317, line 8. Repetitive to say "stored" then in "storage".

Response 3.2

"In storage" has been removed to avoid repetition.

Comment 3.3

Pg 16318, lines 3 and 4. Define ESM as Earth Systems Model?
Response 3.3

Done

Comment 3.4

Pg 16318, line 8. Normally we would have Haverd et al. 2013a cited before Haverd et al. 2013b.

Response 3.4

Not done: this is not easily fixed with reference software.

Comment 3.5

Pg 16324, line 5. Remove "a" after "proportion".

Response 3.5

Done: See Response 1.5 above.

Comment 3.6
Pg 16327, Equations 26 and 27. I am having a hard time reconciling units in these two equations. It seems that the second term will have the same units in both equations, but the primary terms have saturation deficit and temperature, respectively?

Response 3.6

Thank you for pointing out this mistake: an error in the typed equations only, not the model code. The denominator in the second term of Eq 1.26 has been corrected so it is down dimensionally consistent.

Comment 3.7

Pg 16329, line 14. Haverd et al 2012 is not in the reference list.

Response 3.7

Fixed.

Comment 3.8

Pg 16331, line 20. I think that the Isaac reference will likely get published much behind the current paper, so is not useful here. Can it be removed?

Response 3.8
Done.

Pg 16332, line 26. fPAR is usually the fraction of PAR used by plants. Did you mean something different here?

Response 3.9

No, we didn’t mean something different. The term "Vegetation fractional cover" has been removed.

Pg 16334, line 4. Where did the values of 50 and 140 come from?

Response 3.10

We have revisited the divergent estimates of peak root carbon density, and adjusted the text as follows: "The ratio of fine root to leaf mass is a very rough estimate, as estimates of peak fine root mass in Northern Australian tropical savannas are divergent: 1800 g C m$^{-2}$ (range 1050 - 4050 g C m$^{-2}$) (Janos et al., 2008); 1300 g C m$^{-2}$ (Chen et al., 2004); 70 g C m$^{-2}$ (Chen et al., 2002) (assuming a specific root length of 10 m g$^{-1}$, and possibly a factor of 10 too low due to units conversion error (Janos et al., 2008))."
The R^2 values look about the same to me and no statistical test was performed for comparison; can you really say that some are larger and that RMSE is smaller?

Response 3.11

We agree, and have adjusted the text accordingly: "Even without being supplied external vegetation cover information, our new HAVANA model performed comparably to the benchmark (BIOS2) for monthly GPP and ET, based on the R^2 values and RMSE scores (Figure 4)."

Comment 3.12

Pg 16337, line 8. Higgins is not in the reference list.

Response 3.12

Fixed

Comment 3.13

Pg 16337, line 20. You briefly mentioned grazing earlier, but it would help to add something here on the impact of both native and introduced grazers/browsers. The model appears to not consider animals that could limit establishment of woody species, or contribute to the maintenance of grassland dynamics. For many parts of the world, these factors are important in savannas.

Response 3.13

We have inserted the following text at the end of the discussion: "We did not explicitly consider native or introduced grazers or browsers: however these represent a minor disturbance agent compared with fire in northern Australia (Murphy et al. 2015). The approach of HAVANA-POP
remains valid for regions in which savannah vegetation structure is controlled by the disturbance regime."

Comment 3.14

Pg 16338, line 7. Insert "of" after "implementation".

Response 3.14

Done

Comment 3.15

Pg 16342, line 15. "Acacia woodland" needs spaces.

Response 3.15

Done

Comment 3.16

Pg 16353, Figure 4. Label FAPAR as fPAR to be consistent with text?

Response 3.16

Done
Coupling carbon allocation with leaf and root phenology predicts tree-grass partitioning along a savanna rainfall gradient.

Vanessa Haverd\textsuperscript{1,}, Benjamin Smith\textsuperscript{2}, Michael Raupach\textsuperscript{3}, Peter Briggs\textsuperscript{1}, Lars Nieradzik\textsuperscript{1}, Jason Beringer\textsuperscript{4},

Lindsay Hutley\textsuperscript{5}, Cathy M Trudinger\textsuperscript{6}, James Cleverly\textsuperscript{7}

\textsuperscript{1}CSIRO Oceans and Atmosphere, PO Box 3023, Canberra ACT 2601, Australia

\textsuperscript{2}Lund University, Department of Physical Geography and Ecosystem Science, 223 62 Lund, Sweden.

\textsuperscript{3}Australian National University, Climate Change Institute, Canberra, ACT 0200, Australia.

\textsuperscript{4}School of Earth and Environment, The University of Western Australia, M004. 35 Stirling Highway,

Crawley, WA, 6009.

\textsuperscript{5}Research Institute for the Environment and Livelihoods, Charles Darwin University, NT, 0909, Australia

\textsuperscript{6}CSIRO Oceans and Atmosphere, PMB 1 Aspendale, Vic 3195, Australia

\textsuperscript{7}School of Life Sciences, University of Technology, Sydney, PO Box 123, Broadway NSW, 2007, Australia.

* Correspondence to: vanessa.haverd@csiro.au

\textsuperscript{‡}Deceased
Abstract

The relative complexity of the mechanisms underlying savanna ecosystem dynamics, in comparison to other biomes such as temperate and tropical forests, challenges the representation of such dynamics in ecosystem and Earth system models. A realistic representation of processes governing carbon allocation and phenology for the two defining elements of savanna vegetation (namely trees and grasses) may be a key to understanding variations in tree/grass partitioning in time and space across the savanna biome worldwide. Here we present a new approach for modelling coupled phenology and carbon allocation, applied to competing tree and grass plant functional types. The approach accounts for a temporal shift between assimilation and growth, mediated by a labile carbohydrate store. This is combined with a method to maximise long-term net primary production (NPP) by optimally partitioning plant growth between fine roots and (leaves + stem). The computational efficiency of the analytic method used here allows it to be uniquely and readily applied at regional scale, as required, for example, within the framework of a global biogeochemical model.

We demonstrate the approach by encoding it in a new simple carbon/water cycle model that we call HAVANA (Hydrology and Vegetation-dynamics Algorithm for Northern Australia), coupled to the existing POP (Population Orders Physiology) model for tree demography and disturbance-mediated heterogeneity. HAVANA-POP is calibrated using monthly remotely-sensed fraction of absorbed photosynthetically active radiation (fPAR) and eddy-covariance-based estimates of carbon and water fluxes at 5 tower sites along the Northern Australian Tropical Transect (NATT), which is characterized by large gradients in rainfall and wildfire disturbance. The calibrated model replicates observed gradients of fPAR, tree leaf area index, basal area and foliage projective cover along the NATT. The model behaviour emerges from complex feed-backs between the plant physiology and vegetation dynamics, mediated by shifting above- versus below-ground resources, and not from imposed hypotheses about the controls on tree/grass co-existence. Results support the hypothesis that resource limitation is a stronger determinant of tree cover than disturbance in Australian savannas.
Introduction

Savannas constitute one of the world’s most extensive biomes and provide ecosystem services as rangelands and marginal agricultural lands for one-fifth of the world’s population (Lehmann et al., 2009). Being sensitive to variations in rainfall and water availability, they have a primary role in governing interannual variability in biosphere-atmosphere carbon exchange and the CO₂ concentration of the atmosphere (Ahlström et al., 2015; Poulter et al., 2014). For the last three decades, semi-arid ecosystems (including savannas) globally have exhibited a positive net carbon uptake trend (Ahlström et al., 2015), coinciding with regional observations of woody encroachment and increased vegetation greenness when viewed from space (Donohue et al., 2009; Liu et al., 2015). The biogeochemical dynamics of seasonally dry savannas are modulated by stress tolerance and pulse response behaviour of the drought adapted biota as the environment shifts seasonally in the relative availability of above-(light) and below-ground (mainly water) resources. Resource competition—or avoidance of competition through spatial and temporal niche segregation (Ward et al., 2013)—between trees and grasses, as well as disturbances due to grazing animals and fires (Lehmann et al., 2014; Sankaran et al., 2005) drives shifts in allocation and tree versus grass performance that feed back to and tightly couple the water and carbon cycles. The relative complexity of the mechanisms underlying savanna ecosystem dynamics, in comparison to other biomes such as temperate and tropical forests, challenges the representation of such dynamics in ecosystem and Earth system models (Baudena et al., 2015).

Phenology and allocation of carbon to leaves, roots and stems are critical determinants of savanna productivity (Ma et al., 2013; Scholes and Walker, 2004). Savanna vegetation occurs in regions of high rainfall variability and, while vegetation is often water-limited, light can limit production seasonally or during heavy precipitation episodes. (Whitley et al., 2011) Species may partition available carbon seasonally and interannually in order to optimise uptake of variably available resources above and below ground. Resource availability often changes quickly: species respond by producing resource uptake surfaces quickly to optimise uptake of the most limiting resource—leaves to capture light when soil water is abundant, fine roots to increase water uptake as supplies deplete. To enable a rapid response to
changing resources, plants draw on stored non-structural carbohydrates (NSC), which are accumulated during times of plenty. This must lead to a temporal shift between plant growth and carbon capture.

A realistic representation of processes governing carbon allocation and phenology for the defining elements of savanna vegetation (namely trees and grasses) may thus be a key to understanding variations in tree/grass partitioning in time and space in the savanna biome worldwide. Global vegetation models typically treat allocation and phenology as independent processes. One exception is the ADGVM model of Scheiter and Higgins (2009) which is specialised for the simulation of savannas. It uses an individual plant’s carbon status to determine the transition between active and dormant states, dynamically allocating carbon based on resource (light or water) limitation. However, no large-scale vegetation model of which we are aware allows phenology to emerge as a result of allocation of assimilated carbon to leaves and roots in response to changing relative availability of above- and below-ground resources during the course of a growing season or between years.

Here we present a new approach that links phenology and allocation, accounting for a temporal shift between assimilation and growth, which is mediated by a labile carbohydrate store. The novelty of the approach lies in the dynamic constraint of plant growth such that the long term change in store (net primary production minus growth) is zero (a requirement for carbon conservation). This is combined with the use of an optimal response method for analytically predicting the partitioning of plant growth between fine roots and (leaves + stem), which optimises long term NPP. While optimal response methods for carbon allocation are not new (Franklin et al., 2012), and have been applied to savanna vegetation (Schymanski et al., 2009) the computational efficiency of the analytic method used here allows it to be uniquely readily applied at regional scale, as required, for example, within the framework of a land surface model (LSM) or Earth system model.

We demonstrate the approach by encoding it in a simple carbon/water cycle model that we call HAVANA (Hydrology and Vegetation-dynamics Algorithm for Northern Australia), coupled to the POP (Population Orders Physiology) model for tree demography and disturbance-mediated heterogeneity (Haverd et al.,
HAVANA-POP is applied to and tested against observations from the Northern Australian Tropical Transect, featuring gradients in rainfall and wildfire disturbance. In particular, the model is evaluated against a suite of observations that are sensitive to the tree-grass ratio along the transect, namely: eddy-covariance-based estimates of carbon and water fluxes at 5 tower sites; dynamics of remotely-sensed fPAR; tree leaf area index derived from digital hemispheric photography and satellite observations; gradients of tree basal area and foliage projective cover.

2. Model Description
HAVANA is a new model of landscape water balance and plant function. It contains two water stores (upper and lower soil) and leaf and fine root compartments for each of two competing vegetation types: trees and grass. The tree vegetation type also has a stem compartment, which includes coarse roots. The stem compartment is partitioned between sapwood and heartwood via coupling to the POP module (Haverd et al., 2013b), which accounts for tree demography and landscape-heterogeneity mediated by disturbance.

Qualitative relationships between key variables for a single vegetation type (trees) are shown in Figure 1. The schematic also applies to grass, except that the stem component does not apply in grasses, and grass fine-roots do not access the deep soil moisture store. Although not represented in Figure 1, trees and grass interact via competition for water in the shallow upper soil layer, and competition for light.

In the model, soil water stores change in response to input from precipitation and losses due to evapotranspiration, deep drainage and surface runoff (Figure 1). Dynamics of vegetation carbon stores are governed by growth and turnover rates. Growth is constrained to be equal to net primary production (NPP, equal to gross primary production minus autotrophic respiration) in the long term, but is temporarily dependent on the size of an implicit NSC store, soil water availability and the deviation of the structural carbon store from an internally computed carbon carrying capacity, above which growth stops and NPP is stored away as NSC. No assumption is made as to the absolute size of the NSC store; rather it is the cumulative deviation due to the imbalance between NPP and growth that is maintained as a state variable.
of the model. Growth is partitioned between (leaf + stem) and fine root compartments using an optimal response theory in which long term NPP is the fitness proxy. That is, we assume the ecological optimality hypothesis, that evolutionary selection pressures drive ecosystems towards maximal utilization of available resources for the production of biomass, so that long-term NPP over many reproductive cycles takes the largest possible value under the constraints of available resources (Raupach, 2005). This leads to a negative feed-back of soil moisture on allocation to fine roots, in favour of the combined (leaf + stem) compartment. Partitioning of growth between leaf and stem is influenced by the relative magnitudes of leaf and sapwood compartments, which are constrained by the Pipe Model (Shinozaki et al., 1964), in which sapwood cross-sectional area is assumed to be a constant proportion of total leaf area. Leaf and fine root carbon stores are subject to first order decay, while turnover of woody biomass is given by the mortality (both resource-limitation and disturbance components, including fire) computed within the POP module (Section 2.3 and Appendix A).

The carbon and water cycles are primarily linked by the transpiration component of evapotranspiration, with a secondary link being the dependences of growth and growth-partitioning on soil moisture. Transpiration, equivalent to root water extraction, is modelled as the lesser of evaporative demand (dependent on radiation, air temperature and fraction cover) and supply-limited root water uptake, which depends both on soil moisture and root density in each soil layer.

Trees and grass compete for light and water. Tree roots can potentially access water in both shallow and deep soil layers, whereas grass roots are assumed unable to access the deep soil moisture store. Further, grass is partially shaded by trees as a function of tree cover.

A quantitative description of the model follows. All parameter symbols, meaning, values and sources are listed in Table 1. The time-step is one day.
2.1 Water balance model

The water balance model is that of the Australian Water Availability Project (Raupach et al., 2009), with modification to the transpiration terms to allow for root-carbon dependence, and is described here in full for completeness.

**State variables:** The two state variables of the water balance model are soil water stores \(W_1, W_2\) [m-water] corresponding to upper and lower soil layers, the boundary between them corresponding to the approximate vertical extent of the grass root profile (Janos et al. 2008), and the total depth that of the tree roots (Hutley et al., 2000). The layers together encompass the whole soil profile from which water is extracted by plant transpiration. Corresponding dimensionless variables are the relative soil water \((w_1, w_2)\) in the two stores, between 0 and 1 and related to \(W_1\) and \(W_2\) by

\[
w_i = W_i / \left(\theta_S Z_{Wi}\right) \quad (i = 1, 2)
\]

where \(\theta_S [m^3 m^{-3}]\) is the saturated volumetric water content and \(Z_m [m]\) is the thickness of layer \(i\) (Table 1).

**Balance equations:** The dynamic equations governing \(W_1\) and \(W_2\) are the mass conservation equations for soil water:

\[
\frac{dW_1}{dt} = \theta_{S1} Z_{W1} \frac{dw_1}{dt} = F_{W_{Prec}} - F_{W_{Tr1}} - F_{W_{Evap}} - F_{W_{Run}} - F_{W_{Leach1}}
\]

\[
\frac{dW_2}{dt} = \theta_{S2} Z_{W2} \frac{dw_2}{dt} = F_{W_{Leach1}} - F_{W_{Leach2}} - F_{W_{Run}} - F_{W_{Trans12}}
\]

where all water fluxes \(F_w\) are in metres of water per day \([m\cdot H_2O \cdot d^{-1}]\).

**Phenomenological equations:** The phenomenological equations for water fluxes are as follows.

1. Precipitation \(F_{W_{Prec}}\) is an external input.
Transpiration ($F_{Tr}$) is defined for each soil layer ($i = 1, 2$) and each plant type ($j = \text{grass, trees}$) as the lesser of an energy-limited transpiration rate $F_{Tr(EL)}$ and a water-limited transpiration rate $F_{Tr(WL)}$:

$$F_{Tr,i,j} = \min\left(F_{Tr(EL),i,j}, F_{Tr(WL),i,j}\right)$$  \hspace{1cm} (1.0)

(Note here that $F_{Tr(EL),2,\text{grass}}=0$, as it is assumed that grass roots do not access the lower soil moisture store.)

The total energy-limited transpiration rate (summed over two soil layers) is partitioned among soil layers using the water-limited transpiration for each layer under prevailing (energy-limited) conditions, so that:

$$F_{Tr(EL),i,j} = F_{Tr(EL),i} \left[ F_{Tr(WL),i,j} / \left(F_{Tr(WL),1,j} + F_{Tr(WL),2,j}\right) \right]$$  \hspace{1cm} (1.0)

The total energy-limited transpiration rate, $F_{Tr(EL)}$, and the water-limited transpiration for each layer, $F_{Tr(WL)}$, are defined as follows.

The total energy-limited transpiration rate is the evaporation rate from the surface without soil water constraints. It is often defined using the Penman-Monteith equation, but for reasons of both physics and simplicity, it is defined here as

$$F_{Tr(EL),i} = \nu_i F_{Tr(PT)}$$  \hspace{1cm} (1.0)

where $\nu_j$ is the tree or grass vegetation cover fraction and $F_{Tr(PT)}$ is the Priestley-Taylor evaporation rate [m-H$_2$O d$^{-1}$], a thermodynamic estimate of the energy-limited evaporation rate for the whole surface (vegetation plus soil). The factor $\nu_j$ relates energy-limited total evaporation to the plant component only.

From (Raupach 2000) and (Raupach 2001), $F_{Tr(PT)}$ is

$$F_{Tr(PT)} = c_{eP} \Phi_{eq} / (\rho_w \lambda_w)$$  \hspace{1cm} (1.0)

where $\rho_w$ [mol-H$_2$O m$^{-3}$] is the density of liquid water, $\lambda_w$ [J mol-H$_2$O$^{-1}$] is the latent heat of vapourisation of water, $\Phi_{eq}$ [J m$^{-2}$ d$^{-1}$] is the thermodynamic equilibrium latent heat flux, and $c_{eP}$ is the Priestley-Taylor...
coefficient, a number which is well constrained at about 1.26 (Priestley and Taylor, 1972; Raupach, 2001).

The equilibrium latent heat flux is given by

$$\Phi_{eq} = pe\Phi_A^* / (pe + 1)$$  \hspace{1cm} (1.0)

where $\Phi_A^*$ is the isothermal available energy flux, $e$ is the ratio of latent to sensible heat content of saturated air (2.2 at 20°C, roughly doubling with each 13°C temperature increase) and $p$ is a number slightly less than 1 accounting for radiative coupling:

$$p = \frac{G_s}{G_s + G_r}$$  \hspace{1cm} (1.0)

where $G_s$ is the aerodynamic conductance for heat and water vapour transfer; $G_r = 4e\sigma T_a^4 / (\rho_A c_{PA})$ is the radiative conductance; $\rho_A$ [mol m$^{-3}$] is the density of air; and $c_{PA}$ is the specific heat of air at constant pressure [J mol$^{-1}$ K$^{-1}$].

The isothermal available energy flux $\Phi_A^*$ is given by

$$\Phi_A^* = (1 - a)\Phi_{\downarrow}^{s} + e\left(\Phi_{\downarrow}^{l} - \sigma T_a^4\right)$$  \hspace{1cm} (1.0)

where $\Phi_{\downarrow}^{s}$ and $\Phi_{\downarrow}^{l}$ are the downward solar (shortwave) and thermal (longwave) irradiances; $a$ and $e$ are whole-surface albedo and emissivity, respectively; $\sigma$ is the Stefan-Boltzmann constant; $T_a$ [K] is the air temperature at a reference height.

Energy fluxes ($\Phi$) are calculated as averages over daylight hours only, since it is assumed that total evaporation ($F_{\text{TOT}} = F_{\text{WTRA}} + F_{\text{WSOIL}}$) and its components are all zero at night. Downward daytime longwave irradiance is estimated with the Swinbank (1963), formula:

$$\Phi_{\downarrow}^{l} = 335.97 \left( \frac{T_a}{293} \right)^{1.6}$$  \hspace{1cm} (1.0)

using average daytime $T_a$ estimated as $0.75T_{\text{max}} + 0.25T_{\text{min}}$. 
The water-limited transpiration rate in layer $i$ by plant type $j$ is parameterised as:

$$F_{\text{Tr}i,\text{lim}}^j = k_{Ei,j} C_{Ei,j} W_i^{\text{Fwater}}$$ (1.0)

where $k_{Ei,j}$ is a rate per unit root carbon density [$\text{m d}^{-1} \text{mol C m}^{-2}$] for the uptake of water by roots from a drying soil under water-limited transpiration, and $C_{Ei,j}$ is the root carbon density [$\text{mol C m}^{-2}$] of soil layer $i$ and plant type $j$.

(3) Soil evaporation ($F_{\text{Wsoil}}$) is formulated as:

$$F_{\text{Wsoil}} = (1 - v) W_i^{\beta} F_{\text{water}}^j$$ (1.0)

where $\beta$ is an exponent specifying the response of soil evaporation to upper-layer soil water ($w_i$).

(4) Surface runoff ($F_{\text{Wrun}}$) is given by

$$F_{\text{Wrun}} = F_{\text{Water}} \text{Step}(w_i - 1)$$ (1.0)

All precipitation runs off when the upper-layer soil is saturated, and there is no runoff otherwise.

(5) Leaching ($F_{\text{Wleach}}$) or drainage downward out of soil layer $i$ is given by

$$F_{\text{Wleach}} = K_{Si} w_i^g$$ (1.0)

where $g$ is an exponent specifying the response of drainage to relative soil water $w_i$, and $K_{Si}$ [$\text{m d}^{-1}$] is the saturated hydraulic conductivity of soil layer $i$.

2.2 Model of Vegetation Function

State variables and governing equations: The state variables of the vegetation model are carbon pools in leaves and fine roots of trees and grass, and the woody carbon pool (stem plus coarse roots) in trees, and the cumulative difference between NPP and growth, which equates to the deviations of NSC for trees and grasses from an (unknown) baseline value. A single set of parameters was adopted for all trees and all grasses respectively: species were not distinguished. The dynamics of these pools are governed by their...
mass conservation equations, with each pool augmented by a proportion \( \alpha \) of the growth flux. Leaf and fine root pools are depleted by first order decay, while all tree carbon pools are depleted by tree mortality:

\[
\frac{dC_{L,j}}{dt} = \alpha_{L,j} F_{\text{Growth},j} - k_{L,j} C_{L,j} - \frac{C_{L,j}}{C_{\text{stem}}} m_{\text{stem},j} \quad (1.0)
\]

\[
\frac{dC_{R,i,j}}{dt} = \alpha_{R,i,j} F_{\text{Growth},j} - k_{R,i,j} C_{R,i,j} - \frac{C_{R,i,j}}{C_{\text{stem}}} m_{\text{stem},j} \quad (1.0)
\]

\[
\frac{dC_{\text{stem},j}}{dt} = \alpha_{\text{stem}} F_{\text{Growth,tree}} - m_{\text{stem}} \quad (1.0)
\]

In Equations (1.0) to (1.0), \( C \) denotes a carbon pool [mol C m\(^{-2}\)]; \( \alpha \) a carbon allocation coefficient; \( L \) leaves; \( R \) fine roots; stem trunk plus coarse roots \( k \) a first order rate constant [d \(^{-1}\)]; \( j \) a plant type (woody or grassy) and \( i \) a soil layer (upper or lower), \( m_{\text{stem},j} \) is stem biomass turnover [mol C m\(^{-2}\) d\(^{-1}\)], which is zero for grass, and computed by POP for trees (See Section 2.3).

For woody vegetation, we adopt a dependence of leaf turnover on specific leaf area, based on the synthesis of Wright et al. (2002):

\[
k_{L,w} = \frac{1}{365 \left( \frac{A_{S,w}}{60} \right)^{1.2}} \quad (1.0)
\]

**Growth**

Growth (the flux of carbon to structural components) is parameterised by a logistic curve, inspired by Choler et al. (2010), who specified growth of grasses in water-controlled ecosystems as the product of (i) a growth scaling parameter; (ii) relative soil moisture content; (iii) one minus current leaf carbon, relative
to a fixed carrying capacity and (iv) current leaf carbon. In contrast we specify growth following Eq (1.0) as

the product of: (i) a growth scaling parameter \( \beta_{\text{growth}} \); (ii) \( f_{\text{water},j} \), an increasing function of soil water in the
upper soil layer (grass) or lower soil layer (trees) (Eq (1.0)) (n.b. that trees and grass nonetheless compete
for water in the upper soil layer via transpiration) (iii) one minus (leaf + fine root) carbon relative to a
prognostic carrying capacity \( C_{\text{max},j} \), above which growth stops and net primary production is stored away
as non-structural carbohydrate; (iv) the sum of (a) long-term NPP; (b) a multiple of the long-term net flux
(NPP – growth) to the NSC store, and (c) a residual component \( F_{\text{growth}} \), allowing regrowth to occur, should
the plant \( C \) stores decline to zero.

\[
F_{\text{Cgrowth},j} = \beta_{\text{growth}} f_{\text{water},j} \max \left[ 1 - \frac{C_{\text{leaf},j} + \sum C_{\text{fine},j}}{C_{\text{max},j}} \right] \left[ F_{\text{growth}} + \max \left[ \frac{F_{\text{CNP},j}}{C_{\text{max},j}} - F_{\text{growth}} \right], 0.0 \right]
\]

(1.0)

\[
f_{\text{water}} = \frac{1 - \left( 1 + \left( \frac{W}{W_{\text{max}}(F_{\text{water})}} \right)^{-1} \right)}{1 - \left( 1 + \left( \frac{1}{W_{\text{max}}(F_{\text{water})}} \right)^{-1} \right)}
\]

(1.0)

**Dynamic Storage (Coupling of Net Primary Production and Growth)**

Growth is constrained to equal time-averaged NPP over some averaging period \( t_{\text{av},j} \) (set here to 1 year
for grass and 3 y for trees), producing a change in storage of carbohydrate (NPP minus Growth) which
averages to zero. This is achieved by adjusting \( C_{\text{max},j} \) dynamically according to:
where calculated transpired quanta Plant gross primary production
Gross Primary Production respiration of leaves and fine roots, otherwise. \( C_{\text{max}} \) is maintained above \( C_P \).

**Net Primary Production**

Net primary production is the difference between gross primary production \( (F_{\text{C,GPP}}) \) and maintenance respiration of leaves and fine roots, scaled by \((1-c_{\text{growth}})\) to account for growth respiration [Ryan, 1991]:

\[
F_{\text{C,APP},j} = \left(1 - c_{\text{growth}}\right) \left( F_{\text{C,GPP},j} - \sum_i F_{\text{C,In,R},i,j} - F_{\text{C,In,L},j} - F_{\text{C,In,N}} \right) \tag{1.0}
\]

**Gross Primary Production**

Plant gross primary production \( (F_{\text{C,GPP}}) \) is evaluated as the lesser of light- and water-limited components:

\[
F_{\text{C,GPP},j} = \min \left[ \left( \alpha_Q, j \right)^{\alpha_P} F_Q, \left( \alpha_w \rho_w F_{\text{W,in},j} \right) \right] \tag{1.0}
\]

where \( F_Q \) is the incident quantum flux of photosynthetically active radiation (PAR) on the surface \([\text{mol-}
\text{quanta m}^{-2} \text{ d}^{-1}]\), and \( \alpha_Q \) and \( \alpha_w \) are respectively a PAR use efficiency \([\text{molC mol-quantum}^{-1}]\) and a transpired-water use efficiency \([\text{molC mol-H}_2\text{O}^{-1}]\). Of these, \( \alpha_Q \) is a prescribed parameter, and \( \alpha_w \) is calculated as

\[
\alpha_w = m_{w,j} \left( [\text{CO}_2]_a - [\text{CO}_2]_j \right) \left( 1.6 D \right) \tag{1.0}
\]

where \( m_{w,j} \) is a dimensionless multiplier, \( [\text{CO}_2]_a \) is the atmospheric \( \text{CO}_2 \) concentration, \( [\text{CO}_2]_j \) is the \( \text{CO}_2 \) compensation point \([\text{molC molAir}^{-1}]\) calculated using the (Von Caemmerer, 2000) algorithm:

\[
[\text{CO}_2]_j = 37.0 \times 10^{-4} \times 1.37^{-25.0 \text{ MP}} \tag{1.0}
\]
$D_s$ is the surface saturation deficit [mol H$_2$O$^3$ molAir$^{-1}$], calculated from the air saturation deficit $D_a$ as in (Raupach, 1998):

$$D_s = D_a + \frac{e \left( \rho \left( \Phi_A - \Phi_E \right) \right) - \Phi_E}{\rho_A \lambda_a G_a} \quad (1.0)$$

and surface temperature $T_s$ is given by:

$$T_s = T_a + \frac{\rho \left( \Phi_A - \Phi_E \right)}{\rho_A c_p G_a} \quad (1.0)$$

**Maintenance Respiration**

The rate of maintenance respiration for the $j$th compartment (sapwood, leaf or fine roots) is formulated as:

$$R_{m,j} = k_{res} C_j / \text{ratio}_{CtoN,j}(T_a) \quad (1.0)$$

where $k_{res} = 0.0548$ d$^{-1}$ is the rate constant for maintenance respiration (Sprugel et al., 1995), and $g(T)$ is the ecosystem respiration temperature response function of Lloyd and Taylor (1994) adopted by Sitch et al. (2003) in the LPJ model:

$$g(T) = \exp \left[ 308.56 \left( \frac{1}{56.02} - \frac{1}{T - 227.13} \right) \right] \quad (1.0)$$

and ratio$_{CtoN}$ is the mass ratio of carbon to nitrogen in the plant tissue, here taken as 30 for leaves and fine roots, and 300 for sapwood.

**Carbon Allocation**

The allocation scheme governs the partitioning of growth between leaf, root and (for trees) stem compartments. Allocation of assimilated carbon to reproduction is not considered. Following Raupach (2005), we choose time-dependent carbon allocation coefficients to maximise the total carbon gain,
namely the long-term integral of $F_{C,NPP,j}$ for each plant type. As discussed by Raupach (2005), the vector of allocation coefficients has “bang-bang” character, meaning that, at each instant $t$, an allocation coefficient of one is assigned to the pool for which the marginal return on invested growth is largest while all other pools receive zero allocation:

$$\alpha_{L,j} \ast \alpha_{mow,j} = H \left[ \frac{\delta F_{C,NPP,j}}{\delta C_{L,j}} - \frac{\delta F_{C,NPP,j}}{\delta C_{R,1,j}} \right] H \left[ \frac{\delta F_{C,NPP,j}}{\delta C_{L,j}} - \frac{\delta F_{C,NPP,j}}{\delta C_{R,2,j}} \right]$$  (1.0)

$$\alpha_{R,1,j} = H \left[ \frac{\delta F_{C,NPP,j}}{\delta C_{R,1,j}} - \frac{\delta F_{C,NPP,j}}{\delta C_{L,j}} \right] H \left[ \frac{\delta F_{C,NPP,j}}{\delta C_{R,1,j}} - \frac{\delta F_{C,NPP,j}}{\delta C_{R,2,j}} \right]$$  (1.0)

$$\alpha_{R,2,j} = H \left[ \frac{\delta F_{C,NPP,j}}{\delta C_{R,2,j}} - \frac{\delta F_{C,NPP,j}}{\delta C_{R,1,j}} \right] H \left[ \frac{\delta F_{C,NPP,j}}{\delta C_{R,1,j}} - \frac{\delta F_{C,NPP,j}}{\delta C_{R,2,j}} \right]$$  (1.0)

Where $H$ is the Heaviside Step Function, the value of which is zero for a negative argument and one for a positive argument. Partial derivatives in Equations (1.0)-(1.0) are readily evaluated from analytically differentiating $F_{C,NPP,j}$ with respect to each plant carbon pool.

For trees, the total allocation to leaves and wood is partitioned, such that a target ratio of leaf area to sapwood area, $k_{LA:SA}$ is maintained:

$$\frac{\left( C_{L,w} + \alpha_{L,w} F_{Growth} - k_{LA} C_{L,w} \right) A_{SL,w}}{A_{sapwood}} \leq k_{LA:SA}$$  (1.0)

where $A_{SL,w}$ is the specific leaf area for woody vegetation (see Eq (1.0) below).

**Vegetation Cover**

The vegetation cover fraction or green-leaf cover $n$ (dimensionless, between 0 and 1) is assumed equal to the fraction of absorbed photosynthetically active radiation (FAPAR) and related to leaf area index $L$ by

$$v = 1 - \exp \left( -c_{v} K_{sap} A_{v} \right)$$  (1.0)
and

$$v_g = \left(1 - v_min\right)\left(1 - \exp\left(-c_{ext,1}A_{c}\right)\right)$$  \hspace{1cm} (1.0)$$

where $c_{ext}$ is the exponential light extinction coefficient in the canopy (assumed here the same for trees and grass), and $K_{clump}$ is a crown clumping factor related to crown projected cover $A_c$ by (Haverd et al., 2012):

$$K_{clump} = \min\left[A \left(1 - \exp\left(-c_{ext,1}A_{c}/A_{j}\right)\right)/(c_{ext,1}A_{c}), 1.0\right]$$  \hspace{1cm} (1.0)$$

as computed within the POP module.

Leaf area index is related to the leaf carbon pool and specific leaf area $A_{SL}$ [cm$^2$ g(DW)$^{-1}$] by:

$$\Lambda_{j} = 0.0024 \frac{g(DW) \text{ cm}^{-2}}{\text{molC}\text{m}^{-2}} A_{SL,j} C_{L,j}$$  \hspace{1cm} (1.0)$$

For woody vegetation, specific leaf area is known to increase with mean annual precipitation ($P$, mm y$^{-1}$) along the NATT as (Schulze et al., 1998):

$$A_{SL,wo} = 2.0 + 0.025P$$  \hspace{1cm} (1.0)$$

2.3 Woody biomass turnover and tree demography feed-backs on carbon uptake

Woody biomass turnover due to resource-limitation mortality and disturbance mortality (including fire mortality) is computed by coupling HAVANA to the POP module for tree demography and landscape heterogeneity mediated by disturbance. POP has been fully described elsewhere (Haverd et al., 2014), except for updates used in this work, relating to the feed-backs of structure on function, which are documented in Appendix A.

3 Study site and observational data

The North Australian Tropical Transect is a 1000 km transect (Hutley et al., 2011), with a systematic decline in mean annual rainfall (Grant et al., 2008; Jones et al., 2009) with distance (~ 1 mm per km) from
the northern coast of the Northern Territory, Australia. As in (Haverd et al., 2013b), we represent the gradients in rainfall (Figure 2(ii)) and fire regime (Figure 2(iii)) of the NATT transect by selecting 1000 random 0.05° x 0.05″ grid-cells from an area bounded by (19.95°S, 11.4°S, 130.0°E, 134.5°E) (Figure 2(ii)).

The NATT is characterized by largely intact savanna vegetation. In the north of the region (mean annual precipitation > 600 mm), the dominant vegetation is tropical savanna (overstorey of evergreen *Eucalyptus* and *Corymbia* tree species, and an understorey dominated by C4 grasses), while Acacia woodlands, shrublands and hummock grasslands become increasingly prominent at the southern, semi-arid extreme (Hutley et al., 2011). The vegetation is subjected to fire regularly (once every 2 to 7 years, Figure 2(ii), data derived from Craig et al. (2002)). The fraction of early dry-season (pre-August) fires follows a similar latitudinal pattern to the fire frequency, which is an effect of fire management. Fire timing is a predictor of fire intensity, with late-season fires generally being significantly more intense as fuels accumulate and cure and weather becomes more extreme (Williams et al., 1998).

### 3.1 Driving Data

HAVANA was forced using gridded meteorological data and soil properties at 0.05° spatial resolution, which are described fully in Haverd et al. (2013a). Briefly, meteorological data comprise daily gridded rainfall, temperature, and solar irradiance for the period 1900-2013, current at March 2014, from the Bureau of Meteorology’s Australian Water Availability Project data set (BoM AWAP) (Grant et al., 2008; Jones et al., 2009), with temporal gap-filling using climatologies from the same dataset. Soil information is taken from the McKenzie and Hook (1992) and McKenzie et al. (2000) interpretations of the 725 principal profile forms (soil types) mapped in the Digital Atlas of Australian Soils (Northcote et al., 1960; Northcote et al., 1975).

### 3.2 Data for model calibration and validation

**Calibration Data**

Monthly Estimates of GPP and ET from five flux tower sites (Table 2 and located in Figure 2(ii)) were obtained from eddy covariance datasets that were quality assured and quality controlled using the OzFlux
standard processing protocol OzFluxQCv2.8.5 (Eamus et al., 2013). Gaps in missing data were filled, and GPP was resolved from net ecosystem exchange (NEE) using a new processing package called DINGO (Dynamic INtegrated Gap filling and partitioning for OzFlux).

DINGO applies a linear interpolation to gaps of less than two hours, and uses the following methods for gaps longer than two hours. For temperature, humidity, pressure, precipitation and wind speed, DINGO searches for the 10 closest Australian Bureau of Meteorology (BoM) monitoring sites from a localised database and gap fills using data from the site for which correlation with site data is the highest. Gaps in incoming solar radiation gaps are filled using solar exposure data, derived by the BoM from satellite imagery, while reflected solar radiation is filled using the MODIS albedo product. Soil moisture and temperature gaps are filled from half-hourly outputs from a biogeochemical land surface model (Haverd et al., 2013a). A feed-forward artificial neural network (ANN), described in Beringer et al., (2007) is used to gap fill NEE and sensible, latent, and soil heat fluxes. DINGO estimates GPP as NEE minus ecosystem respiration ($\text{R}_e$), with $\text{R}_e$ estimated as follows. During the night, CO$_2$ fluxes are assumed to equal $\text{R}_e$, as no photosynthesis occurs. It is also assumed that NEE, being biologically determined, is independent of atmospheric turbulence and remains constant above a friction velocity ($u^*$) threshold (Goulden et al., 1996), also assuming that stored CO$_2$ is drained completely from beneath the canopy before re-initiation of turbulence (Aubinet, 2008) This last assumption is likely to be violated at the southern-most Alice Springs site (Cleverly et al., 2013). Based on these assumptions, we used a $u^*$ threshold for selecting nights of adequate ventilation to determine the respiration component of carbon flux. The $u^*$ threshold applied is based on Reichstein et al. (2005), where the $u^*$ filtering dataset is split into six equal sample size temperature classes, and into 20 $u^*$ classes within each temperature class. When the $u^*$ value falls below the threshold, DINGO removes the value of NEE during that half-hour and the subsequent half-hour. The maximum $u^*$ threshold and gap filled soil moisture, soil temperature, air temperature and normalised difference vegetation index (NDVI) variables are inputs to an ANN for calculating $\text{R}_e$. 
A monthly time series of fPAR for January 1982 to December 2013 was derived from the third generation (NDVI3g) of the GIMMS NDVI time series (Tucker et al., 2005; Zhu et al., 2013). A monthly maximum composite was created from the original 15-day series, and the data were resampled from the original 0.0833° resolution (8 km) to 0.05° (5 km). NDVI values from 0.1 (bare ground) to 0.75 (full cover) were linearly rescaled between 0 and 1 to represent vegetation fractional cover. For calibration, we used 2000-2013 data at the locations of the flux sites (Table 1).

Validation Data
For model evaluation, we used predictive empirical models describing the decline of basal area and projected foliage cover with rainfall, developed by Williams et al. (1996) from a data-set of ~1000 quadrats (each 20 m x 20 m) lying north of 18°S within the Northern Territory. We also utilized observations reported by Sea et al. (2011) of dry-season (September 2008) tree leaf area index (LAI) based both on digital hemispheric photography (DHP) and the MODIS Collection 5 (MODC5) remote-sensing LAI product. Additionally, we used monthly fPAR (as described in Calibration Data above) along the entire rainfall gradient.

4 Model-Data Fusion
We calibrated HAVANA parameters by optimisation against monthly observations of ET, GPP and fPAR, subject to prior constraints. The parameters subject to calibration are shown in Table 1. The search algorithm was the Levenberg-Marquardt method implemented in the PEST software package (Doherty, 2004). The cost function to be minimised was the weighted sum of squared residuals, $\Phi = \sum w_i r_i^2$, where the residual $r_i$ can be either the residual between a model prediction and corresponding observation, or the residual between prior and posterior variables. Relative observation weights ($w_i$) were set such that each observation data type and each prior constraint contributed equally to the prior cost function.
Prior constraints consisted of estimates of leaf and fine-root carbon pools at Howard Springs. We assume prior estimates of time-averaged leaf carbon to be 50 gCm\(^{-2}\) and 100 gCm\(^{-2}\) for grassy and woody vegetation respectively, and a ratio of time-averaged fine root mass to leaf mass of 2. Leaf carbon estimates are based on Chen et al. (2003). The ratio of fine root to leaf mass is a very rough estimate, as estimates of peak fine root mass in Northern Australian tropical savannas are divergent: 1800 g C m\(^{-2}\) (range 1050 – 4050 g C m\(^{-2}\)) (Janos et al., 2008); 1300 g C m\(^{-2}\) (Chen et al., 2004); 70 g C m\(^{-2}\) (Chen et al., 2002) (assuming a specific root length of 10 m g\(^{-1}\), and possibly a factor of 10 too low due to units conversion error (Janos et al., 2008)).

5 Results

5.1 Calibration

We assessed the calibrated HAVANA predictions of monthly fluxes of ET and GPP, and monthly mean remotely-sensed fPAR. Time series of the three modelled variables for each flux site are shown in Figure 3 as coloured patches, with colour coding to represent the flux-partitioning between transpiration from upper and lower soil and soil evaporation (ET) and between tree and grass components (fPAR and GPP). The observed quantities are also shown along with a benchmark, being a state-of-the-art biogeochemical land surface model (LSM, CABLE, as implemented in BIOS2 (Haverd et al., 2013a)), forced using LAI derived from the GIMMS-3g fPAR product (Zhu et al., 2013), and calibrated here against GPP and ET from the five flux sites. ET, fPAR and GPP determined from HAVANA-POP increasingly matched observations toward the northern end of the NATT, where a more predictable seasonal cycle was observed than at the southernmost semi-arid site (Figure 4). Even without being supplied external vegetation cover information, our new HAVANA model performed comparably to the benchmark (BIOS2) for monthly GPP and ET, based on the R\(^2\) values and RMSE scores (Figure 4). There was a tendency in HAVANA and BIOS2 to under-predict ET (slope > 1), whereas the modelled range in GPP closely matched the observed range (Figure 4). While ET, and to a lesser extent GPP, was under-predicted by BIOS2 at Howard Springs, the bias was not apparent in the
HAVANA results (Figure 4). Both models over-predict the small values of ET and GPP at the Alice Springs site (Figure 4). HAVANA soil evaporation is a small proportion of ET at all sites.

5.2 Evaluation

We evaluated the performance of HAVANA-POP along the entire rainfall gradient (Figure 5). Each model point represents a spatial average across “65 points lying within a latitude bin of width 0.5°”, with error bars representing one standard deviation. The model replicates observed variations with rainfall of GPP, foliage projective cover, tree basal area and dry season tree LAI along the transect. Modelled tree foliage projective cover is higher than the observation-based estimates by about 0.06. This likely reflects a bias between the observation-based estimates, and the satellite-based fPAR that was used for calibration.

5.2 HAVANA dynamics along the NATT

Figures 6a and 6b illustrate the dynamics of key HAVANA variables from north (top row) to south (bottom row) along the NATT. Soil moisture (Fig 6a(i)) shows strong seasonality in the top layer, which is smoothed out in the lower layer, resulting in respective seasonal and persistent transpiration (root water extraction) from the two layers (Fig 6a(ii)). This leads to woody vegetation cover persisting throughout the year (Fig 6a(iii-iv)) and only small seasonal fluctuations in associated GPP (Fig 6a(v)), compared with grassy vegetation cover, which is completely absent by the late dry season. The decline in fPAR southward along the NATT accords well with satellite observations (Fig 6a(v)), as does the interannual variability which is largely absent at the northern end of the NATT, and clearly evident below 970 mm MAP.

Grassy vegetation is characterised by significant temporal shifts in NPP and growth, leading to large changes in the NSC store (Fig 6b(i)). This ability for growth to draw on NSC reserves is critical for rapid production of resource uptake surfaces (leaves and roots) at the beginning of the wet season (Fig 6b(iii)). The change in storage flux (relative to NPP) increases down the transect as both woody and grassy vegetation become more reliant on the NSC pool for growth in times of stress (Fig 6b(i-ii)). For grass, root carbon increases with aridity relative to leaf carbon. This is less evident for woody vegetation, because leaf carbon in woody vegetation is also influenced by a gradient in specific leaf area (Eq (1.0)). Allocation
patterns for grass (Fig 6b(v)) show an increasing fine root component as aridity increases down the transect, with temporal dynamics dictated by whether fine roots or leaves are limiting NPP (Eq (1.0)-(1.0)). (These are monthly-averaged C-allocation coefficients, which don’t necessarily sum to one because allocation coefficients are zero when growth is zero.) For trees (Fig 6b(vi)), allocation to surface roots occurs in the early wet season, when soil moisture in the upper layer exceeds that in the lower layer. Thus tree and grass roots compete in the surface layer. When soil moisture is plentiful (eg 2011), root growth is small and the remainder is partitioned between stems and leaves (Fig 6b(vi)). Leaf carbon is constrained by sapwood area (Eq (1.0)), leading to periods of high allocation to stems in wet periods.

Discussion

There is ongoing debate about the mechanisms governing tree and grass cover and maintaining the stability of savanna ecosystems relative to grassland or closed woody ecosystems (Bond, 2008; Torello-Raventos et al., 2013). While it is widely acknowledged that both resource limitation (especially water) and disturbance (fire and grazing) may control tree cover, their roles differ along environmental gradients and between continents (Africa, Australia, and South America), to the extent that Lehmann et al. (2014) claimed that “a single model cannot adequately represent savanna woody biomass across these regions”. Sankaran et al. (2005) found woody carrying capacity in African savannas to be limited by rainfall, but that savannas were typically held below woody carrying capacity by fire or grazing. Supporting the influential role of disturbance, Bond et al. (2005) used a dynamic vegetation model to infer that fire suppression has the potential to convert vast areas of C4 grassland and savannas to forests, roughly doubling the global area covered by forest. Sea and Hanan (2012) highlight the importance of self-thinning of smaller trees as they compete with grass for resources, in contrast to the Walter hypothesis (Ward et al., 2013) that tree-grass co-existence is made possible by separation of the rooting niche. While root partitioning is important in controlling relative performance of trees and grasses (e.g. Kulmatiski and Beard (2013)), there is good evidence that long-term stand dynamics are modulated by life-history disturbance interactions on demography (Higgins et al., 2000).
In Australian savannas (in contrast to other continents), Bond (2008) noted a roughly linear relationship between mean annual precipitation and tree cover, indicative of a stronger limitation by water availability and less impact from fire given the remarkable fire tolerance of the dominant woody genera of Australian savanna, *Eucalyptus* and *Corymbia* (Lawes et al., 2011). Murphy et al. (2015) suggested that fire impacts controlling *Eucalyptus* and *Corymbia* woody cover have been exaggerated in north Australian savanna, with intraspecific competition for limited water and nutrient resources a far stronger driver of cover.

Our findings support the view that Australian savannah tree cover is primarily controlled by availability of soil resources rather than disturbance. Simulated tree cover emerges from the balance between production – controlled by resource availability – and turnover, controlled both by resource availability and the frequency and intensity of disturbance. In our simulations for Australia, a high proportion of biomass loss was attributable to resource-limitation. Of the total biomass lost to mortality, 68% was attributable to resource-limitation at the wet northern end of the NATT, increasing to 84% at the arid southern end. The remaining minority of biomass turnover was attributable to disturbance loss, largely from fire. We did not explicitly consider native or introduced grazers or browsers; however these represent a minor disturbance agent compared with fire in northern Australia (Murphy et al. 2015). The approach of HAVANA-POP remains valid for regions in which savannah vegetation structure is controlled by the disturbance regime.

Future Prospects

The principles encoded in HAVANA-POP have been demonstrated to suffice as a “single-model” to account for savanna tree cover for the case of Australia. However the model in its current form has limitations, warranting further development for use in carbon-water-nutrient cycle modelling. For example: (i) nutrient resources are not accounted for; (ii) fire frequency is prescribed; (iii) leaves have a fixed turnover rate, which may explain e.g. the lack of modelled seasonality in tree vegetation cover (Fig 6a(iv)), known from observations to have an amplitude of about 30% at the northern end of the transect (Chen et al., 2003); (iv) soil evaporation (Fig 4(i)) is low compared with limited observations (eg Hutley et
al. (2000) observed soil evaporation fluxes that accounted for 50% of total evapotranspiration during the wet season at Howard Springs).

To overcome the above limitations, and to test the HAVANA principles of coupled allocation-phenology describing savannas globally, future work will entail implementation of these principles within a full biogeochemical land-surface model, coupled to the POP module for tree demography and landscape heterogeneity (e.g. CABLE-POP (Haverd et al. 2014)). In particular we propose implementing formulations developed here for growth (Eq (1.0)), NSC dynamics via coupling of growth and NPP (Eq (1.0)) and dynamic C allocation to maximise long-term NPP (Eqs (1.0)-(1.0)), while maintaining sufficient sapwood cross-sectional area to support leaf transpiration (Eq (1.0)). Such an implementation would require the following of the (modified) biogeochemical model: (i) root-water extraction dependence on root carbon; (ii) association of root carbon with vertical structure of soil moisture stores; (iii) partial derivatives of NPP (and hence GPP) with respect to plant carbon stores. Since GPP in the biogeochemical model may not be analytically differentiable, we suggest running the HAVANA GPP model (Eq (1.0)) in parallel with the full GPP model at daily time scale and with key parameters (water-use and light-use efficiencies) supplied by the full model at each daily time-step.

Conclusion

We have shown that HAVANA-POP predicts tree/grass partitioning along a wide rainfall gradient within a biozone of the Australian savanna belt. The model behaviour emerges from complex feed-backs (Figure 1) between the plant physiology and vegetation dynamics, mediated by shifting above- versus below-ground resources, and not from imposed hypotheses about the controls on tree/grass co-existence.

Appendix A: Updates to the POP module

POP simulates woody ecosystem stand dynamics, demography and disturbance-mediated heterogeneity. In previous work, POP has been coupled to the CABLE land surface scheme (Wang et al., 2011) and demonstrated to successfully replicate both the effects of rainfall and fire disturbance gradients on
vegetation structure along the NATT (Haverd et al., 2013b), and leaf-stem allometric relationships derived from global forest data (Haverd et al., 2014).

**POP Coupling**

In the above-mentioned applications, the CABLE-Pop coupling consisted of just two exchanges: (i) stem NPP passed from the host LSM to POP; (ii) woody biomass turnover returned from POP to the host LSM.

In contrast, in the current work, the HAVANA-Pop coupling also includes the return of sapwood area and sapwood volume to HAVANA, where these variables respectively influence C-allocation to leaves (Eq (1.0)) and autotrophic respiration (Eq (1.0)). Further, in previous applications of POP, LAI was exogenous, being imposed using remote-sensing. In contrast, in the HAVANA-Pop set-up, LAI is endogenous, being computed from leaf carbon (Eq (1.0)). Figure A1 illustrates the HAVANA-Pop coupling and key inputs and outputs.

**POP Biomass partitioning amongst patches and cohorts**

Stem biomass increment for each patch $\Delta C$ (kgC m$^{-2}$), is assumed equal to the grid-scale value, accumulated over the POP model time step $\Delta t(y)$.

In the original model, it was assumed that individuals capture resources in a varying proportion to their size, following a power relationship to biomass with an exponent ($s$). On this basis, annual stem biomass increment was partitioned among cohorts in proportion to the population-weighted current biomass of individuals within each cohort:

$$\frac{\Delta C_y}{\Delta t} = \sum \frac{(C_i / N_i) N_i}{\sum (C_i / N_i) N_i} \frac{\Delta C}{\Delta t} \quad (A.0)$$

where $C_i$ is the stem biomass summed across individuals of cohort $N_i$.
In the current work, gross primary production and autotrophic respiration are each passed from the host model to POP, and each is partitioned amongst patches and cohorts. Net resource uptake for each patch and cohort is evaluated as its gross primary production minus autotrophic respiration.

Gross resource uptake $\Delta C_g$ is partitioned amongst cohorts and patches in proportion to light interception, evaluated from vertical profiles of gap probabilities. These require the maximum leaf area $LAI_{\text{max}}$, inherited from the host model to be partitioned amongst patches and cohorts in proportion to sapwood area in the $y^{th}$ cohort and $p^{th}$ patch $A_{s,y,p}$:

$$LAI_{\text{max},y,p} = N_{y,p}A_{s,y,p} \frac{\sum_{i=1}^{n} N_{y,i}A_{s,y,i}}{\sum_{j=1}^{m} w_j \left(\sum_{i=1}^{n} N_{y,i}A_{s,y,i}\right)} LAI_{\text{max}} \quad \text{(A.0)}$$

Autotrophic respiration is also partitioned amongst cohorts and patches, with leaf and root carbon pools partitioned in proportion to LAI.

Stem biomass is the sum of sapwood $C_{s,y,p}$ and heartwood components $C_{h,y,p}$, with sapwood converted to heartwood at a rate $k_s = 0.05 \text{ y}^{-1}$:

$$\frac{\Delta C_{s,y,p}}{\Delta t} = \frac{\Delta C_{s,y,p}}{\Delta t} - k_s C_{s,y,p} \quad \text{(A.0)}$$

$$\frac{\Delta C_{h,y,p}}{\Delta t} = k_s C_{s,y,p} \quad \text{(A.0)}$$

The sapwood area is related to sapwood biomass and tree dimensions by:

$$A_{s,y,p} = \frac{\pi D_{s,y,p}^2}{4} - \frac{C_{s,y,p} N_{s,y,p}}{H_{s,y,p} \rho_n} \quad \text{(A.0)}$$
Sapwood area is returned to the host model, where it constrains the relative C-allocation to leaves and wood (Eq (1.0)).

Acknowledgements
The contributions of VH and PRB were made possible by the support of the Australian Science Change Program. BS acknowledges funding as an OCE Distinguished Visiting Scientist to the CSIRO Oceans & Atmosphere Flagship, Canberra.

We are grateful to Prof. Ranga Myneni and Dr. Jian Bi for the supply of GIMMS NDVI3g updated to 2013, and to Dr Randall Donohue for processing of these data for this study. This study is a contribution to the strategic research areas BECC and MERGE.

References


### Table 1: Model Parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>units</th>
<th>Value</th>
<th>Meaning</th>
<th>Equation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\theta_{S1}$</td>
<td>[$m^3 m^{-3}$]</td>
<td>Spatially variable</td>
<td>Saturated volumetric Water content (upper soil layer)</td>
<td>(1.0)</td>
<td>Section 3.1</td>
</tr>
<tr>
<td>$\theta_{S2}$</td>
<td>[$m^3 m^{-3}$]</td>
<td>Spatially variable</td>
<td>Saturated volumetric Water content (lower soil layer)</td>
<td>(1.0)</td>
<td>Section 3.1</td>
</tr>
<tr>
<td>$Z_{W1}$</td>
<td>[m]</td>
<td>0.2</td>
<td>Depth of upper soil layer</td>
<td>(1.0)</td>
<td>[Janos et al., 2008]</td>
</tr>
<tr>
<td>$Z_{W2}$</td>
<td>[m]</td>
<td>4.0</td>
<td>Depth of lower soil layer</td>
<td>(1.0)</td>
<td>[Hutley et al., 2000]</td>
</tr>
<tr>
<td>$c_{PT}$</td>
<td></td>
<td>1.26</td>
<td>Priestley-Taylor Coefficient</td>
<td>(1.0)</td>
<td>[Priestley and Taylor, 1972]</td>
</tr>
<tr>
<td>$G_o$</td>
<td>[$m s^{-1}$]</td>
<td>0.015</td>
<td>Aerodynamic Conductance</td>
<td>(1.0)</td>
<td>This work (fixed)</td>
</tr>
<tr>
<td>$\rho_{extract}$</td>
<td></td>
<td>0.421</td>
<td>Exponent in root water extraction</td>
<td>(1.0)</td>
<td>This work (calibrated)</td>
</tr>
<tr>
<td>$k_{x,g}$</td>
<td>[$m d^{-1} (mol C m^{-3})^{-1}$]</td>
<td>6.14x10^{-4}</td>
<td>Rate constant for root water extraction (grass)</td>
<td>(1.0)</td>
<td>This work (calibrated)</td>
</tr>
<tr>
<td>$k_{x,w}$</td>
<td>[$m d^{-1} (mol C m^{-3})^{-1}$]</td>
<td>6.12x10^{-4}</td>
<td>Rate constant for root water extraction (trees)</td>
<td>(1.0)</td>
<td>This work (calibrated)</td>
</tr>
<tr>
<td>$\beta$</td>
<td></td>
<td>8.88</td>
<td>exponent specifying the response of soil evaporation to upper-layer soil water</td>
<td>(1.0)</td>
<td>This work (calibrated)</td>
</tr>
<tr>
<td>$g$</td>
<td></td>
<td>1.30</td>
<td>exponent specifying the response of drainage to relative soil water</td>
<td>(1.0)</td>
<td>This work (calibrated)</td>
</tr>
<tr>
<td>$K_{S1}$</td>
<td>[$m d^{-1}$]</td>
<td>Spatially variable</td>
<td>saturated hydraulic conductivity of soil layer 1</td>
<td>(1.0)</td>
<td>See section 3.1</td>
</tr>
<tr>
<td>$K_{S2}$</td>
<td>[$m d^{-1}$]</td>
<td>Spatially variable</td>
<td>saturated hydraulic conductivity of soil layer 2</td>
<td>(1.0)</td>
<td>See section 3.1</td>
</tr>
<tr>
<td>$k_{L,g}$</td>
<td>[$d^{-1}$]</td>
<td>1/67</td>
<td>first order rate constant for leaf turnover (grass)</td>
<td>(1.0)</td>
<td>This work (calibrated)</td>
</tr>
<tr>
<td>$k_{R,g}$</td>
<td>[$d^{-1}$]</td>
<td>$k_{L,g}$</td>
<td>first order rate constant for fine root turnover (grass)</td>
<td>(1.0)</td>
<td>[Janos et al., 2008]</td>
</tr>
<tr>
<td>$k_{R,w}$</td>
<td>[$d^{-1}$]</td>
<td>1/256</td>
<td>first order rate constant for fine root turnover (trees)</td>
<td>(1.0)</td>
<td>[Vogt et al., 1995]</td>
</tr>
<tr>
<td>$b_{growth}$</td>
<td></td>
<td>6.17</td>
<td>growth scaling</td>
<td>(1.0)</td>
<td>This work (calibrated)</td>
</tr>
<tr>
<td>Parameter</td>
<td>Units</td>
<td>Description</td>
<td>Reference</td>
<td>Calibration Status</td>
<td></td>
</tr>
<tr>
<td>-----------</td>
<td>-------</td>
<td>-------------</td>
<td>-----------</td>
<td>-------------------</td>
<td></td>
</tr>
<tr>
<td>$F_{\text{growth}}$</td>
<td>[mol C m$^{-2}$ d$^{-1}$]</td>
<td>Residual growth flux to allow for regeneration from seed or resprouting</td>
<td></td>
<td>This work (calibrated)</td>
<td></td>
</tr>
<tr>
<td>$k_{\text{store}}$</td>
<td>[ ]</td>
<td>Parameter controlling contribution of flux to NSC store to growth rate</td>
<td></td>
<td>This work (fixed)</td>
<td></td>
</tr>
<tr>
<td>$p_{\text{growth}}$</td>
<td>[ ]</td>
<td>Parameter controlling steepness of soil moisture function used in growth formulation</td>
<td></td>
<td>This work (fixed)</td>
<td></td>
</tr>
<tr>
<td>$W_{\text{thresh}}$</td>
<td>[ ]</td>
<td>Relative soil moisture threshold in soil moisture function used in growth formulation</td>
<td></td>
<td>This work (calibrated)</td>
<td></td>
</tr>
<tr>
<td>$K_{\text{growth}}$</td>
<td>[ ]</td>
<td>Scaling parameter controlling rate of change of the dynamic carrying capacity.</td>
<td></td>
<td>This work (fixed)</td>
<td></td>
</tr>
<tr>
<td>$C_0$</td>
<td>[mol C m$^{-2}$]</td>
<td>Minimum carrying capacity</td>
<td></td>
<td>This work (fixed)</td>
<td></td>
</tr>
<tr>
<td>$c_{\text{growth}}$</td>
<td>[ ]</td>
<td>Growth respiration coefficient</td>
<td>(Ryan, 1991)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\alpha_Q$</td>
<td>[mol mol-quantum$^{-1}$]</td>
<td>PAR use efficiency (trees &amp; grass)</td>
<td></td>
<td>This work (calibrated)</td>
<td></td>
</tr>
<tr>
<td>$m_{\alpha,n-e}$</td>
<td>[ ]</td>
<td>Dimensionless multiplier in equation for water use efficiency, grass</td>
<td>(Singh and Misra, 1985)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$m_{\alpha,n-w}$</td>
<td>[ ]</td>
<td>Dimensionless multiplier in equation for water use efficiency, trees</td>
<td></td>
<td>This work (calibrated)</td>
<td></td>
</tr>
<tr>
<td>$k_{\text{resp}}$</td>
<td>[d$^{-1}$]</td>
<td>Rate constant for maintenance respiration</td>
<td>(Sprugel et al., 1995)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\text{ratio}_{\text{C:N,sapwood}}$</td>
<td>[gC (gN)$^{-1}$]</td>
<td>Carbon to nitrogen mass ratio in sapwood</td>
<td>(Sitch et al., 2003)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\text{ratio}_{\text{C:N,leaf}}$</td>
<td>[gC (gN)$^{-1}$]</td>
<td>Carbon to nitrogen mass ratio in leaves</td>
<td>(Sitch et al., 2003)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\text{ratio}_{\text{C:N,roots}}$</td>
<td>[gC (gN)$^{-1}$]</td>
<td>Carbon to nitrogen mass ratio in fine roots</td>
<td>(Sitch et al., 2003)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$k_{\text{LA,SA}}$</td>
<td>[ ]</td>
<td>Ratio of leaf area to sapwood cross-sectional area</td>
<td>(McDowell et al., 2002)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$c_{\text{Ext}}$</td>
<td>[ ]</td>
<td>Extinction coefficient for</td>
<td></td>
<td>This work (fixed)</td>
<td></td>
</tr>
<tr>
<td>PAR</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-----</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$A_{sl,g}$ [cm$^2$ g(DW)$^{-1}$]</td>
<td>120.0</td>
<td>Specific Leaf Area, grass (1.0)</td>
<td>Lower than the recommended values of 175 (Hutley, pers comm) to account for clumping.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2: Locations and characteristics of OzFlux sites (after Hutley et al. (2011))

<table>
<thead>
<tr>
<th>Site</th>
<th>Coordinates</th>
<th>Reference</th>
<th>Ecosystem</th>
<th>Dominant vegetation</th>
<th>Data period</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Howard Springs (HS)</td>
<td>12.4952 S 131.1501 E</td>
<td>(Beringer et al., 2003; Beringer et al., 2011)</td>
<td>Open-forest savanna</td>
<td>Eucalyptus miniata and E. tetrodonta, Sorghum intrans, S. plumosum Heteropogon triticeus grassy understorey</td>
<td>01/2001-12/2013</td>
</tr>
<tr>
<td>5. Alice Springs (AS)</td>
<td>22.283 S 133.249 E</td>
<td>(Cleverly et al., 2013)</td>
<td>Acacia woodland</td>
<td>Acacia aneura</td>
<td>09/2010-12/2013</td>
</tr>
</tbody>
</table>
Figure 1: Schematic showing the key elements of HAVANA, and the qualitative relationships between them. Carbon and water pools are represented by red boxes; fluxes by blue boxes. Blue (red) arrows show positive (negative) feed-backs. Less intuitive feed-backs are: (i) Soil water influence on growth: soil water positively impacts on total growth, while there is a negative feed-back of soil moisture on allocation to fine roots, in favour of the combined (leaf + stem) compartment; (ii) Growth responds negatively to the structural carbon store as it approaches carbon carrying capacity (Eq (1.0)); (iii) Partitioning of growth between leaf and stem is influenced by the relative magnitudes of leaf and sapwood compartments, which are constrained by the Pipe Model (Shinozaki et al., 1964), in which sapwood cross-sectional area is assumed to be a constant proportion of total leaf area.
Figure 2. (i) Map of 1000 points representative of the study area, and locations of flux sites (red dots) for use in calibration/validation. Flux site abbreviations are given in Table 2; (ii) latitudinal variation of mean annual precipitation (1900-2013) and (iii) latitudinal variation of fire frequency and fraction of fires occurring in the early part of the dry season (pre-August) (1989-2011). Each point represents a spatial average across ~65 points lying within a latitude bin of width 0.57°, with error bars representing one standard deviation.
Figure 3: Monthly (2005-2013) time-series of (i) ET, (ii) fPAR and (iii) GPP at five flux stations: HAVANA-POP (stacked plots); BIOS2 (full biogeochemical model with prescribed vegetation cover) and observations. HAVANA-POP ET is partitioned into soil evaporation and transpiration from each of the upper (1) and lower (2) soil layers. HAVANA-POP fPAR and GPP are partitioned into tree and grass components. Flux site abbreviations (left of figure) are given in Table 2.
Figure 4: Scattergrams of model predictions vs observations of monthly values at 5 Flux Sites of (i) ET; (ii) GPP; (iii) fPAR. (a) HAVANA-POP and (b) CABLE in BIOS2, a full biogeochemical model with prescribed phenology and vegetation cover.
Figure 5: Time-averaged (1964–2013) HAVANA-POP output variables: variation with rainfall and comparison with observation-based estimates. (i) Gross primary production (combined tree and grass components) and comparison with mean annual GPP from flux data (averaged over observation period); (ii) Annual average tree foliage projected cover and comparison with Williams et al. (1996); (iii) tree basal area and comparison with Williams et al. (1996); (iv) Dry season tree LAI (September 2008) and comparison with Sea et al. (2011) estimated from digital hemispheric photography (DHP) and the MODIS Collection 5 product (MODC5).
Figure 6a: Monthly time series (2009-2014) of (i) soil moisture ($w_1$ and $w_2$); (ii) ET; (iii) leaf area index (LAI) (iv) FPAR and (v) GPP, as predicted by HAVANA-POP. Corresponding observed FPAR is also shown. Each row represents a spatial average over the randomly sampled gridcells (Figure 2(i)) falling within the range of mean annual precipitation shown on the left.
Figure 6b: Monthly mean time series (2009-2014) of (i) NPP, growth and change in storage (grass); (ii) NPP, growth and change in storage (trees); (iii) leaf and fine root carbon pools (grass); (iv) leaf and fine root carbon pools (trees); (v) C allocation coefficients to leaves and fine roots (grass); (vi) C allocation coefficients to leaves, fine roots and stems (trees). Spatial aggregation is the same as in Figure 6a.
Figure A1: HAVANA-POP coupling