RESEARCH ARTICLE

Key Points:
- An optimality model incorporating ecohydrological theory can predict long-term average steady state leaf area index
- Terrestrial vegetation models could incorporate this approach to improve leaf area index predictions

Applying the Concept of Ecohydrological Equilibrium to Predict Steady State Leaf Area Index

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Abstract Leaf area index (LAI) is a key variable in modeling terrestrial vegetation because it has a major impact on carbon and water fluxes. However, several recent intercomparisons have shown that modeled LAI differs significantly among models and between models and satellite-derived estimates. Empirical studies show that LAI is strongly related to precipitation. This observation is predicted by the ecohydrological equilibrium theory, which provides an alternative means to predict steady state LAI. We implemented this theory in a simple optimization model. We hypothesized that, when water availability is limited, plants should adjust steady state LAI and stomatal behavior to maximize net canopy carbon export, under the constraint that canopy transpiration is a fixed fraction of total precipitation. We evaluated the predicted LAI (L_{opt}) for Australia against ground-based observations of LAI at 135 sites and continental-scale satellite-derived estimates. For the site-level data, the root-mean-square error of predicted L_{opt} was 1.07 m^2 m^{-2}, similar to the root-mean-square error of a comparison of the data against 9-year mean satellite-derived LAI (L_{sat}) at those sites. Continentally, L_{opt} had an R^2 of 0.7 when compared to L_{sat}. The predicted L_{opt} increased continental-wide with rising atmospheric [CO_2] over 1982–2010, which agreed with satellite-derived estimations, while the predicted stomatal behavior responded differently in dry and wet regions. Our results indicate that long-term equilibrium LAI can be successfully predicted from a simple application of ecohydrological theory. We suggest that this theory could be usefully incorporated into terrestrial vegetation models to improve their predictions of LAI.

1. Introduction

Leaf area index (LAI; or L in equations) is a key biophysical variable in terrestrial biosphere models (TBMs), as it determines the exchange of carbon and water between the vegetation and the atmosphere. However, current TBMs systematically overestimate LAI when compared to satellite-derived estimates (Anav et al., 2013; Mahowald et al., 2016; Murray-Tortarolo et al., 2013). At individual sites, recent model intercomparisons have shown that there is a sizable spread among models (>4 m^2 m^{-2}) in predicted maximum LAI (Medlyn et al., 2016; Walker et al., 2014). Models also disagree about the size of the projected change in LAI in response to warming and increasing atmospheric carbon dioxide (C_a; De Kauwe et al., 2014; Mahowald et al., 2016). Typically, these models predict LAI as the outcome of leaf growth (dependent on net primary productivity, its allocation to leaves, and leaf mass per area) and turnover processes (usually constant input parameters). Uncertainty across models arises from differences in the way these processes are implemented, reflecting a lack of mechanistic understanding of the controls of these processes (De Kauwe et al., 2014).

An alternative approach that could be used to predict LAI is based on the idea of ecohydrological equilibrium: the LAI comes into equilibrium with the water availability at a given location (Eagleson, 1982). There is strong empirical support for a relationship between LAI and water availability especially in evergreen ecosystems. In *Eucalyptus*-dominated ecosystems in Australia, Specht and Specht (1989) found a strong ($R^2 = 0.8$) relationship between LAI and an evaporative coefficient, represented as relative evapotranspiration/precipitation. Similarly, Ellis and Hatton (2008) reported a linear relationship between LAI and precipitation ($R^2 = 0.8$) across eucalypt woodlands in southern Australia. Donohue et al. (2013) demonstrated a strong correlation between precipitation and satellite-derived maximum foliage coverage in dry regions of Australia. Across rainfall gradients of California, USA, Jin and Goulden (2014) analyzed precipitation and satellite-derived absorbed photosynthetically active radiation (Q_{APAR}; generally assumed to be proportional to LAI) and found a saturating relationship with the sensitivity of Q_{APAR} to precipitation

being higher in drier regions. Globally, Iio et al. (2014) reported a strong LAI correlation with wetness index (precipitation/potential evapotranspiration [PET]) in dry regions, although the relationships varied with plant functional types (R varying from 0.13 to 0.57).

There have been relatively few attempts to incorporate this well-understood control on LAI into vegetation models. Woodward (1987) was the first to apply the idea of ecohydrological equilibrium in a large-scale model, predicting equilibrium LAI (L_{equ}) from considerations of water and energy balance. In his approach, transpiration was calculated using the Penman-Monteith equation, in which increasing LAI was assumed to increase both canopy absorbed radiation and surface conductance. L_{equ} was given by the maximum value of LAI for which transpiration is less than incoming precipitation. Thus, L_{equ} maximized the absorbed radiation subject to the constraint of water availability. Since this calculation was based only on energy and water balance, it did not predict any change in L_{equ} with rising C_a.

Nemani and Running (1989) also used this theory to predict L_{equ} at stand scale. These authors used the FOREST-BGC model and empirical data to estimate the baseline transpiration and associated L_{equ} in one experimental pine stand in Montana, USA. They then modeled transpiration for 20 other similar stands and, by assuming the L_{equ}-transpiration relationship is constant, predicted L_{equ} for each stand. They found a strong correlation with the observed LAI ($R^2 = 0.87$). However, this approach cannot be applied more broadly, since the relationship between transpiration and L_{equ} will vary with ecosystem type.

Kergoat (1998) suggested that a combination of water and carbon limitations would predict more realistic L_{equ} than consideration of water limitation alone and included two constraints on L_{equ}: (i) Plant transpiration (a function of both stomatal conductance [g_s] and LAI) must not deplete soil moisture below a critical point, and (ii) the bottom layer of the canopy must have a positive carbon balance. L_{equ} was then predicted as the maximum LAI that satisfies these constraints. The predicted L_{equ} captured the LAI variation by biome globally, and the associated runoff matched observations in 28 sites. Kergoat (2002) expanded the model in Kergoat (1998) by additionally accounting for the construction cost of leaves and reported improved accuracy as compared to satellite-derived LAI. The approach proposed by Kergoat (2002) has not been widely adopted, possibly because of computational demands of a daily optimization.

Beerling and Woodward (2001) incorporated L_{equ} as a component of Sheffield Dynamic Global Vegetation Model (SDGVM). The L_{equ} in SDGVM was based on similar carbon constraints as Kergoat (2002) but differed in the water balance constraint: They assumed that plant transpiration should be less than the precipitation reaching the ground. They also avoided the need to iterate by calculating LAI from the water and carbon balances of the previous year in a multiyear simulation. Woodward and Lomas (2004) validated the LAI predicted by SDGVM against optical measurements from the FLUXNET network and found a strong correlation ($R^2 = 0.8$) across 52 sites. The L_{equ} model in SDGVM is more practical than the Kergoat models because of the simplification of water balance calculation. The goodness of fit of SDGVM L_{equ} to observations suggested that such a simplification may be reasonable and necessary considering the limitation in computational capacity. However, some recent applications of the SDGVM model have found it to significantly overestimate LAI at specific sites (De Kauwe et al., 2017; Medlyn et al., 2016).

One feature common to all the models described above is that the g_s response to drying soil is fixed. However, there is increasing empirical evidence to suggest that there are important differences in plant stomatal behavior across ecosystems and climatic zones (Lin et al., 2015). We take an alternative approach to predicting the ecohydrological equilibrium, based on the MATEY (Model Any Terrestrial Ecosystem–Yearly) model proposed by McMurtrie et al. (2008). In the original MATEY model, plants are assumed to maximize net carbon export by regulating both g_s and LAI, subject to the constraint that evapotranspiration cannot exceed a given fraction of incoming precipitation. The MATEY model thus optimizes both LAI and g_s at the same time. McMurtrie et al. (2008) evaluated their model at two forest stands but not on larger scales. We identified that a potential issue of optimizing both g_s and LAI is that the variabilities of g_s and LAI are on different temporal scales (minutes versus weeks). Hence, we characterized the variability of g_s using a model of stomatal behavior in which variation is represented by the stomatal slope parameter g_1 (equation (S7) in the supporting information; Medlyn et al., 2011; Prentice et al., 2014). The term g_1 is related to the water cost per unit carbon gain introduced by Cowan and Farquhar (1977) and is similar to the fitted slope in the widely used Ball-Berry model (Ball et al., 1987).
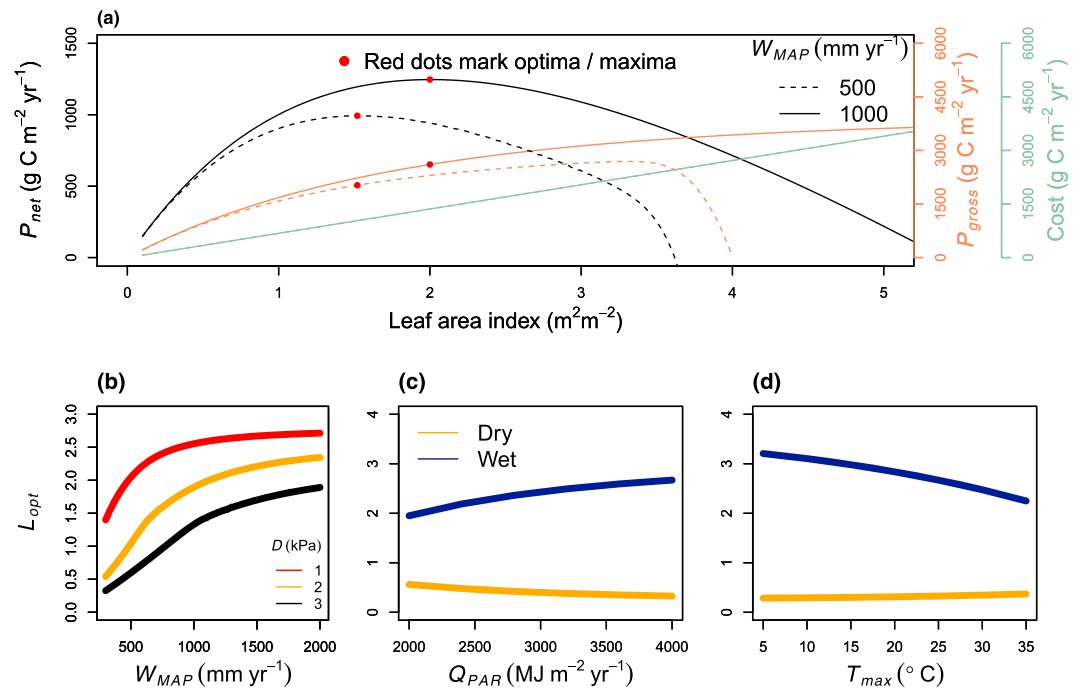
Figure 1. Model behavior and sensitivity. (a) Two examples of how model optima are obtained for two mean annual precipitation scenarios, W_{MAP} (500 and 1,000 mm; solid lines and dashed lines, respectively). Other inputs are set to $D = 1.5$ kPa, $Q_{PAR} = 3,000$ MJ PAR m^{-2} yr^{-1}, and $T_{max} = 25$ °C. The orange lines indicate gross primary production (P_{gross}, scale on right-hand axis); the green lines indicate foliage cost (scale on right-hand axis); the black lines indicate canopy net carbon export (P_{net}), which equals $P_{gross} - C_{total}$ (equation (7)). Sensitivity of predicted L_{opt} to climate factors for two scenarios: dry ($W_{MAP} = 300$ mm yr^{-1}; $D = 3$ kPa) and wet ($W_{MAP} = 1,500$ mm yr^{-1}; $D = 1$ kPa). (b) The relationship of L_{opt} to mean annual precipitation (W_{MAP}) for three values of vapor pressure deficit (D). Mean annual photosynthetically active radiation (Q_{PAR}) and mean annual maximum temperature of each month (T_{max}) were fixed to 4,000 MJ m^{-2} yr^{-1} and 25 °C, respectively. (c and d) The impact of Q_{PAR} and T_{max} in conditions, respectively.

Here we investigate whether this optimality theory can successfully predict LAI across the Australian continent. Following McMurtrie et al. (2008) we take the approach of implementing the theory as simply as possible, applying a minimal set of equations to predict the long-term equilibrium. This approach allows us to focus on evaluating the performance of the theory independent of other model assumptions. Success of this simple parsimonious approach would indicate that the theory could usefully be incorporated into TBMs as an alternative to existing foliage carbon allocation schemes. We chose Australia as an example to evaluate the applicability of the concept of ecohydrological equilibrium because abundant and high-quality data are available for model construction (i.e., plant physiology and meteorology) and evaluation (i.e., g_1 and LAI data). In addition, Australia is dominated by evergreen ecosystems, for which the steady state approach is more easily interpreted. Utilizing the theory to predict LAI of deciduous ecosystems would require an additional set of assumptions regarding phenology (e.g., Caldararu et al., 2014).

The goal of this research is thus to explore the capacity of ecohydrological equilibrium theory to predict LAI at large scales. The outcome from this study should indicate whether incorporation of this theory is a potential avenue to improve the foliage carbon allocation schemes in existing TBMs. We tested several alternative implementations of the theory, identified the best-performing model, and evaluated the predictions against in situ data and satellite-derived estimates for Australia. To test its capacity to predict LAI in novel environmental conditions, we also used the model to predict the recent trend in LAI with the increase in atmospheric carbon dioxide and compared the predictions to satellite-derived observations.

2. Materials and Methods

2.1. Model

The model is a variant of the MATEY model (McMurtrie et al., 2008). It optimizes canopy net carbon export (P_{net}; g C m^{-2} yr^{-1}), the difference between canopy production and leaf construction and respiration

costs, for a given long-term climate, which is specified by the atmospheric CO_2 concentration (C_a; μmol mol^{-1}), mean annual precipitation (W_{MAP}; mm yr^{-1}), vapor pressure deficit (D; kPa), and annual total photosynthetically active radiation (Q_{PAR}; MJ PAR m^{-2} yr^{-1}). P_{net} is optimized based on a trade-off between LAI (m^2 m^{-2}) and water use per unit leaf area, here represented by g_1 (kPa$^{0.5}$), the stomatal slope parameter (Medlyn et al., 2011). In the original MATEY model (McMurtrie et al., 2008), the optimization was a trade-off between LAI and stomatal conductance (g_s; mol H$_2$O m^{-2} s^{-1}). Here instead of using g_s directly, we model g_s as a function of the carbon assimilation rate, g_1, D, and C_a, with the optimal stomatal behavior model of Medlyn et al. (2011). We chose to use g_1 because (i) g_1 is related to plant water cost per unit carbon gain (Cowan & Farquhar, 1977; Medlyn et al., 2011) and thus combines the impacts of plant physiology, genetics, and prior environmental conditions; (ii) g_1 is less temporally variable than g_s (Lin et al., 2015). A further difference from the original MATEY model is that our model considers the cost of foliage (both construction and maintenance), modeled as a function of LAI instead of being a fixed fraction of production (McMurtrie et al., 2008).

The trade-off between LAI and g_1 in the model is represented by the responses of light use efficiency (ε_l; g C MJ^{-1}), water use efficiency (ε_w; g C mm^{-1}), the foliage cost per unit ground area (C_{total}; g C m^{-2} ground), and the absorbed photosynthetically active radiation (Q_{APAR}; MJ PAR m^{-2} yr^{-1}). Increasing LAI not only increases the fraction of absorbed Q_{PAR} and the transpiration fraction but also adds to C_{total}, while increasing g_1 enhances ε_l but reduces ε_w. The total possible transpiration is set by W_{MAP} and the transpiration fraction, leading to a negative relationship between LAI and g_1. As a result, there are optimal values of LAI and g_1 (L_{opt} and $g_{1.opt}$) that maximize P_{net} under a given W_{MAP} (Figures 1 and 2). This L_{opt} is different from the L_{equ}, which is based on eco-hydrological equilibrium, by incorporating optimization. All symbols are defined at first use and again in Table S1 in the supporting information. Equations are defined in the following paragraphs and Text S1 in the supporting information. The model assumes the same equations and parameters for all plant functional types. Alternative assumptions were tested in developing the model (Appendix A) but showed little improvement of the prediction and were thus not incorporated for parsimony.

The water constraint in the model is represented by W_T (plant transpiration; mm yr^{-1}), which was assumed to be a fraction of evapotranspiration following (Wang et al., 2014):

$$W_T = a_T \cdot L^{b_T} \cdot W_{ET} \tag{1}$$

where a_T and b_T are fitted parameters from Wang et al. (2014), with values of 0.77 and 0.1, respectively; L is LAI (m^2 m^{-2}). W_{ET} is evapotranspiration (mm yr^{-1}), which is related to mean annual precipitation following Zhang et al. (2001):

$$W_{ET} = \frac{W_{MAP} + 2 \cdot c_w}{1 + \frac{2 \cdot c_w}{W_{MAP}} + \frac{W_{MAP}}{c_w}} \tag{2}$$

where W_{MAP} is the mean annual precipitation (mm yr^{-1}) and c_w is an empirical constant (fitted PET) in Zhang et al. (2001), with data for forest ecosystems. Our model here differs from McMurtrie et al. (2008), who assumed that a constant fraction (0.8) of rainfall was used by the plant. We used the more complicated calculation of transpiration because (i) transpiration can be less than half of total evapotranspiration (Kool et al., 2014; Sutanto et al., 2012; Wang et al., 2010; Wang & Dickinson, 2012; Yepez et al., 2005) (ii) and the fraction of transpiration in evapotranspiration is related to vegetation cover (Liu et al., 2017). The impacts of using these functions on the prediction are shown in Appendix A1.

The canopy carbon uptake is related to transpiration by the water use efficiency:

$$P_{gross} = \varepsilon_w \cdot W_T \tag{3}$$

where P_{gross} is gross primary production (g C m^{-2} yr^{-1}); ε_w is the transpiration efficiency (g C kg^{-1}), calculated following Medlyn et al. (2011; equation (S1)). P_{gross} calculated with water limitation has to equal to that calculated with absorbed radiation:

$$P_{gross} = \varepsilon_l \cdot Q_{APAR} \tag{4}$$
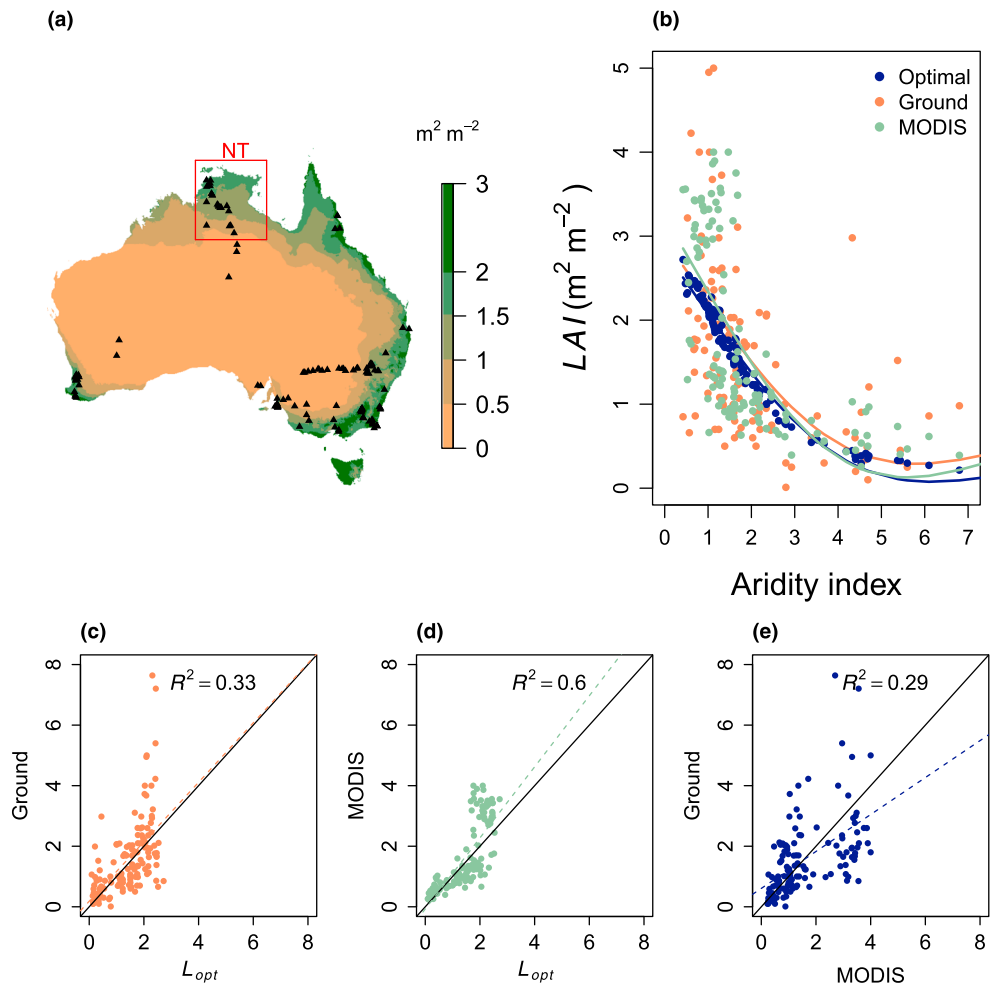
Figure 2. Optimal equilibrium leaf area index (LAI; L_{opt}) plotted against AI (aridity index; potential evapotranspiration over mean annual precipitation). (a) L_{opt} for Australia, with site locations marked by triangles. The red square marks Northern Territory region discussed in section 3.3 and shown in Figure 4. (b) The mean of optimal, ground, and Moderate Resolution Imaging Spectroradiometer (MODIS) LAI of each site ($n = 135$) plotted against AI. The smooth lines are generalized additive model fits. Linear regressions are shown for (c) ground versus L_{opt}, (d) MODIS versus L_{opt}, and (e) ground versus MODIS with R^2. The 1:1 line is shown by a solid line, while the colored, dashed lines are regression fits.

where ε_l is light use efficiency (g C MJ^{-1} PAR), estimated with the model of Sands (1995,1996; equations (S2)–(S7)), and Q_{APAR} (absorbed photosynthetically active radiation; MJ PAR m^{-2} yr^{-1}) of the canopy is related to LAI by the Beer-Lambert law (equation (S8)). This Q_{APAR} is the long-term average value: The model does not consider interannual and intraannual variation of climate conditions or of LAI. The responses of ε_l to T_{max} and D are described in equations (S4)–(S6) following Bernacchi et al. (2001), Medlyn et al. (2002), Medlyn et al. (2007), and Medlyn et al. (2011).

Equations (3) and (4) are the key equations describing the water and light constraints in the model and the trade-off between g_1 and LAI. Combining equations (3) and (4), g_1 can be solved as a function of LAI. As a result, P_{gross} can be calculated as an implicit function of LAI, which is solved by iteration. The carbon cost of building leaves is given by C_{total}, which includes the maintenance respiration, construction respiration, and construction cost per unit ground area (g C m^{-2} yr^{-1}), defined as a function of LAI:

$$C_{\text{total}} = c_r \cdot R_m \cdot L + C_{\text{cost}} \cdot L \tag{5}$$

where c_r converts μmol C m^{-2} s^{-1} to g C m^{-2} yr^{-1}; R_m is maintenance respiration per unit leaf area (μmol m^{-2} s^{-1}); C_{cost} is the carbon cost of construction, including construction respiration per unit leaf

area (g C m^{-2} leaf). To estimate R_m, we used the Australian subset of the GLOBRESP data set (Atkin et al., 2015) and took the mean across available data. We assumed that the rate of respiration acclimates to the prevailing mean temperature and thus the value for R_m is taken to be a constant. We also considered two alternative assumptions for R_m, namely, a relationship with W_{MAP} or a relationship with leaf mass per area. The effects of these alternative assumptions are shown in Appendices A2 and A3.

The construction cost, C_{cost}, is calculated as

$$C_{cost} = c_c \cdot b_c \cdot \frac{M_{area}}{t_f} \tag{6}$$

where c_c is the assumed proportion of carbon in dry mass (0.5 g C g^{-1} DM) and b_c is the construction respiration ratio (g C g^{-1} C). Villar and Merino (2001) reported a mean cost of 1.66 g of glucose per gram of dry mass for xeric forest. Assuming half of the dry mass is carbon and 40% of the glucose is carbon, we calculated the fraction of construction respiration (b_c) to be 1.3 (g C g^{-1} C). M_{area} is leaf mass per area (g DM m^{-2} leaf), and t_f is the leaf lifespan (year). The values of M_{area} and t_f were taken as the mean from the GLOPNET data set (Wright et al., 2004; values are given in Table S1).

The model also relies on J_{max}, the maximum electron transport rate. We compiled a data set of Australian observations from the literature (Ali et al., 2015; De Kauwe et al., 2016; Walker et al., 2014; data available in Table S5) and tested for relationships with climate. J_{max} was not correlated with any climate factor used in the model (Figure S1 in the supporting information). Thus, we used the mean of the measurements from the data set. Similar to R_m, the temperature dependence of J_{max} is not included in the model.

The optimization target of the model, canopy net carbon export (P_{net}; g C m^{-2} yr^{-1}), is then defined as the difference between production and cost:

$$P_{net} = P_{gross} - C_{total} \tag{7}$$

2.2. Data

The model was applied to predict L_{opt} and $g_{1.opt}$ using gridded climate data and was evaluated against ground-based measurements (stand level) as well as satellite-derived estimates (0.06-degree grid). L_{opt} and $g_{1.opt}$ were evaluated together for 10 sites where both measurements were available. To minimize anthropogenic effects, evaluation of the model at the continental scale was constrained to natural reserves.

2.2.1. Climate Inputs

Potential evapotranspiration (mm yr^{-1}), W_{MAP}, actual vapor pressure, Q_{PAR}, and T_{max} are obtained from Ecosystem Modeling and Scaling Infrastructure (Whitley et al., 2014). We selected a 21-year period, 1991–2011, matching the satellite record (2000–2011). For computational efficiency, the climate data (0.01° native resolution) were aggregated to 0.06°. D was calculated as the difference of saturation vapor pressure and actual vapor pressure with the former being a function of T_{max}. We also calculated an aridity index (AI), defined as PET/W_{MAP}. All the other gridded data sets in the following sections were aggregated to match the climate grids (0.06°). We used the long-term (21-year) mean of the four inputs for each grid cell. Plots of W_{MAP}, D, Q_{PAR}, and T_{max} are shown in Figure S2. The model predicted a paired L_{opt} and $g_{1.opt}$ for each grid cell with no temporal variation.

2.2.2. Ground-Based Data

Ground-based LAI and g_1 data were used for evaluation. Ground-based LAI measurements were taken from six sources: Ellis & Hatton (2008; 37 sites), Zeppel et al. (2008; one site), Mitchell et al. (2009; one site), Iio et al. (2014; 134 sites), Duursma et al. (2016; one site), and eight sites from the Terrestrial Ecosystem Research Network (TERN; Beringer & McHugh, 2015a, 2015b; Bradford, 2015; Eamus & Cleverly, 2015a, 2015b; Liddell & Laurance, 2015; Prober & Macfarlane, 2013; Prober & Macfarlane, 2015; Rowlings & Grace, 2015; van Gorsel, 2015). For sites that are close together (<0.01°), the mean of the reported LAI values was taken, giving a total of 135 sites. Both Duursma et al. (2016) and the data from TERN used the estimated gap fraction to estimate the LAI of the canopy. As a result, both data sets are plant area index. The data from Ellis and Hatton (2008) were a synthesis and thus the methods used to estimate LAI varied by source. Iio et al. (2014) synthesized a similar data set with various methods to estimate LAI but reported ecosystem LAI (sum of understory and canopy) instead of canopy when possible. Notably, the understory LAI could be as

high as canopy, and thus, these LAI measurements were likely underestimates. There are some notable inconsistencies among sources regarding their methodology: plant versus LAI, different methods to correct leaf clumping, and canopy versus ecosystem LAI. Moreover, the measurements are on stand level and are not scaled to the spatial resolution of satellite-derivatives and the modeled LAI. These LAI data were mostly one-time measurements and thus could not represent intraannual and interannual LAI variations. Corresponding ground-based g_1 values were estimated from in situ leaf gas exchange measurements at the top of the canopy (Cernusak et al., 2011; Gimeno et al., 2016; Kelly, 2013; Medlyn et al., 2007; Mitchell et al., 2009; Zeppel et al., 2008), which were available for 10 of these sites (Table S4). Values were estimated from data using the "fitBB" routine (R package "plantecophys"; Duursma, 2015), which uses the nonlinear least squares method to fit g_1 to measurements of stomatal conductance, photosynthesis, and environmental variables.

2.2.3. Satellite-Derived LAI Data

To evaluate the model's performance at large spatiotemporal scales, we used the satellite-derived LAI product, MODIS (Moderate Resolution Imaging Spectroradiometer; Knyazikhin et al., 1999). The 8-day MODIS LAI (collection 5; MOD15A2) tiles for Australia were mosaicked and reprojected from their native sinusoidal projection to a regular latitude-longitude grid (GDA94; see Paget & King, 2008). The LAI estimates were averaged for the period 2000 to 2011. Only LAI data estimated from the main radiative transfer algorithm and deemed to be of the best quality (i.e., no cloud contamination or saturation data used; quality assurance flag = 0) were used.

2.2.4. Land Cover, Soil Attribute, and Digital Elevation Maps

The model used land cover type information taken from Australian Bureau of Agricultural and Resource Economics and Sciences product, National scale land use version 4 (2005–2006; http://www.agriculture.gov.au/abares/aclump/Pages/land-use/data-download.aspx). The soil attribute maps with total nitrogen (N_{soil}; %) and phosphorus (P_{soil}; %) of the top layer (0–5 cm) were obtained from CSIRO (Viscarra Rossel et al., 2014a, 2014b). The N_{soil} and P_{soil} data represented the total N and P in the soil and were aggregated from a native resolution (0.00083°) to 0.06°. The soil attributes were used for the statistical analysis of the importance of soil nutrients for LAI. We used the digital elevation model version 3 and flow direction grid 2008 obtained from Geoscience Australia (http://www.ga.gov.au/metadata-gateway/metadata/record/66006/).

### 2.2.5. Statistical Benchmark and Model Evaluation

We derived a statistical bench mark (Abramowitz, 2005) for the model by a generalized additive model (GAM) fitting LAI measurements as a function of climate. The fitting used a cubic spline basis with no interaction. This benchmarking is important because it quantifies the explanatory power of climate for LAI. We compared the model performance to this bench mark in order to determine how much of the information contained in the inputs is captured by the model.

We evaluated the model first at site level with measurements of both LAI and g_1. Then, we compared predicted L_{opt} to satellite derivatives at the scale of the whole continent, and for a sample region in the Northern Territory where there is a natural rainfall gradient spanning ~1,700 to ~300 mm (1 mm km^{-1}; Cernusak et al., 2011). The predictions should be linearly related to the observations if the model captures the key processes. Assessment of observed increase of LAI in response to rising C_a was done using Advanced Very High Resolution Radiometer NDVI (1982–2010; cf. Donohue et al., 2013). We applied the model to predict the response of L_{opt} and $g_{1.opt}$ to this increase in C_a (holding long-term mean climate constant) and evaluated the predicted response of L_{opt} against these observations.

3. Results

3.1. L_{opt} Sensitivity to Climate

Predicted L_{opt} was driven primarily by W_{MAP} and D, with Q_{PAR} and T_{max} modifying the results to a lesser extent. The impact of W_{MAP} was explained by the fact that the rainfall gradient (more than 20-fold) across Australia is much larger than that of D, Q_{PAR}, or T_{max} (see Figure S2). The influence of D is the result of the sensitivity of light use efficiency to D. Assuming fixed D, Q_{PAR}, and T_{max}, and at a given W_{MAP}, P_{gross} showed a humped relationship with LAI due to the trade-off with g_1; the peak occurred much earlier at lower W_{MAP} (orange lines in Figure 1a). Cost increases linearly with increasing LAI and does not vary with W_{MAP} (green line in Figure 1a). The optimum P_{net} is reached when the difference between P_{gross} and cost is maximized (shown as red dots). The predicted sensitivity (slope) of L_{opt} to W_{MAP} was stronger at low W_{MAP} and at low D, both of
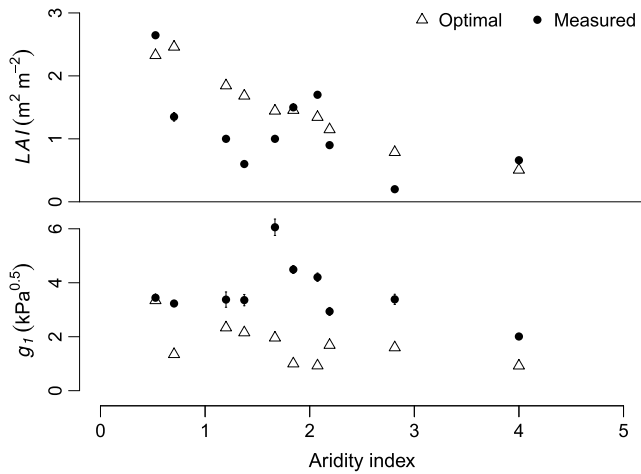
Figure 3. Optimal steady state leaf area index (L_{opt}) and g_1 ($g_{1.opt}$) compared with data from sites across Australia. The error bars show standard errors of measurements.

which suggested more severe water limitation (Figure 1b). Q_{PAR} increased L_{opt} when water was abundant but slightly decreased L_{opt} as water became limiting (Figure 1c; see equations (4) and (S3)). T_{max} reduced L_{opt} when water was abundant but slightly increased L_{opt} under water limitation (Figure 1d; see equation (S5)).

3.2. Site-Scale Evaluation of L_{opt}

Figure 2a shows L_{opt} for Australia and locations of site-scale LAI measurements. L_{opt} was predicted to decrease with increasing AI (Figure 2b). This response to water availability was consistent with both ground-based and satellite-derived (MODIS) estimates. Both predicted L_{opt} and MODIS were evaluated against ground-based measurements. L_{opt} had equivalent root-mean-square error (1.066 versus 1.170 m^2 m^{-2}) but more negative bias (mean of the difference between model and observations; -0.158 versus 0.016 m^2 m^{-2}) than MODIS, suggesting that the model tended to underpredict in situ estimates, while MODIS was both higher and lower than ground data. Overall, L_{opt} values were of a similar accuracy to satellite estimates when compared to in situ measurements. L_{opt} correlated well with in situ LAI (Figure 2c; $R^2 = 0.33$), suggesting that despite the difference in scales between measurements and predictions, in situ LAI may not deviate much from the long-term equilibrium. L_{opt} predictions were also consistent with satellite-derived values (Figure 2d; $R^2 = 0.6$). L_{opt} had a nonlinear relationship with both sets of measurements, showing that the model performance is close to measurements at low values of LAI but it tends to underpredict at high values of LAI. The model had comparable R^2 values to statistical bench mark (GAM fits) of MODIS LAI for the sites (0.6 compared to 0.77; Table S2) but worse to that of the situ measurements and climate (0.33 compared to 0.68; Table S2). This better agreement with satellite-derived values than with in situ measurements is most likely to be due to a more consistent spatial sampling footprint between satellite and modeled data (0.06° or ~6 km).

Since the prediction of L_{opt} is balanced with g_1 in the model, we also examined the optimal g_1 ($g_{1.opt}$) and in situ estimates to probe our results further (Figure 3; site details in Table S4). Measured LAI and g_1 both declined with increasing AI. Predicted L_{opt} and $g_{1.opt}$ tracked this decline in measured values. The model tended to overpredict LAI but systematically underpredict g_1.

3.3. Continental Evaluation

To evaluate model behavior at larger scales, we compared L_{opt} to satellite-derived estimates across Australian natural reserves (Figure 4a). Predicted L_{opt} captured the 9-year average from MODIS with an R^2 of 0.7, a bias of -0.022 (m^2 m^{-2}), and a root-mean-square error of 0.370 (m^2 m^{-2}). The model tended to slight overpredict LAI in most regions relative to the satellite-derived estimates and underpredict only at extreme wet coastal spots and at extreme dry center (Figure 4a). Again, the model had comparable R^2 values to the statistical bench mark of MODIS LAI and climate (0.7 versus 0.81; Table S2). The nonlinear relationship in Figure 4b was consistent with the site-scale evaluation (Figure 2). Similar to the continental-wide pattern, L_{opt} was lower than MODIS at the extreme dry and wet sites in Northern Territory (Figure 4c). However, at the same MODIS LAI, the relative difference was smaller in the drier regions (higher AI; red versus blue dots in Figure 4d).

3.4. Change in L_{opt} With Elevated C_a

To evaluate the modeled LAI response to the recent increase in C_a (340 to 389 μmol mol^{-1}), we compared the predictions against Donohue et al. (2013), who calculated the change of the slope of LAI against W_{MAP} in the driest areas ($W_{MAP} < 400$ mm yr^{-1}) and found a 11.3% increase. We followed the same methodology and found the model predicted a 14.8% increase of slope. The predicted L_{opt} responses depended on water availability: L_{opt} remained relatively insensitive to C_a in wet areas, while it increased by up to 20% in dry areas (Figure 5a). We then used the model to predict the response to future changes (a doubling of C_a from 340 to 680 μmol mol^{-1}). The impact of future CO$_2$ fertilization on model predictions was also determined by water availability: In the mesic regions (e.g., $W_{MAP} = 1,200$ mm; $D = 0.5$ kPa), a doubling of C_a (340 to
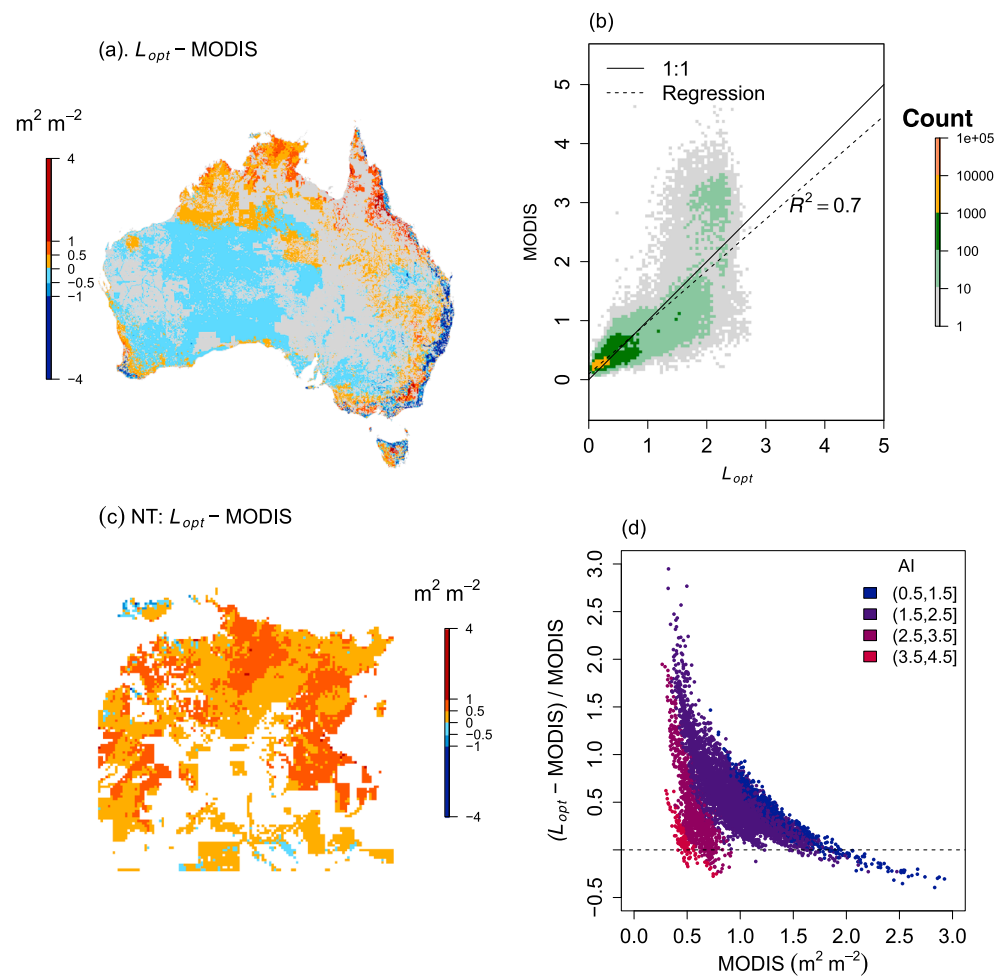
Figure 4. L_{opt} for Australian natural reserves compared to satellite products. (a) L_{opt} for natural reserves across Australia (gray indicates nonreserves). (b) Moderate Resolution Imaging Spectroradiometer (MODIS) versus L_{opt} with color-marked density. (c) The difference between L_{opt} and MODIS leaf area index (LAI) for Northern Territory (NT) natural reserves. (d) Relative difference between L_{opt} and MODIS LAI of NT, as function of MODIS LAI, with colors indicating aridity index.

680 μmol mol^{-1}) raised L_{opt} by ~20% compared to a >100% increase in xeric regions (e.g., W_{MAP} = 400 mm; D = 3 kPa; Figure 5b).

We also examined how $g_{1.opt}$ is predicted to change with increased C_a (340 to 389). On average, $g_{1.opt}$ was predicted to be reduced by ~7.98% (change of geometric mean) across Australia (Figure 5c), but the direction of change differed in dry versus wet areas. In dry areas, elevated C_a reduced $g_{1.opt}$ (blue region in Figure 3c and orange lines in Figure 3d), while in wet areas, $g_{1.opt}$ was predicted to increase (~20%) increased with rising C_a (red region in Figure 3c and blue lines in Figure 3d). Since the predicted percentage increase of LAI and g_1 to elevated C_a was nearly linear in both dry and wet conditions (Figures 5b and 5d, dashed lines), responses of LAI and g_1 to rising C_a should follow the current trajectories at least to C_a ~680 μmol mol^{-1}.

4. Discussion

4.1. Model Performance

Predicting LAI is an important yet challenging step in the simulation of carbon and water fluxes, especially under climate change and rising C_a. We found that a parsimonious optimality model incorporating the concept of ecohydrological equilibrium could successfully predict long-term average LAI across the Australian
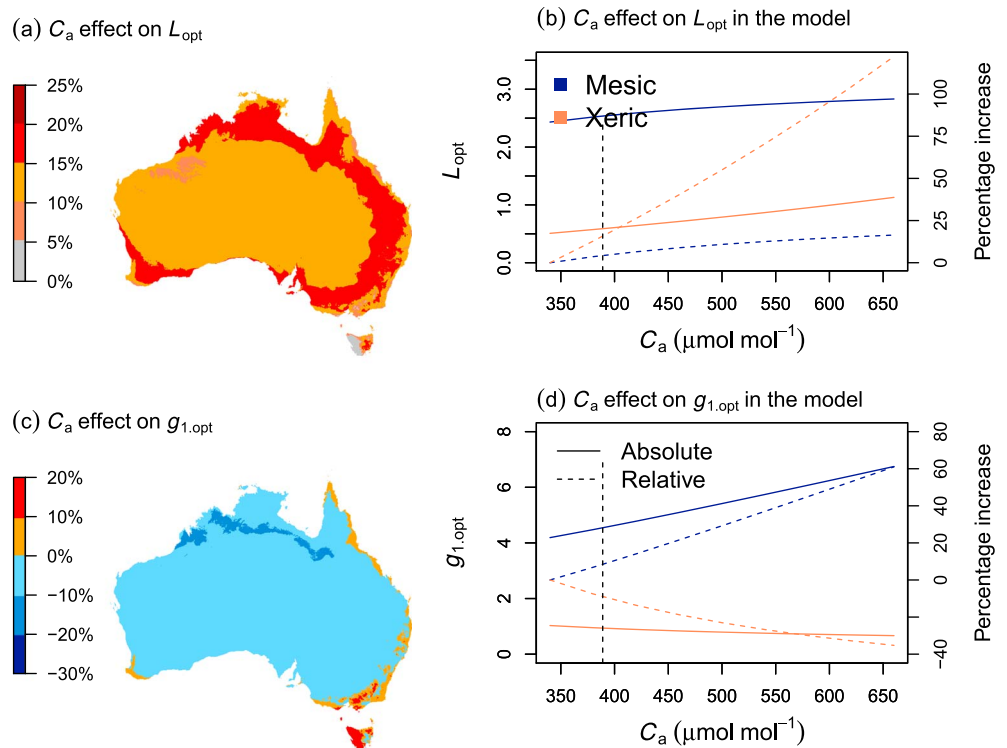
Figure 5. (a) Predicted effect of the 1980–2012 increase in C_a (from 340 to 389 μmol mol^{-1}) on L_{opt} in Australia. (b) Doubling C_a (340 to 680 μmol mol^{-1}) stimulates L_{opt} in the xeric regions by over 100% (orange dashed line) while ~20% in mesic regions (blue dashed line). The dotted vertical lines mark 389 μmol mol^{-1} corresponding to (a). (c) Predicted response of $g_{1.opt}$ to the 1980–2012 increase in C_a. (d) Doubling C_a (340 to 680 μmol mol^{-1}) has different effects on g_1 depending on water availability.

continent. This theory is thus a promising approach to incorporate into existing TBMs to improve predictions of foliage carbon allocation and LAI.

The optimality model showed good agreement with ground-based and satellite measurements. Previous assessments of satellite-derived products suggested an R^2 of 0.56–0.85 among products (Fang et al., 2012, 2013; Hill et al., 2006; Garrigues et al., 2008). The model thus had an R^2 comparable to that of satellite inter-product assessments. Our results suggested that LAI could be adequately predicted from consideration of the ecohydrological equilibrium. Since L_{opt} captured long-term mean MODIS, it should be possible to use L_{opt} in TBMs to reduce the current differences among models and satellite-derived products. The L_{opt} could, for example, be used as a target LAI for allocation routines, around which modeled LAI would vary dynamically according to phenology. Phenological variation of LAI could potentially be accounted for with a satellite-derived climatology (e.g., Broxton et al., 2014) or linked to existing process-based or optimization phenology models (e.g., Caldararu et al., 2014).

Although the model performed well overall, there was a discrepancy for high-LAI systems (Figure 4b). The predicted L_{opt} saturated at ~3 m^2 m^{-2}, while the observed values continued to increase. There are several potential causes for the discrepancy between our parsimonious model and observations at high LAI. First, R_m, which is assumed to be a constant, might be lower in higher-rainfall regions (Appendix A2). However, there is relatively little evidence to support such a variation in R_m, and the mechanism which would cause reduced R_m with higher water availability is not clear. In addition, nutrient limitation may be more important in regions with high LAI, and thus, consideration of nutrient availability may be necessary in these areas (McMurtrie & Dewar, 2013). Furthermore, the model does not take into account the decoupling between the vegetation and boundary layer, which may be significant in high-LAI systems (De Kauwe et al., 2017). These limitations of our simple, parsimonious approach could potentially be overcome if the theory were implemented in a TBM which treats these processes in more detail.

One key reason why our model improves LAI predictions is that it allows for variation in g_1 (via g_s) strategies in different climates. Lin et al. (2015) found, based on an analysis of a large database of leaf gas exchange measurements, that g_1 varies with climate and plant functional type. Previous optimal LAI models either fixed stomatal behavior (Kergoat, 2002; Woodward & Lomas, 2004) or considered trade-offs between g_s and LAI (McMurtrie et al., 2008). Our approach optimized g_1 simultaneously with LAI and thus represented a more realistic trade-off between the canopy (LAI) and leaf-level (g_1) water use strategies. These predictions also potentially provide a means to inform TBM parameterization of g_1—currently using fixed parameters.

The pattern of $g_{1.opt}$ agreed well with measurements, although there was a tendency to underpredict. There may be several reasons for this underprediction. First, $g_{1.opt}$ is the ecosystem average g_1 instead of only upper-canopy values. Consequently, one potential reason for overprediction of g_1 at site scale is that measurements focus on the upper canopy. g_1 varies with light availability and thus should be higher under light limitation (Campany et al., 2016). Another potential reason is the disagreement between g_1 estimates on different scales: Plant water use efficiency (a function of g_1; equation (S1)) measured on leaf and canopy scales were statistically different (Knauer et al., 2017; Medlyn et al., 2017). Moreover, the underprediction of g_1 suggests that there may be potentially other trait-related costs (e.g., stem and root respiration and construction) that are currently unaccounted for in the model. The temporal distribution of rainfall may also add to the difference between observed and modeled g_1 as stomatal conductance should respond not only to the amount of rainfall but also to the frequency (Lu et al., 2016).

An important benefit of this model is the ability to provide climate-constrained estimates of long-term changes in LAI with respect to increasing C_a. The increase of L_{opt} predicted by the model to rising C_a was consistent with satellite-derived observations. This evaluation focused on the effect of increased C_a alone; we assumed no change in long-term mean climate with rising C_a. The change of C_a during the evaluation period was accompanied by an average +7% of M_{MAP} (Donohue et al., 2009) and +8% D (Donohue et al., 2013). We did not consider these changes here because the impact of the M_{MAP} and D roughly canceled. However, in the future, rising C_a could be accompanied by larger changes in M_{MAP}. The sensitivity of L_{opt} to water availability in Australia suggests that the uncertainty in climate predictions of rainfall for Australia (e.g., ±100% with large intermodel variations; Mehran et al., 2014) could very likely transfer into uncertain vegetation feedbacks through changes in LAI.

The model also provides insights into the trade-off between LAI and g_1 in the context of rising C_a. Previous studies of stomatal behavior (Manzoni et al., 2013; Lu et al., 2016; Wolf et al., 2016; Prentice et al., 2014) have examined leaf-scale optimization but generally do not consider whole-plant trade-offs such as the balance between stomatal conductance and LAI (but see Kelly et al., 2015). Leaf-scale optimization models generally predict no change in g_1 under elevated C_a. As a result, larger scale studies have also assumed constant g_1 with increasing C_a when assessing LAI responses (e.g., Cheng et al., 2017; Donohue et al., 2017; Yang et al., 2016). Here the predicted $g_{1.opt}$ had distinct responses to rising C_a under different water availability scenarios. Under dry conditions, the model predicted reduced $g_{1.opt}$ and increased L_{opt} with elevated C_a, suggesting that it is beneficial for the plant to use the increased available C to grow leaves. Increased LAI in water-limited areas brings a double benefit to the plant because it increases both the transpiration fraction (equation (1)) and PAR interception (equations (S8a) and (S8b)). Reduced g_1 also indicates a decrease in the marginal carbon cost of water (Cowan & Farquhar, 1977), which suggests that elevated C_a releases water stress to some extent. Under wetter conditions, both $g_{1.opt}$ and L_{opt} and predicted to increase slowly with rising C_a, indicating the diminishing return from increasing C_a with increasing water availability. Both the direction and the magnitude of g_1 responses to C_a under different water availability are consistent with the findings in Schymanski et al. (2015), who predicted that marginal carbon cost of water would reduce by ~14% in a dry site but increase ~13% in a wet site with 20% increase of C_a. The predicted change in $g_{1.opt}$ with C_a adds to our general understanding of marginal carbon cost of water use: Previous meta-analyses of elevated C_a experiments not only found overall no change in g_1 with increasing C_a (e.g., Ainsworth & Rogers, 2007; Medlyn et al., 2001; but see Keenan et al., 2013) but also indicated variation across experiments. Our model specifically predicts that g_1 would increase with increased C_a in wet conditions and decrease in dry conditions—a testable hypothesis.

4.2. Alternative Model Assumptions

Our optimality model included two important empirical assumptions: (1) Plant transpiration is constrained to be a function of mean annual precipitation and LAI (equations (1) and (2)), and (2) maintenance respiration,

leaf mass per area, and life lifespan do not vary with climate. We tested alternative assumptions in each of these two areas, but none led to better model performance (Appendix A). The model prioritized parsimony and did not incorporate assumptions that did not improve model performance. However, these parameters are inputs to the model and can thus be changed upon the emergence of new theories and evidence.

Water availability to the plant, or transpiration in the model, is crucial to model predictions. The model showed that L_{opt} was sensitive to water input and thus the uncertainty in water availability contributed to the errors in the predictions. Water resources such as groundwater and surface flow are not included in the model but can be used for transpiration in certain regions (Evaristo et al., 2015; Liu et al., 2017). Topography has impacts on local water availability and thus plant water use strategies (Méndez-Toribio et al., 2017). Incorporation of the ecohydrological equilibrium theory into a more detailed TBM which accounts for topography and soil type would allow these effects to be incorporated in LAI predictions.

The temporal variation of water availability is also important to determine equilibrium LAI. In extreme cases such as tropical savanna in the Northern Territory, the majority of rainfall falls during the wet half of the year (Cernusak et al., 2011). The equilibrium LAI for average rainfall in dry and wet seasons would be very different. Indeed, the model agreed more with the long-term average MODIS LAI estimates than ground-based LAI, which are typically one-off measurements (Figure 2), suggesting the potential importance of variability of water availability and other parameters (e.g., respiration). Here we used an annual time step for simplicity. However, in strongly seasonal rainfall environments, it may be more appropriate to evaluate L_{opt} on subannual time scales. Hence, we aim to predict optimal seasonality along with L_{opt} in future developments of the model.

Empirical studies have suggested variation in the four plant traits used in the model (R_m, J_{max}, M_{area}, and t_f) with climate (Ali et al., 2015; Atkin et al., 2015; Dong et al., 2017; Heskel et al., 2016; Wright et al., 2004). This variation is potentially important to modeling carbon and water (Pappas et al., 2016). We examined existing data sets for these relationships but only found weak correlations, which, when implemented into the model, did not improve model performance nor substantially modify model behavior (Appendix A). We also did not discover any relationship between our literature-compiled values of J_{max} across Australia and climate (Figure S1). Consequently, we assumed here that R_m, J_{max}, M_{area}, and t_f were independent of climate. However, including empirical relationships between these parameters and W_{MAP} tends to increase predicted LAI where high LAI is observed (Figures A2 and A3). As a result, including variable parameters may help reduce the discrepancy between the modeled and observed LAI at high LAI (Figure 4d). New data sets and theories for variation in traits with climate are emerging: The correlation between plant traits and climate could be explained by physiological trade-offs (Onoda et al., 2017) and thus should be predictable by optimality models (e.g., Xu et al., 2017). The model is flexible enough to incorporate these new theories.

There is substantial evidence that leaf photosynthesis and respiration rates depend on leaf nitrogen content (Norby et al., 2017; Ryan, 1991). Nitrogen and phosphorus limitation have been suggested to be particularly common in Australian ecosystems due to the old, weathered soils (Chapin et al., 1986; Elser et al., 2007; Ellsworth et al., 2017; Wild, 1958). The lack of representation of nutrient limitation may contribute to the underprediction at high LAI seen in Figure 4d. McMurtrie et al. (2008) included a dependence of photosynthetic rate on leaf nitrogen content and considered the three-way trade-off between leaf nitrogen, stomatal conductance, and LAI. However, their approach requires knowledge of the canopy nitrogen uptake rate, which precludes application at the continental scale. To determine whether omitting nutrient availability impacts model success, we fitted GAMs to observed LAI and climate, with and without soil nitrogen and phosphorus as predictor variables. We found that including soil nutrients in the GAM did not capture more variation of measured LAI (Table S2). We also found that the water and carbon constrained L_{opt} agreed with existing data well, despite not incorporating the impacts of nutrient limitation. However, this result does not invalidate the importance of nutrient limitation, due to correlations between soil nutrient availability and water availability (Table S3). The impacts of nutrient limitations may thus already be incorporated in the water limitation.

J_{max} and R_m are known to be sensitive to temperature in the short term, but here we ignored this temperature dependence because both J_{max} and R_m have been reported to acclimate to growth temperature (Aspinwall et al., 2016; Reich et al., 2016; Smith et al., 2015). We found no correlation between J_{max} and R_m with temperature (section A2, Figure S1). As a result, we decided to use constant values of J_{max} and R_m. Temperature
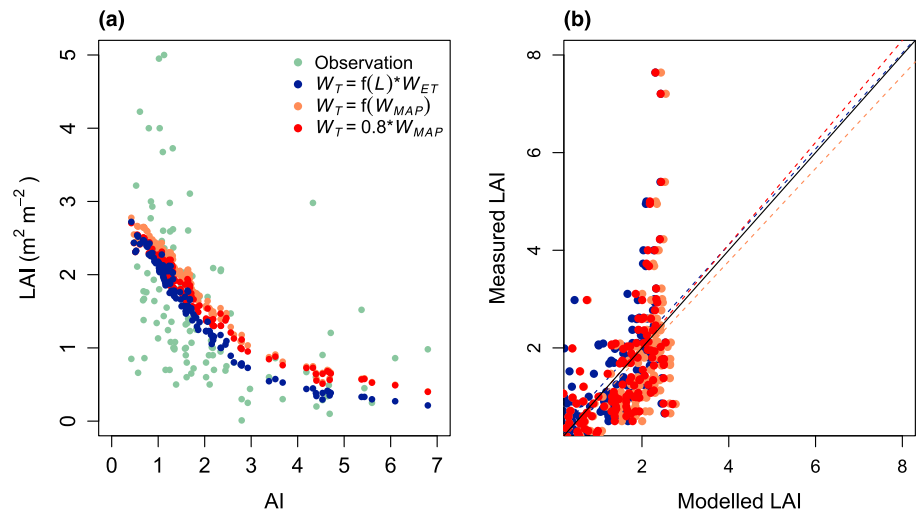
Figure A1. Impact of different transpiration fraction assumptions on L_{opt}. (a) The impact of different assumptions along the aridity index (gradient) and how they compared to observations. The L_{opt} from final model are the blue dots. "$W_T = f(W_{MAP})$" means substituting equation (1) with a constant fraction of 1. "$W_T = 0.8 * W_{MAP}$" means neither equation (1) nor (2) is used but instead a constant fraction is implemented (0.8). (b) Scatterplot of measured and modeled leaf area index with the solid line being 1:1 ratio and dashed line regression colored by assumptions.

dependence could be explored further in future; the model is flexible and could adopt a temperature dependence if necessary.

5. Conclusion

We showed that a parsimonious optimization model incorporating ecohydrological theory can accurately predict long-term average LAI in Australian ecosystems. The inputs (i.e., climate) and outputs (i.e., LAI and g_1) of the model are all being measured and thus enable convenient application and evaluation. Although set to be constant or calculated via empirical equations, all the parameters used in the model can be taken as inputs enabling accommodation to different purposes of studies. This approach could readily be incorporated into vegetation models to set a target long-term LAI, with the short-term variation modified as a function of water balance dynamics and phenology. Although the evaluation is limited to Australia, these findings may also apply to other water-limited ecosystems. Consequently, we suggest that TBMs could constrain leaf area predictions under climate change and rising C_a in water-limited regions to realistic values by incorporating a climate-constrained trade-off between leaf area and canopy conductance into their foliage submodel.

Appendix A: Alternative Assumptions

There are several potential options to calculate the key parameters (i.e., M_{area}, t_f, W_T, and R_m) in the model. It is therefore important to investigate how the underlying assumptions differ among equations and how those differences affect the predictions. In the following section, we compared the alternative functions to those implemented, illustrated the differences among the assumptions, and explained the reasoning behind our choice of assumptions for the final model.

A1. The Transpiration Fraction

The final model included the assumptions that the transpiration fraction varies with LAI (equation (1); Wang et al., 2014) and with precipitation (equations (2); Zhang et al., 2001). An alternative potential assumption is to take transpiration as a constant fraction (0.8) of precipitation as in McMurtrie et al. (2008). A constant transpiration fraction resulted in higher prediction at low observed LAI (red dots and lines in Figures A1a and A1b). Including the Zhang et al. (2001) relationship with precipitation only slightly improved the result (orange dots and lines in Figures A1a and A1b). Assuming the transpiration fraction to be a function of LAI gave the lowest results of all three assumptions tested here (blue dots and lines in Figures A1a and A1b).
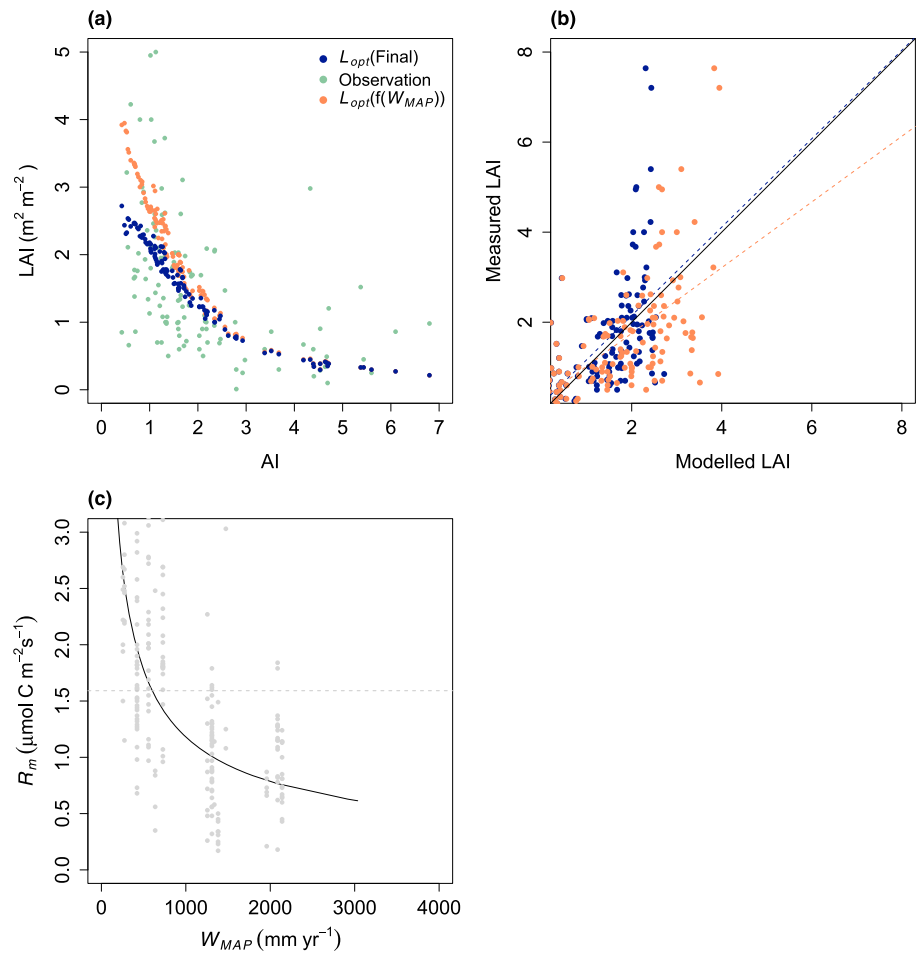
Figure A2. Comparison of the impacts of different R_m assumptions. (a) L_{opt} under different R_m assumptions compared to the in situ measurements along an aridity index gradient. Note that the final model uses constant R_m (blue dots). (b) The difference between constant R_m and the final model. (c) The tested R_m-W_{MAP} relationship with the dashed line indicating the value used in the final model and gray dots being the measurements from the Australian subset of the GLOBRESP data set (Atkin et al., 2015). Note that different assumptions are used here and in Figure A3d.

Although calculating transpiration fraction as a function of LAI added complexity and required iteration, we included this assumption in the final model for its fitness to data (blue line in Figure A1b). Alternatively, it may be viable to reduce prediction error at high AI by increasing respiration cost at high AI empirically (see the following section).

A2. Maintenance Respiration

R_m, maintenance respiration per unit leaf area ($\mu mol\ m^{-2}$ leaf s^{-1}), is a key factor in determining the cost of leaf growth. The final model assumed a constant value (1.59 $\mu mol\ m^{-2}\ s^{-1}$). This section explained the alternative assumptions we considered for R_m and showed how they affected the model predictions. We fitted an empirical relationship between R_m and W_{MAP} ($R^2 = 0.36$) to data from the Australian subset of the GLOBRESP data set (Atkin et al., 2015):

$$\ln(R_m) = a_r \cdot \ln(W_{MAP}) + b_r \tag{A1}$$

where a_r and b_r are fitted parameters, -0.589 and 4.235, respectively.

A constant R_m was chosen over the empirical relationship for the final model because: (i) The R_m-W_{MAP} relationship does not improve prediction at low in situ LAI (AI from 3 to 7 in Figure A2a); (ii) the final
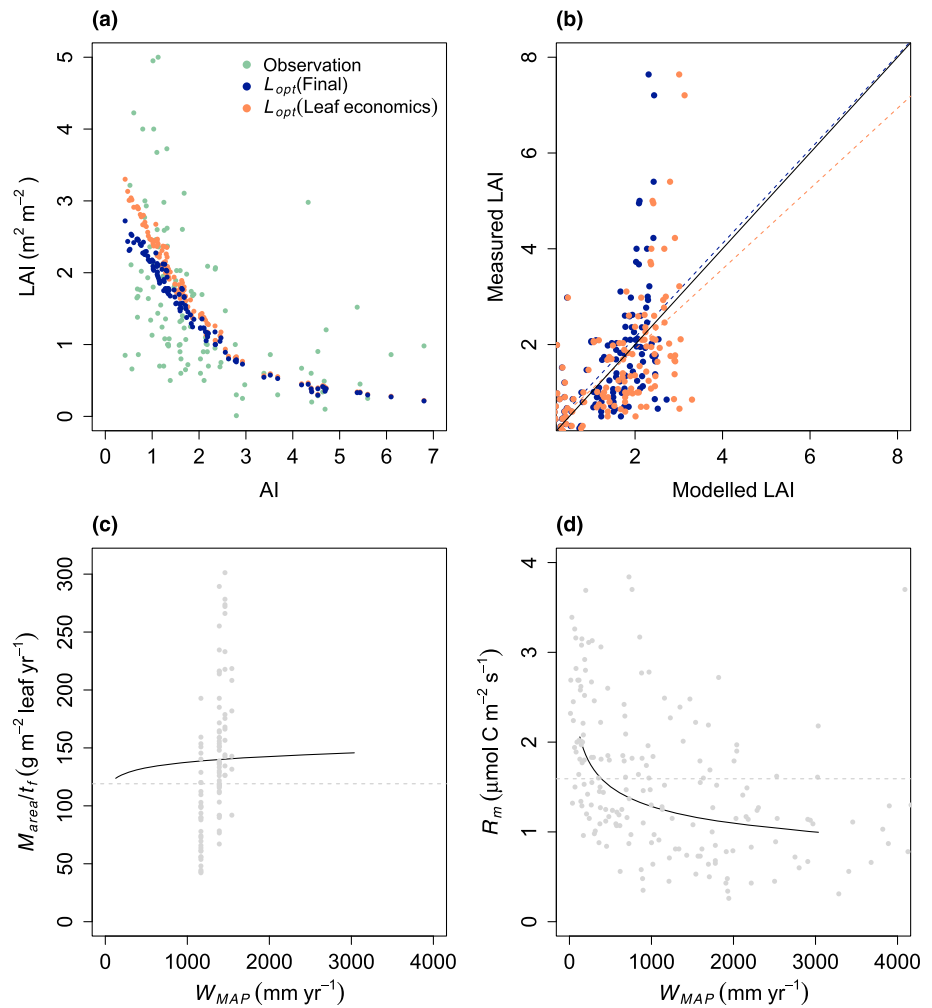
Figure A3. L_{opt} based on leaf economics compared to that of the final model. (a) L_{opt} based on leaf economics and final model compared to the measurements along an aridity index gradient. (b) The scatterplots of measurements against leaf economics and final model. (c) The change of leaf carbon investment (M_{area}/t_f) over a rainfall gradient. (d) The change of R_m based on M_{area} over a rainfall gradient. The solid lines show the regression. The gray dashed lines in (c) and (d) mark the values used in the final model. The gray dots are measurements.

model captured the observations better overall (blue dashed line was closer to 1:1 ratio than the orange dashed line in Figure A2b); and (iii) a climate-modified R_m added unnecessary complexity to the model assumptions.

Equation (A1) predicts an exponential decline of R_m with W_{MAP} (Figure A2c). However, the impact of incorporating this relationship on model predictions did not follow the same pattern. The difference between the two assumptions was negligible at low LAI because when LAI is very low, R_m has limited impact on the optimization compared to the exponential relationships of f_{APAR} (equation (S8a)) and transpiration fraction to LAI (equation (1)). However, at high LAI, both f_{APAR} and transpiration fraction were nearly saturated and thus a small change in R_m has a large impact on the prediction.

The impact of the R_m assumption would be larger if the model did not include the transpiration fraction to LAI relationship. As mentioned in the previous section, the model prediction could be improved by either incorporating the transpiration fraction-LAI relationship or a climate-modified R_m. The transpiration fraction-LAI assumption is more empirically justifiable but requires iteration to solve. It may thus be possible to improve the computational efficiency of the model by using an empirical R_m-W_{MAP} relationship instead of the transpiration fraction-LAI relationship, but this risks the limited applicability of the empirical relationship.

A3. Leaf Economics

The parameters describing leaf economics in the model are R_m, M_{area}, and t_f, which are assumed constant in this study (section 2 and Table S1). Previous studies (e.g., Wright et al., 2004) have suggested correlations among R_m, M_{area}, and t_f. In this section, we test the alternatives of calculating R_m, M_{area}, and t_f with empirical relationships and the impacts on predictions.

t_f correlates best with M_{area} according to GLOPNET data set ($R^2 = 0.44$; Wright et al., 2004):

$$\ln(t_f) = a_l \cdot \ln(M_{area}) - b_l \tag{A2}$$

where a_l and b_l are fitted parameters equal to 1.14 and -5.64, respectively. Similarly, R_m can be expressed as a function of M_{area}:

$$\ln(R_m) = a_{rm} \cdot \ln(M_{area}) - b_{rm} \tag{A3}$$

where a_{rm} and b_{rm} are fitted parameters and equal to 0.63 and -2.94, respectively. Here equation (A3) was derived from the Australian subset of GLOBRESP (Atkin et al., 2015) with an R^2 of 0.25. M_{area} correlates best with mean annual precipitation according to the same data set ($R^2 = 0.22$; Atkin et al., 2015):

$$\ln(M_{area}) = a_m \cdot \ln(W_{MAP}) + b_m \tag{A4}$$

where a_m and b_m are fitted parameters with values of -0.36 and 7.52, respectively.

Although these relationships are statistically significant, we did not implement them in the final model because making M_{area} and t_f functions of climate had no effect on model predictions in dry regions (AI > 2 in Figures A3a and A3b). The reason is that the carbon investment per unit time (proportional to M_{area}/t_f) and R_m is relatively insensitive to climate (Figures A3c and A3d). (ii) The regression line between the final model and observations was closer to 1:1 ratio than the one based on leaf economics (blue versus orange dashed lines in Figure A3b). For parsimony, the final model thus used the constant M_{area} and t_f. The values M_{area} and t_f in the final model were based on GLOPNET, while the M_{area} correlation with W_{MAP} was derived from GLOBRESP. The reason we tested the correlation from GLOBRESP is that the same correlation is not significant in GLOPNET. We chose to use the constant values of M_{area} and t_f from GLOPNET because t_f is not reported in GLOBRESP. We thus used values from one data set for consistency. Consequently, the gray line in Figure A3c was not the mean of the dots.

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