1 A test of an optimal stomatal conductance scheme within the

2 CABLE Land Surface Model

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19 Abstract

Stomatal conductance (g_s) affects the fluxes of carbon, energy and water between the 20 vegetated land surface and the atmosphere. We test an implementation of an optimal stomatal 21 22 conductance model within the Community Atmosphere Biosphere Land Exchange (CABLE) land surface model (LSM). In common with many LSMs, CABLE does not differentiate 23 24 between g_s model parameters in relation to plant functional type (PFT), but instead only in relation to photosynthetic pathway. We constrained the key model parameter " g_1 ", which 25 represents plant water use strategy, by PFT, based on a global synthesis of stomatal 26 27 behaviour. As proof of concept, we also demonstrate that the g_1 parameter can be estimated 28 using two long-term average (1960-1990) bioclimatic variables: (i) temperature and (ii) an 29 indirect estimate of annual plant water availability. The new stomatal model, in conjunction

with PFT parameterisations, resulted in a large reduction in annual fluxes of transpiration (~30 % compared to the standard CABLE simulations) across evergreen needleleaf, tundra and C4 grass regions. Differences in other regions of the globe were typically small. Model performance against upscaled data products was not degraded, but did not noticeably reduce existing model-data biases. We identified assumptions relating to the coupling of the vegetation to the atmosphere and the parameterisation of the minimum stomatal conductance as areas requiring further investigation in both CABLE and potentially other LSMs. We conclude that optimisation theory can yield a simple and tractable approach to predicting stomatal conductance in LSMs.

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55 1 Introduction

56 Land surface models (LSMs) provide the lower boundary conditions for the atmospheric 57 component of global climate and weather prediction models. A key role for LSMs is to calculate net radiation available at the surface and its partitioning between sensible and latent 58 59 heat fluxes (Pitman, 2003). To achieve this, LSMs calculate latent heat exchange between the 60 soil, vegetation and the atmosphere. This latent heat exchange involves a transfer of water vapour to the atmosphere; for vegetated surfaces this transfer (i.e. transpiration) occurs mostly 61 62 through the stomatal cells on the leaves as they open to uptake CO₂ for photosynthesis, but 63 also includes interception losses from the canopy. Transpiration from the vegetation has been 64 estimated to account for 60-80% of evapotranspiration (ET) across the land surface (e.g., Miralles et al. 2011; Jasechko et al. 2013; Schlesinger and Jasechko, 2014, but see Schlaepfer 65 66 et al. 2014). The stomata are thus the principal control over the exchange of water and the 67 associated flux of carbon dioxide (CO₂) between the leaf and the atmosphere. Stomatal 68 conductance (g_s) plays a significant role in the global carbon, energy and water cycles, hence 69 it modulates climate feedbacks and plays a critical role in global change (Henderson-Sellers et al., 1995; Pollard and Thompson, 1995; Cruz et al., 2010; Sellers et al. 1996; Gedney et al. 70 71 2006; Betts et al. 2007; Cao et al. 2010).

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In both ecosystem and land surface models, it is common to represent g_s with empirical 73 models (Jarvis, 1976; Ball et al. 1987; Leuning, 1995; see Damour et al. 2010 for a review). 74 75 In a recent inter-comparison study, 10 of the 11 ecosystem models considered applied some form of the "Ball-Berry-Leuning" approach (De Kauwe et al. 2013a). The empirical nature of 76 77 these models means that we cannot attach any theoretical significance to differences in model parameters across datasets or among species. As a consequence, models which use these 78 79 schemes commonly either assume the model parameters only vary with photosynthetic 80 pathway, or tune the parameters to match a specific experiment where necessary. Whilst more 81 mechanistic g_s models have been proposed (e.g. Buckley et al. 2003; Wang et al. 2012), they have not been widely applied due to their relative complexity and the need to obtain 82 83 additional model parameters, for which we have no (or limited) observational data across a 84 variety of PFTs.

An alternative approach, originally proposed by Cowan and Farquhar (1977) and Cowan (1982), is to model stomatal conductance using an optimisation framework (Hari et al. 1986; Lloyd, 1991; Arneth et al. 2002; Katul et al. 2009; Schymanski et al. 2009; Medlyn et al. 2011). This approach hypothesises that optimal stomatal behaviour occurs when the carbon gain (photosynthesis, A) is maximised, whilst minimising water loss (transpiration, E) over some period of time (t_2 - t_1). Therefore, optimal stomatal behaviour is the result of maximising:

$$\int_{t_1}^{t_2} \left(A(t) - \lambda E(t) \right) dt \tag{1}$$

- 92 where λ (mol⁻¹ C mol⁻¹ H₂O) is the marginal carbon cost of water use.
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94 Medlyn et al. (2011) recently proposed a tractable model that analytically solves the 95 optimisation problem. This model has great potential because it combines a simple functional form, similar to current empirical approaches, with a theoretical basis. Biological meaning 96 97 can be attached to the parameters, which can then be hypothesised to vary with climate and plant water use strategy (Medlyn et al. 2011; Héroult et al. 2013; Lin et al. 2015). In addition, 98 99 the behaviour of this model has been widely tested at the leaf scale and it has been shown to 100 perform at least as well, if not better than, the more widespread empirical approaches 101 currently used (Medlyn et al. 2011; De Kauwe et al. 2013a; Duursma et al. 2013; Medlyn et 102 al. 2013; Héroult et al. 2013). We also note that it is possible to implement a numerical 103 solution of this optimisation problem into a LSM (Bonan et al. 2014).

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105 Here, we present an implementation of the Medlyn et al. (2011) optimal stomatal conductance 106 model within the Community Atmosphere Biosphere Land Exchange (CABLE) LSM (Wang 107 et al. 2011). CABLE is the LSM used within the Australian Community Climate Earth System Simulator (ACCESS, see http://www.accessimulator.org.au; Kowalczyk et al. 2013), 108 109 a fully coupled earth system model used as part of the Coupled Model Intercomparison 110 Project (CMIP-5), which in turn informed much of the climate projection research underpinning the 5th assessment report of the Intergovernmental Panel on Climate Change. 111 CABLE currently implements an empirical representation of g_s following Leuning et al. 112 113 (1995). The existing CABLE parameterisation of stomatal conductance, similar to other

114	LSMs, including the Community Land Model version 4.5 (CLM4.5: Oleson et al. 2013) and
115	the ORganizing Carbon and Hydrology in Dynamic EcosystEms model (ORCHIDEE:
116	Krinner et al. 2005), only characterises differences in stomatal behaviour relating to
117	photosynthetic pathway, rather than PFT. The implementation assumes that all PFTs can be
118	adequately described by three parameters, two of which vary with photosynthetic pathway.
119	Simulated latent heat (LE) by CABLE has been shown to be sensitive to these parameters (Lu
120	et al. 2013), but the origin of this parameterisation has not been well documented in the
121	literature. In contrast, here we seek to constrain the new Medlyn model implementation with
122	data derived from a recent global synthesis of stomatal behaviour (Lin et al. in 2015). We first
123	test the implementation of the new g_s scheme at a series of flux tower sites and then undertake
124	a series of offline simulations to examine the model's behaviour at the global scale.
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139 2 Methods

140 **2.1 Model description**

141 The CABLE LSM has been used extensively for both coupled (Cruz et al. 2010; Pitman et al. 2011; Mao et al. 2011; Lorenz et al. 2014) and offline simulations (Abramowitz et al. 2008; 142 143 Wang et al. 2011; Kala et al. 2014) at a range of spatial scales. CABLE represents the canopy 144 using a single layer, two-leaf canopy model separated into sunlit and shaded leaves (Wang and Leuning, 1998), with aerodynamic properties simulated as a function of canopy height 145 146 and leaf area index (LAI) (Raupach 1994; Raupach et al. 1997). The Richards' equation for 147 soil water and heat conduction is numerically integrated using six discrete soil layers, and up 148 to three layers of snow can accumulate on the soil surface. A complete description can be 149 found in Kowalczyk et al. (2006) and Wang et al. (2011). The source code can be accessed 150 after registration at https://trac.nci.org.au/trac/cable.

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152 **2.2** Stomatal model and parameterisation.

153 In CABLE, g_s (stomatal conductance, mol m⁻² s⁻¹) is modelled following Leuning (1995):

$$g_s = g_0 + \frac{a_1 \beta A}{(C_s - \Gamma) \left(1 + \frac{D}{D_0}\right)}$$
(2)

where A is the net assimilation rate (μ mol m⁻² s⁻¹), C_s (μ mol mol⁻¹) and D (kPa) are the CO₂ 154 concentration and the vapour pressure deficit at the leaf surface, respectively, Γ (µmol mol⁻¹) 155 is the CO₂ compensation point of photosynthesis, and g_0 (mol m⁻² s⁻¹), D_0 (kPa) and a_1 are 156 fitted constants representing the residual stomatal conductance as net assimilation rate reaches 157 158 zero, the sensitivity of stomatal conductance to D and the slope of the sensitivity of stomatal 159 conductance to assimilation, respectively. In CABLE, the fitted parameters g_0 and a_1 vary with photosynthetic pathway (C3 vs C4) but not PFT, and D_0 is fixed for each PFTs. g_0 is scaled 160 161 from the leaf to the canopy by accounting for LAI, following Wang and Leuning (1998). β 162 represents an empirical soil moisture stress factor:

$$\beta = \frac{\theta - \theta_w}{\theta_{fc} - \theta_w}; \, \beta[0, 1] \tag{3}$$

163 where θ is the mean volumetric soil moisture content (m³ m⁻³) in the root zone, θ_w is the 164 wilting point (m³ m⁻³) and θ_{fc} is the field capacity (m³ m⁻³).

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166 In this study we replaced Eq. (2) with the g_s model of Medlyn et al. (2011) using the same β 167 factor as above:

$$g_s = g_0 + 1.6 \left(1 + \frac{g_1 \beta}{\sqrt{D}} \right) \frac{A}{C_s} \tag{4}$$

where g_1 (kPa^{0.5}) is a fitted parameter representing the sensitivity of the conductance to the assimilation rate. In this formulation of the g_s model, the g_1 parameter has a theoretical meaning and is proportional to:

$$g_1 \propto \sqrt{\frac{\Gamma^*}{\lambda}}$$
 (5)

171 where λ is defined by Eq. (1) and Γ^* (µmol mol⁻¹) is the CO₂ compensation point in the 172 absence of mitochondrial respiration. As a result, g_1 is inversely related to the marginal 173 carbon cost of water, λ (Medlyn et al. 2011).

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Figure 1 shows the stomatal sensitivity to D predicted by the two models in the absence of 175 soil water stress. In this comparison, the Medlyn model has been calibrated using least 176 177 squares against g_s values predicted by the Leuning model, where D varies between 0.05 and 3 178 kPa. The Leuning model was parameterised in the same way as the CABLE model, for C3 species: $a_1 = 9.0$, $D_0 = 1.5$ kPa and for C4 plants: $a_1 = 4.0$, $D_0 = 1.5$ kPa. The calibrated 179 parameters for the Medlyn model were $g_1 = 3.37 \text{ kPa}^{0.5}$ and $g_1 = 1.10 \text{ kPa}^{0.5}$ for C3 and C4 180 species, respectively. Over low to moderate D ranges (<1.5 kPa), the g_s calculated by the 181 182 Medlyn model declines more steeply than the Leuning model. There is then a crossover between the two models, such that at high D the Leuning model predicts g_s to be more 183 184 sensitive to increasing D than the Medlyn model. We use this calibration of the Medlyn model 185 (MED-L) to the Leuning model (LEU) throughout this manuscript, in order to distinguish 186 structural difference between the models from differences resulting from model 187 parameterisation (MED-P) based on a global synthesis of stomatal behaviour (see below).

189 Lin et al. (2015) compiled a global database of stomatal conductance and photosynthesis from 190 314 species across 56 field studies, which covered a wide range of biomes including Arctic 191 tundra, boreal, temperate forests and tropical rainforest. We estimated parameter values for g_1 192 for each of the 10 PFTs in CABLE (Fig. 2) by fitting Eq. (4) to this dataset, using the non-193 linear mixed-effects model approach presented by Lin et al. (2015). We used only data from 194 ambient field conditions, excluding elevated [CO₂], temperature, or other treatments. The 195 model was fit to data for each PFT separately, using species as a random effect on the g_1 196 parameter (to account for correlation of observations within species groups). For all mixed-197 effects models, we used the *lme4* package in R version 3.1.0 (R Core Development Team 198 2014). For this fitting, we set the parameter g_0 equal to zero. The reasons for this choice, and 199 the consequences, are discussed in detail below.

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The dataset compiled by Lin et al. (2015) did not have measurements from the deciduous needleleaf PFT. As Lin et al. hypothesised that the high marginal cost of water in evergreen conifers is a consequence of the lack of vessels for water transport in conifer xylem, we assumed that the marginal cost of water for deciduous needleleaf trees would be similar to that of evergreen needleleaf.

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Lin et al. (2015) also demonstrated a significant relationship ($r^2 = 0.43$) between g_1 and two long-term average (1960-1990) bioclimatic variables: temperature and a moisture index representing an indirect estimate of plant water availability. First, they estimated g_1 for each species separately using non-linear regression, and then they fit the following equation to these individual estimates of g_1 :

$$\log(g_1) = a + b \times MI + c \times \overline{T} + d \times MI \times \overline{T}$$
(6)

where *a*, *b*, c, and *d* are model coefficients, \overline{T} is the mean surface air temperature during the period of the year when the surface air temperature is above 0°C, *MI* is a moisture index calculated as the ratio of mean precipitation to the equilibrium evapotranspiration (as described in Gallego-Sala et al. 2010). Equation 6 was fit using a linear mixed-effects model, where PFT was used as random intercept, because we assume g_1 observations were independent observations for a given PFT.

We derived global MI and \overline{T} values from Climate Research Unit (CRU) CL1.0 climatology data set (1961-1990), interpolating the 0.5 degree data to 1.0 degree to match the resolution of the global offline forcing used, using a nearest neighbour approach. We masked land surface areas in the CRU data which did not correspond to one of CABLE 10 PFTs. In addition, we also masked pixels where MI and \overline{T} estimates were not available (40 out of a possible 54,000 pixels). To directly evaluate the differences in g_1 responses to the two climatic variables amongst PFTs, we modified Eq. (6):

$$\log(g_1) = a + b \times MI + c \times \overline{T} + d \times MI \times \overline{T} + e \times PFT$$
(7)

where a, b, c, d and e are model coefficients (Table, 2). We fitted Eq. (7) to the individual 226 227 estimates of g_1 by species (see above), but this time with a linear regression model (because PFT here is assumed to be a fixed effect). We then used the model coefficients to predict g_1 228 values (MED-C) based on the PFT, MI and \overline{T} values for each pixel. In the MED-C 229 230 simulations therefore the predicted g_1 values vary within a PFT as a function of the 231 bioclimatic indices. Standard errors of the prediction were calculated with standard methods 232 for linear regression. Finally, we masked pixels where MI or \overline{T} values are outside the range $(MI > 3.26; \overline{T} > 29.7^{\circ}C)$ covered by the g_s synthesis database (126 out of a possible 54,000 233 234 pixels) to avoid extrapolation of the model.

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236 **2.3 Model simulations**

In addition to the control simulation using the Leuning model (LEU), we carried out three 237 238 model simulations using the Medlyn model, testing the impact of model structure (MED-L), 239 parameterisation synthesised from experimental data (MED-P) and parameterisation based on 240 a set of climatic indices (temperature and aridity) (MED-C) (Table 3). Simulations were first 241 carried out at 6 flux sites selected from the FLUXNET network (http://www.fluxdata.org/) to 242 cover a range of PFTs included in CABLE: (i) deciduous broadleaf forest; (ii) evergreen 243 broadleaf forest; (iii) evergreen needleaf forest; (iv) C3 grassland; (v) C4 grassland; and (vi) 244 cropland (Table 4). In both site and global simulations, each site/pixel contained only a single 245 PFT type. Site data were obtained through the Protocol for the Analysis of Land Surface models (PALS; pals.unsw.edu.au; Abramowitz, 2012) which has previously been pre-246 247 processed and quality controlled for use within the LSM community. This process ensured that all site-years had near complete observations of key meteorological drivers (as opposed
to significant gap-filled periods). CABLE simulations at the 6 flux sites were not calibrated to
match site characteristics; instead default PFT parameters were used for the appropriate PFT
for each site.

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253 Next, we performed global offline simulations using the second Global Soil Wetness Project 254 (GSWP-2; Dirmeyer et al. 2006a) multi-model, 3-hourly, offline, meteorological forcing 255 (precipitation (rain and snowfall), downward shortwave and longwave radiation, surface air 256 temperature, surface specific humidity, surface wind speed and surface air pressure) over the period 1986-1995 at a resolution of 1° by 1° with a 30-year spin-up. Although CABLE has the 257 258 ability to simulate carbon pool dynamics, this feature was not activated for this study, given 259 the relatively short simulation periods. For both the site-scale and global simulations, LAI 260 was prescribed using CABLE's gridded monthly LAI climatology derived from Moderate-261 resolution Imaging Spectroradiometer (MODIS) LAI data. In all simulations, we used the 262 standard soil moisture stress function, β , defined in Eq. (3).

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264 The GSWP-2 driven simulation used the soil and vegetation parameters similar to those 265 employed when CABLE is coupled to the ACCESS coupled model, rather than those 266 provided by the GSWP-2 experimental protocol. This was to ensure that any discrepancies 267 between different CABLE simulations could be attributed to the differences in the stomatal 268 model only. When CABLE is coupled to ACCESS model, differences in surface fluxes and 269 temperature as simulated by CABLE with different stomatal models can also influence the 270 surface forcing fields provided by the atmospheric model, which further modify the 271 simulation results by CABLE. Therefore, to ensure that the results here are comparable to 272 future ACCESS coupled simulations, we use the same soil and vegetation parameters using 273 by CABLE within ACCESS, rather than those specified by the GSWP-2 protocol.

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277 **2.4 Data sets for global evaluation**

278 2.4.1 LandFlux-EVAL ET

The LandFlux-EVAL dataset (Mueller et al. 2013) provides a comprehensive ensemble of 279 global ET estimates at a 1° by 1° resolution over the periods 1989-1995 and 1989-2005, 280 derived from various satellites, LSMs driven with observationally based forcing, and 281 282 atmospheric re-analysis. We used the ensemble combined product (i.e. all sources of ET and associated standard deviations) over the period 1989-1995 (that overlaps with the GSWP-2 283 284 forcing period). The rationale for comparing the simulated ET against the LandFlux-EVAL 285 ET was to test that the uncertainties propagated to the ET estimates based on the 286 parameterisation of g_1 , were within the uncertainty range of the ensemble of existing models 287 and observational estimates.

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289 2.4.2 GLEAM ET

290 While zonal mean comparisons provide a useful measure of uncertainty, it is also useful to 291 identify regions where the model deviates more strongly from more observational ET 292 estimates. We therefore compared the gridded simulated seasonal ET against the latest 293 version of the GLEAM ET product (Miralles et al. 2014). This product is an updated version 294 of the original GLEAM ET (Miralles et al. 2011), that is part of the LandFlux-EVAL 295 ensemble (Mueller et al. 2013). The GLEAM product assimilates multiple satellite 296 observations (temperature, net radiation, precipitation, soil moisture, vegetation water 297 content) into a simple land model to provide estimates of vegetation, soil and total 298 evapotranspiration. Although estimates of vegetation transpiration are available, we only use 299 the total ET product, as the latter has been vigorously evaluated against flux-tower 300 measurements (Miralles et al. 2011, 2014).

301 2.4.3 Upscaled FLUXNET data

To estimate the influence of the new g_s parameterization on gross primary productivity (GPP), we compared our simulations against the up-scaled FLUXNET model tree ensemble (FLUXNET-MTE) dataset of Jung et al. (2009). This dataset is generated by using outputs from a dynamic global vegetation model (DGVM) forced with gridded observations as the surrogate truth to upscale site-scale quality controlled observations. The product is more reliable where there is a high density of high quality observations, mostly restricted to North America. Nonetheless, the DGVM used to generate this product is one of the most extensively evaluated biosphere models (Jung et al. 2009). The FLUXNET dataset provides two versions of up-scaled GPP, which differ slightly in the way they are derived. We use the mean of the two products.

330 3 Results

331 3.1 Flux-site results

Figure 3 shows a site-scale comparison during daylight hours (8 am - 7 pm) between
observed and predicted GPP, LE and transpiration (E) at 6 FLUXNET sites. Table 5 shows a
series of summary statistics (RMSE, bias and index of agreement) between modelled and
observed LE.

336 Impact of model structure

Figure 3 shows that the differences in simulated fluxes due to model structure, shown by comparing LEU with MED-L, are small across the 6 flux tower sites. Differences due to the structure of the model, shown by comparing LEU with MED-L in Fig. 3, are small across sites. These small differences indicate that the replacement of the Leuning model with the Medlyn model (calibrated to the Leuning model, MED-L) does not significantly alter CABLE simulations.

343 Impact of new g_1 parameterisation

344 Differences introduced by the PFT parameterisation, shown by comparing MED-P with LEU, 345 are also typically small across sites (Fig. 3), with the exception of Howard Springs (discussed 346 below) and the LE and E fluxes at Hyytiälä. At Hyytiälä, the parameterisation of a 347 conservative water use strategy for needleleaf trees leads to a reduction in both E and LE 348 fluxes (see Table 1); the change in LE is consistent with measured FLUXNET data. At 349 Bondville and Cabauw, MED-P predicts marginally higher peak fluxes as a result of a less 350 conservative water use strategy parameterisation of C3 grasses and crops, respectively. 351 Finally, for the two other sites represented by tree PFTs, Harvard and Tumbarumba, the 352 differences between modelled fluxes are negligible. The impact of g_s on LE fluxes is 353 noticeably smaller than the impact on E because modelled (and observed) LE also includes a 354 flux component from the soil.

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The PFT parameterisation (MED-P) does not have a noticeable impact on predicted fluxes of GPP, with the exception of Howard Springs. GPP is insensitive to the stomatal parameterisation because of the non-linear relationship between g_s and A. When stomata are

- fully open, A is limited by the rate of ribulose-1,5-bisphosphate (RuBP) regeneration, and is
- 360 relatively insensitive to the changes in C_i caused by small reductions in stomatal conductance.

The differences between models at Howard Springs do not stem from the new g_1 parameterisation (MED-P), but instead result from the large positive g_0 parameter assumed for C4 grassland in CABLE. The assumed g_0 of 0.04 mol m⁻² leaf s⁻¹ is multiplied by LAI meaning that the minimum canopy stomatal conductance at this site can be as high as 0.1 mol m⁻² ground s⁻¹. By contrast, in the MED-P model we assumed $g_0 = 0$, meaning that g_s goes to zero under low light and, importantly, high VPD conditions.

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Figure 4 shows that at Howard Springs, high afternoon VPD caused stomatal closure, represented by reduced E, in the MED-P model but not the MED-L or LEU models (Fig. 4), due to the assumption of a high g_0 as *A* tends towards zero. Consequently, daily fluxes are significantly lower in the MED-P when compared to the LEU and MED-L models.

373 Decoupling factor

The relative insensitivity of modelled fluxes to the new g_s parameterisation (MED-P) results 374 375 from CABLE's assumptions about the coupling of the vegetation to the surrounding 376 atmosphere boundary layer. In CABLE, transpiration from the vegetation to the atmosphere is 377 controlled by several resistances operating in series, both above (aerodynamic) and within the 378 canopy (stomatal and leaf boundary layer), and a longwave radiative balance through 379 radiative conductance on net available energy (Leuning et al. 1995; Kowakczyk et al. 2006). 380 These resistances in serial, result in a relatively weak coupling between the canopy surface 381 and the atmosphere.

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Figure 5 shows the average seasonal cycle of g_s and the decoupling coefficient (Jarvis and McNaughton, 1985; McNaughton and Jarvis, 1991) simulated by CABLE at the 6 flux tower sites. The decoupling coefficient (Ω) represents how well coupled the vegetation is to the surrounding atmosphere, with a value of 0 representing fully coupled behaviour, where transpiration is controlled by g_s , and a value of 1 representing completely decoupled behaviour, where transpiration is controlled by the available energy. The moderate to high Ω at all sites, with the exception of Hyytiälä, explains the lack of sensitivity in the E, LE and GPP fluxes to changes in g_s . At Hyytiälä, Ω is low, and becomes lower when g_1 is reduced in the MED-P model, resulting in an effect on E is more apparent than at the other sites (see Fig. 3).

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394 3.2 Global results

395 Global maps of g_1

396 To facilitate global comparisons, we have derived global maps of the g_1 parameter. Figure 6a 397 shows a clear latitudinal gradient, with lower values of g_1 , which represent a more 398 conservative water use strategy, found in mid-latitudes (20-60°N), whilst higher values of g_1 399 are located towards more tropical regions. When within-PFT variation with bioclimatic 400 indices is included (Fig. 6b) there is more variability in g_1 , particularly across the tropics, due 401 to spatial variability in temperature. Parameter uncertainty maps (± 2 standard errors) of the g_1 402 parameter are shown in Fig. S1. These maps indicate considerable uncertainty in deriving the 403 g₁ parameter as a function of these climate relationships (Fig. S1c,d), particularly for C3 grasses (mean (μ) range = 1.42–8.80) and C3 crops (μ range = 3.99–8.89) PFTs. 404

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406 Impact of model structure on simulated GPP and E

407 We next extend our comparison by examining the impact of different stomatal conductance 408 models on the simulated seasonal and annual GPP and E, the fluxes most directly impacted by 409 g_s in the model. Figures 7 and 8 show mean seasonal (December–January–February: DJF, and June–July–August: JJA) difference maps of predicted GPP and E, respectively. Tables 6 and 410 7 summarise changes in GPP and E in terms of mean annual totals across all the GSWP-2 411 412 years. Similar to Fig. 3, changes in simulated fluxes due to the different model structure (shown by LEU-MED-L, Figs. 7a, b and 8a, b), are typically small (µ change in GPP and E 413 414 relative to the control (LEU) < 7 %, with the exception of the shrub PFT, which has $\mu \sim 12$ %). 415 The largest differences (relative to the LEU) in GPP occur over grass (C3 GPP μ = 47.7 gC m⁻ 2 y⁻¹, μ change = 4.6 %; C4 GPP μ = 93.0 gC m⁻² y⁻¹, μ change = 5.6%) and shrub PFTs (GPP 416 $\mu = 69.3 \text{ gC m}^{-2} \text{ y}^{-1}$, μ change = 12 %), where the LEU model predicts higher fluxes (Figs. 417

418 7a,b). Figures 8a and b shows that the largest differences (relative to the LEU) in E occur 419 across the tropics, where fluxes in broadleaf forest PFTs are higher (E μ = 34.3 mm y⁻¹, μ 420 change = 5.5 %) in the MED-L model. These differences are consistent with the different 421 sensitivities of the modelled stomatal conductance to *D*, as show in Fig. 1. The LEU model 422 would tend to predict higher *g*_s fluxes at low to moderate *D* (<2 kPa), whereas the calibrated 423 MED-L model would predict higher *g*_s fluxes at moderate to high *D* (>2kPa).

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425 Impact of empirically fitted g_1 parameterisation on the simulated GPP and E

The key differences introduced by the MED-P model (Figs. 7c, d and 8c, d) are 29 % 426 reduction in E relative to the control (MED-C) simulation for evergreen needleleaf, C4 grass 427 and Tundra PFTs. Fluxes were reduced across the boreal zone (E μ = 76.1 mm y⁻¹), over C4 428 grass areas (GPP $\mu = 302.9 \text{ gC m}^{-2} \text{ y}^{-1}$, μ change = 16.5 %; E $\mu = 107.7 \text{ mm y}^{-1}$, μ change = 429 27.1 %) and the tundra PFT (E μ = 24.1 mm y⁻¹, μ change = 28.5 %). Fluxes are also 430 431 predicted to decrease over deciduous needleleaf PFTs, but this result should be viewed with 432 caution, as this was the PFT for which there were no synthesis data available. As such, this 433 result just reflects the assumption that these PFTs behave in the same way as evergreen needleleaf PFTs. The MED-P model also predicts increases over regions of C3 crop (GPP μ = 434 64.9 gC m⁻² y⁻¹, μ change = 5.5 %; E μ = 30 mm y⁻¹, μ change = 10.9 %) and C3 grasses (GPP 435 $\mu = 66.8 \text{ gC m}^{-2} \text{ y}^{-1}$, μ change = 5.9 %; E $\mu = 17.4 \text{ mm y}^{-1}$, μ change = 7.6 %). 436

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438 Impact of predicted g_1 parameterisation on the simulated GPP and E

Figures 7e,f and 8e,f show the predicted fluxes when g_1 is allowed to vary within a PFT 439 440 according to climate indices. Generally, the changes are in line with the changes introduced by the MED-P parameterisation. The largest change is a 32 % reduction in E relative to the 441 442 control simulation for evergreen needleleaf pixels. The notable difference compared to the 443 MED-P simulation occurs over C4 grass pixels. The MED-C model predicts fluxes that are 444 approximately half those predicted by the MED-P model for both GPP and E. This suggests a 445 less conservative water use strategy than is obtained through the PFT-specific parameterisation alone, i.e. MED-P. 446

447 3.3 Comparison with benchmarking products

448 Global simulations by the CABLE model using different models of stomatal conductance 449 were compared to the FLUXNET-MTE GPP and GLEAM ET data products (not shown). 450 Differences between these data products and CABLE simulations generally are much larger 451 than the differences among different CABLE simulations with different stomatal conductance 452 model (MED-P/C). Both products suggest that CABLE over-predicts GPP across the globe and ET across mid-latitudes (20-60°N). The MED-P/C models slightly improve agreement 453 454 with the FLUXNET-MTE GPP (Table 8) and GLEAM ET for the evergreen needleleaf PFT 455 (Table 9). Agreement is also improved for C4 grasses and Tundra PFTs. However, when considering all PFTs, the MED-P/C models do not noticeably improve agreement with the 456 457 GLEAM or FLUXNET-MTE products.

458

459 Figure 9 shows zonal means by latitude for DJF and JJA compared to the upscaled 460 FLUXNET-MTE GPP and LandFlux-EVAL ET products. As described above, across all 461 latitudes, the differences between the GPP from the data products and those fluxes predicted 462 by the models (LEU, MED-P and MED-C) are generally large and the impact of the new 463 stomatal scheme is typically negligible (Figs. 8a,b). By contrast, the comparison with ET 464 from the observational data product (Figs. 8c,d) is broadly consistent across all latitudes. 465 Notably, in JJA, the lower ET fluxes predicted by the MED-P/C models across mid (20-60°N) to high latitudes (> 60°N) are in agreement with the LandFlux-EVAL product, though the 466 467 modelled ET from the MED-L model is not outside the uncertainty envelope of the product. 468 In DJF, the MED-P model also predicts lower GPP and ET fluxes across the tropics (20°S-469 20°N) which would be towards the low end of the uncertainty envelope from the LandFlux-470 Eval product, but still falls outside the uncertainty range of FLUXNET-MTE.

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477 4 Discussion

478 4.1 Optimisation theory in LSMs

479 In this study we have implemented a simple stomatal conductance model, which was derived using optimisation theory, into a LSM. By calibrating parameters to match the existing 480 481 parameterisation of the original empirical stomatal model (MED-L), we were able to show 482 that the new model structure for stomatal conductance does not degrade overall model 483 performance. This result is similar to that of Bonan et al. (2014), who implemented the 484 optimal stomatal conductance scheme into the CLM LSM, following Williams et al. (1996). 485 In their implementation they solve the optimisation problem numerically (Eq. 1), with the 486 additional assumption that leaf water potential cannot fall below a minimum value, effectively replacing the empirical soil water scalar used here (Eq. 3). Our results and those of Bonan et 487 488 al. (2014) demonstrate that model performance using the optimisation scheme was 489 comparable to the original empirical stomatal conductance (Ball et al. 1987) scheme.

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491 Optimisation of key plant attributes is a viable alternative to empirical or overly complex 492 mechanistic model algorithms (Dewar et al. 2009). Optimisation is readily achieved via 493 numerical methods, but these are typically computationally intensive, which is a concern for 494 models used in long-term climate projections. Analytical approximations to optimisation such 495 as the stomatal conductance model used here (Medlyn et al. 2011) provide an operational 496 alternative. In this instance, the analytical solution is preferable to the numerical optimisation 497 because it correctly captures stomatal responses to rising atmospheric CO₂ concentration, 498 whereas the full numerical solution does not. In the full numerical solution, optimal stomatal 499 behaviour differs depending on whether RuBP regeneration or Rubisco activity is limiting 500 photosynthesis, and the predicted CO₂ response is incorrect when Rubisco activity is limiting, 501 unless the stomatal slope g_1 is assumed to vary with atmospheric CO₂ (Katul et al. 2010; 502 Medlyn et al. 2013). The analytical solution, in contrast, assumes that stomatal behaviour is 503 regulated as if photosynthesis were always RuBP-regeneration-limited, which yields the 504 correct CO₂ response.

506 The advantage of using an analytical model based on optimisation theory rather than an 507 empirical model is that it provides a basis for model parameterisation. Our implementation of the optimal model has one key parameter, g_1 , which is related to the marginal carbon cost of 508 509 water. It is possible to use theoretical considerations to predict how this parameter should 510 vary among PFTs and with mean annual climate (e.g. Prentice et al. 2014; Lin et al. 2015). 511 The parameter can also be readily and accurately estimated from data, meaning that the 512 predicted parameter values can be tested. For example, Héroult et al. (2013) predicted and 513 demonstrated a negative correlation between the g_1 parameter and wood density, and a 514 positive correlation with the root-to-leaf hydraulic conductance. Lin et al. (2015) examined 515 these relationships with their global stomatal dataset and concluded that such a relationship is 516 consistent across angiosperm tree species but not gymnosperm species.

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In this study we extended the work of Lin et al. (2015) by predicting g_1 values as a function of bioclimatic variables (temperature and aridity) (MED-C). The estimated parameter values were employed in the LSM and resulted in large changes to predicted fluxes in evergreen needleleaf and C4 vegetation. We have highlighted how the key stomatal conductance parameter could in theory be predicted, rather than calibrated, or, alternatively, linked to other traits (wood density) in the model. This work paves the way for broader implementations of optimisation theory in LSMs and other large-scale vegetation models.

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526 As g_1 represents plant water use strategy, there is also potential to hypothesise how it may 527 vary during drought. Inadequate simulation of soil moisture availability by LSMs is often 528 identified as a key weakness in surface flux prediction (Gedney et al. 2000; Dirmeyer et al. 529 2006b; Lorenz et al. 2012; De Kauwe et al. 2013b). In LSMs, as soil moisture declines, gas 530 exchange is typically reduced through an empirical scalar (Wang et al. 2011) accounting for 531 change in soil water content, but not plant behaviour (isohydric vs. anisohydric) (Egea et al. 532 2011). Bonan et al. (2014) showed that during drought periods, the formulation of the soil 533 moisture stress scalar was likely to be the cause of error in g_s calculations, rather than the g_s 534 scheme itself. Zhou et al. (2013, 2014) demonstrated that the g_1 parameter could be linked to 535 a more theoretical approach to limit gas exchange during water-limited periods, by 536 considering differences in species water use strategies.

537 4.2 Performance of the new model and parameterisation

We tested an implementation of a new stomatal conductance model within the CABLE LSM, at site and global scales to assess the impact on the simulated carbon, water and energy fluxes. We utilised a dataset that synthesised stomatal behaviour across the globe in order to constrain g_1 for each PFT (MED-P). In addition, we demonstrated that g_1 can be predicted from bioclimatic temperature and aridity datasets and tested the impact of model simulations using this parameterisation (MED-C).

544

545 Introducing the Medlyn g_s model with g_1 parameterisations (MED-P/C) to the CABLE LSM 546 resulted in reductions in E of \sim 30 % compared to the standard CABLE simulations across 547 evergreen needleleaf, tundra and C4 grass regions (Figs. 7c-f and 8c-f). This large difference 548 represents the conservative behaviour of these PFTs as reported by Lin et al. (2015), currently 549 not captured by the standard CABLE parameters. In other regions of the globe, the differences 550 between fluxes predicted by the models was typically small (Figs. 7, 8 and Tables 6 and 7). 551 Changes of ~30% in E across evergreen needleleaf, tundra and C4 grass PFTs has the 552 potential to affect regional and conceivably global scale climate.

553

554 In comparison to the LandFlux-EVAL ET product, across mid to high latitudes, the ET 555 predicted by the MED-P/C models is closer to the mean of the LandFlux-EVAL products, 556 though the LEU simulations were still within the uncertainty range of the ensemble (Fig. 9). 557 Across the tropics, the MED-P model predicted a reduction in ET fluxes when compared with 558 LandFlux-EVAL estimate and the LEU model, however simulations were still within the 559 uncertainty envelope. Interestingly, over this region the MED-C scheme predicted fluxes closer to the LEU model than the MED-P. Lorenz et al. (2014) showed that CABLE, when 560 561 coupled to ACCESS, predicted excessive ET across much of the northern hemisphere, leading 562 to unrealistically small diurnal temperature ranges. The new stomatal parameterisation predicts reduced transpiration across northern latitudes (Figs. 8d and 9d). We note that this 563 564 only results in a small improvement in the spatial agreement when compared with the GLEAM ET product (Table 9), suggesting that there are other causes not related to g_s for the 565 model-data bias. 566

568 Across all latitudes, the changes introduced by the new stomatal scheme did not degrade the 569 agreement with the FLUXNET-MTE GPP data product (Table, 8), although it was notable 570 that CABLE over-predicted (outside the uncertainty range) GPP across the tropics. The MED-571 P model did predict lower GPP fluxes for this region and the direction of the change was supported by the data product, but the change in fluxes was small and still outside the 572 573 uncertainty range of the FLUXNET-MTE product. Data from Lin et al. (2015) for 3 species in the Amazon suggests that a g_1 value of 4.23 kPa^{0.5} would be appropriate, which is close to the 574 575 PFT derived evergreen broadleaf value used in MED-P simulations (4.12 kPa^{0.5}). This line of 576 evidence, in combination with the GPP over-prediction, would tend to suggest that the 577 mismatch between model and data stems from other biases (in model and/or forcing) unrelated to g_s. Zhang et al. (2013) previously identified a bias in predicted ET and runoff 578 579 fluxes from CABLE over the Amazon region, but argued that this bias was unlikely to result 580 from the meteorological forcing data.

581

Another avenue of potential bias may relate to the use of a prescribed (as is typical in LSMs) 582 583 MODIS LAI climatology, which has been reported to be inaccurate over forested regions 584 (Shabanov et al. 2005; De Kauwe et al. 2011; Sea et al. 2011; Serbin et al. 2013). The 585 sensitivity to stomatal parameterisation may be larger when using prognostic LAI. In 586 prognostic LAI simulations there may be feedbacks from changes in g_s to LAI that could 587 cause larger differences between the Medlyn and the standard Leuning model, both in terms 588 of the different timings of predicted flux maximums and associated feedbacks on carbon and 589 water fluxes. We cannot resolve these wider issues of model bias here, but these issues 590 warrant further investigation.

591

592 4.3 Implications for other models

We anticipate that the new stomatal model could also be readily incorporated into other LSMs. However, other LSMs may show more or less sensitivity to the introduction of a new stomatal model and parameters, depending on how they represent boundary layer conductance. Models with low boundary layer conductance will have low stomatal control of fluxes, and highly decoupled canopies, whereas models with relatively high boundary layer conductance will have strong stomatal control and highly coupled canopies.

600 De Kauwe et al. (2013) previously showed decoupling to be a key area of disagreement 601 between 11 ecosystem models. In this comparison, CABLE appeared as a relatively 602 decoupled model because it considers multiple conductances in series, including aerodynamic 603 (above the canopy), boundary layer (within the canopy), and a radiative conductance, 604 accounting for differences in longwave radiation balance between isothermal and non-605 isothermal conditions (Wang and Leuning, 1998). In comparison, some other LSMs, for 606 example the Joint UK Land Environment Simulator (JULES; Best et al. 2011; Cox et al. 607 1999) and O-CN (Zaehle and Friend, 2010), only consider a bulk aerodynamic conductance 608 term, and thus would typically predict considerably more coupling. Therefore, such LSMs 609 would predict a larger influence of changes in stomatal conductance than CABLE. This 610 sensitivity was demonstrated by Booth et al. (2012), who used the Met Office Surface 611 Exchange System (MOSES; from which JULES was developed) to highlight that the stomatal 612 conductance parameter was a key driver of uncertainty in future estimates of the atmospheric 613 concentration of CO₂ from a coupled carbon cycle model (HadCM3C). They showed that by 614 perturbing the stomatal slope parameter (i.e. g_1 in our notation), their model predicted a large 615 uncertainty in the 1900 to 2100 atmospheric CO₂ change of between 380 to 850 ppm. The 616 Ecosystem Demography model v2 (ED2; Medvigy et al. 1999) is another relatively coupled model, with high sensitivity to g_s . Dietze et al. (2014) estimated that that ~10 % of the 617 618 uncertainty in net primary productivity (NPP) predicted by the ED2 model across North 619 America Biomes was directly due to the stomatal slope parameter (i.e. g_1). This uncertainty 620 was found to be largest in the evergreen PFTs (~21 %), whereas estimates of NPP from 621 grassland PFTs were largely insensitive. It is clear that levels of coupling between the canopy 622 and the atmosphere vary between LSMs and this presents a key area of model uncertainty.

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Determining the appropriate level of decoupling is not a trivial task. Previous estimates of the decoupling coefficient (Ω) based on flux data have either estimated the aerodynamic resistance from the wind speed and the friction velocity u^* (e.g. Lee and Black 1993; Hasler and Avissar, 2006), or from wind speed, stand height and roughness length (e.g. Stoy et al. 2006); both approaches ignore within-canopy turbulence. Launiainen et al. 2010 reported an average (1997-2008) July-August $\Omega = 0.32$ (standard deviation = 0.07) for the Hyytiälä site. By comparison, CABLE predicted a more coupled canopy, July-August (1996-2006) $\Omega =$ 631 0.21 (standard deviation = 0.11) from the standard Leuning model. Other literature studies for 632 coniferous forests suggest a lower $\Omega \sim 0.1$ -0.2 (Jarvis 1985; Jarvis and McNaughton 1986; Lee and Black, 1993; Meinzer 1993). Ranges suggested for other PFTs are typically broad; 633 between 0.5-0.9 for broadleaf tropical forest species (Meinzer 1993; Meinzer et al., 1997; 634 Wullschleger et al. 1998; Cienciala et al. 2000) and 0.4-0.9 for crops (Meinzer 1993). This 635 broad range in Ω makes it difficult to conclude which LSM most correctly simulates coupling. 636 However, as a major source of disagreement among models, we emphasise that coupling 637 638 strength is an important issue to address.

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640 4.4 Minimum stomatal conductance, g_0

641 The empirical Leuning g_s model includes a minimum stomatal conductance term, g_0 . This 642 term can also be added to the optimal Medlyn model. The value of this parameter can have a 643 significant impact on predicted ecosystem fluxes, as we found at the Howard Springs site (Figs. 3 and 4). The values used in the standard CABLE model ($g_0 = 0.01$ and 0.04 mol m⁻² s⁻¹ 644 645 for C3 and C4 species respectively) were taken from the Simple Biosphere Model version 2 646 (SiB2) (Sellers et al. 1996), but the original source of these parameter values is unclear. 647 Replacing these values with zeroes had a large impact on predicted fluxes, particularly under 648 high VPD conditions at the C4-dominated Howard Springs. This result agrees with a recent 649 study by Barnard and Bauerle (2013), who concluded that g_0 was in fact the most sensitive 650 parameter for correctly estimating transpiration fluxes. It is clear that further investigation is 651 needed on the impact of different g_0 assumptions in land surface and ecosystem models. Here 652 we offer some thoughts about the directions such investigations could take.

653 First, it will be important to query the way in which g_0 is incorporated into the stomatal 654 model. Adding a g₀ term as a model intercept, as is currently done, is not based on theory, and 655 has the unintended consequence that it affects predicted stomatal conductance at all times, not 656 only when photosynthesis approaches zero, resulting in high sensitivity to this model 657 parameter. Alternative model structures incorporating g_0 can be derived depending on what g_0 658 is assumed to represent. If we assume, for example, that g_0 represents a physical lower limit to 659 stomatal conductance, below which it is not possible for g_s to fall, the optimal behaviour would be for g_0 to be a lower bound to stomatal conductance predicted by the standard model. 660 Thus, an alternative model structure to consider would be the maximum of g_0 and the optimal 661

 $662 g_s$, rather than the sum of the two.

663 It will also be important to carefully consider how to parameterise the value of g_0 . Some 664 authors suggest using night-time stomatal conductance values (e.g. Zeppel et al. 2014). 665 However, minimum stomatal conductance values measured during the day are considerably 666 lower than measured night-time values (Walden-Coleman et al. 2013). We extracted the minimum g_s values for each species from the dataset of Lin et al. (2015) and plotted them as a 667 668 function of the minimum recorded photosynthesis values (Fig. S2). It can be seen that the 669 minimum g_s values tend to zero with minimum recorded A, and are much lower than the 670 values currently assumed in CABLE and the night-time g_s values estimated from the literature 671 by Zeppel et al. (2014). Consequently, we suggest that values of g_0 used in the stomatal model 672 applied during the day should be estimated from daytime, rather than night-time 673 measurements.

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676 Acknowledgements

677 This work was supported by the Australian Research Council Centre of Excellence for Climate System Science through grant CE110001028, and by ARC Discovery Grant DP 678 679 DP120104055. This study uses the LandFlux-EVAL merged benchmark synthesis products of 680 ETH Zurich produced under the aegis of the GEWEX ILEAPS and 681 projects (http://www.iac.ethz.ch/url/research/LandFluxEVAL/). We thank CSIRO and the 682 Bureau of Meteorology through the Centre for Australian Weather and Climate Research for 683 their support in the use of the CABLE model. We thank the National Computational 684 Infrastructure at the Australian National University, an initiative of the Australian 685 Government, for access to supercomputer resources. The up-scaled Fluxnet dataset was 686 provided by Martin Jung from the Max Planck Institute for Biogeochemistry. This work used 687 eddy covariance data acquired by the FLUXNET community for the La Thuile FLUXNET release, supported by the following networks: AmeriFlux (U.S. Department of Energy, 688 689 Biological and Environmental Research, Terrestrial Carbon Program (DE-FG02-04ER63917 690 and DE-FG02-04ER63911)), AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, CarboItaly, 691 CarboMont, ChinaFlux, Fluxnet-Canada (supported by CFCAS, NSERC, BIOCAP, 692 Environment Canada, and NRCan), GreenGrass, KoFlux, LBA, NECC, OzFlux, TCOS-

693	Siberia, USCCC. We acknowledge the financial support to the eddy covariance data
694	harmonization provided by CarboEuropeIP, FAO-GTOS-TCO, iLEAPS, Max Planck Institute
695	for Biogeochemistry, National Science Foundation, University of Tuscia, Université Laval
696	and Environment Canada and US Department of Energy and the database development and
697	technical support from Berkeley Water Center, Lawrence Berkeley National Laboratory,
698	Microsoft Research eScience, Oak Ridge National Laboratory, University of California -
699	Berkeley, University of Virginia. D.G.M. acknowledges financial support from Netherlands
700	Organisation for Scientific Research (NWO) through grant 863.14.004. All data analysis and
701	plots were generated using the Python language and the Matplotlib Basemap Toolkit (Hunter,
702	2007).
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720	References
721	Abramowitz, G., Leuning, R., Clark, M., Pitman, A., 2008. Evaluating the Performance of
722	Land Surface Models. J. Clim. 21, 5468–5481.
723	
724	Abramowitz, G. (2012) Towards a public, standardized, diagnostic benchmarking system for
725	land surface models, Geoscientific Model Development, 5, 819-827, doi:10.5194/gmd-5-819-
726	2012.
727	
728	Aphalo, P., Jarvis, P., 1991. Do stomata respond to relative humidity? Plant Cell Environ. 14,
729	127–132.
730	
731	Arneth, A., Lloyd, J., Šantrŭčková, H., Bird, M., Grigoryev, S., Kalaschnikov, Y., Gleixner,
732	G., Schulze, ED., 2002. Response of central Siberian Scots pine to soil water deficit and
733	long-term trends in atmospheric CO2 concentration. Glob. Biogeochem. Cycles 16, 5-1.
734	
735	Ball, M.C., Woodrow, I.E., Berry, J.A., 1987. Progress in Photosynthesis Research, in:
736	Biggins, I. (Ed.), Martinus Nijhoff Publisheres, Netherlands, pp. 221-224.
737	
738	Barnard, D., Bauerle, W., 2013. The implications of minimum stomatal conductance on
739	modeling water flux in forest canopies. J. Geophys. Res. Biogeosciences., 118, 1322-1333.
740	
741	Beringer, J., Hutley, L.B., Tapper, N.J., Cernusak, L.A., 2007. Savanna fires and their impact
742	on net ecosystem productivity in North Australia. Glob. Change Biol. 13, 990-1004.
743	
744	Betts, R.A., Boucher, O., Collins, M., Cox, P.M., Falloon, P.D., Gedney, N., Hemming, D.L.,
745	Huntingford, C., Jones, C.D., Sexton, D.M., Webb, M.J., 2007. Projected increase in
746	continental runoff due to plant responses to increasing carbon dioxide. Nature 448, 1037-
747	1041.
748	

- 749 Best, M.J., Pryor, M., Clark, D.B., Rooney, G.G., Essery, R.L.H., Ménard, C.B., Edwards,
- J.M., Hendry, M.A., Porson, A., Gedney, N., Mercado, L.M., Sitch, S., Blyth, E., Boucher,
- 751 O., Cox, P.M., Grimmond, C.S.B., Harding, R.J., 2011. The Joint UK Land Environment
- 752 Simulator (JULES), model description Part 1: Energy and water fluxes. Geosci. Model Dev.
- 753 Discuss. 4, 595–640.
- 754
- 755 Booth, B.B., Jones, C.D., Collins, M., Totterdell, I.J., Cox, P.M., Sitch, S., Huntingford, C.,
- 756 Betts, R.A., Harris, G.R., Lloyd, J., 2012. High sensitivity of future global warming to land
- carbon cycle processes. Environ. Res. Lett. 7, 024002.
- 758
- 759 Bonan, G., Williams, M., Fisher, R., Oleson, K., 2014. Modeling stomatal conductance in the
- 760 Earth system: linking leaf water-use efficiency and water transport along the soil-plant-
- atmosphere continuum. Geosci. Model Dev. Discuss. 7, 3085–3159.
- 762
- Buckley, T., Mott, K., Farquhar, G., 2003. A hydromechanical and biochemical model of
 stomatal conductance. Plant Cell Environ. 26, 1767–1785.
- 765
- 766 Cao, L., Bala, G., Caldeira, K., Nemani, R., Ban-Weiss, G., 2010. Importance of carbon
- dioxide physiological forcing to future climate change. Proc. Natl. Acad. Sci. U. S. A. 107,9513–9518.

- Cox, P., Betts, R., Bunton, C., Essery, R., Rowntree, P., Smith, J., 1999. The impact of new
 land surface physics on the GCM simulation of climate and climate sensitivity. Clim. Dyn.
 15, 183–203.
- 773
- Cienciala, E., Kučera, J., Malmer, A., 2000. Tree sap flow and stand transpiration of two
 Acacia mangium plantations in Sabah, Borneo. J. Hydrol. 236, 109–120.
- 776
- Cowan, I., Farquhar, G., others, 1977. Stomatal function in relation to leaf metabolism and
 environment, in: Symposia of the Society for Experimental Biology. p. 471.

780	Cowan, I.R. 1982. Regulation of water use in relation to carbon gain in higher plants. In
781	Encyclopedia of Plant Physiology, New Series. Vol. 12B. Eds. O.L. Lange, P.S. Nobel and
782	C.B. Osmond. Springer-Verlag, Berlin. pp 589-613.
783	
784	Cruz, F.T., Pitman, A.J., Wang, YP., 2010. Can the stomatal response to higher atmospheric
785	carbon dioxide explain the unusual temperatures during the 2002 Murray-Darling Basin
786	drought? J. Geophys. Res. Atmospheres 1984–2012 115.
787	
788	Damour, G., Simonneau, T., Cochard, H., Urban, L., 2010. An overview of models of
789	stomatal conductance at the leaf level. Plant Cell Environ. 33, 1419–1438.
790	
791	De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Walker, A.P., Dietze, M.C., Hickler, T., Jain,
792	A.K., Luo, Y., Parton, W.J., Prentice, C., others, 2013a. Forest water use and water use
793	efficiency at elevated CO2: a model-data intercomparison at two contrasting temperate forest
794	FACE sites. Glob. Change Biol. 19, 1759–1779.
795	
796	De Kauwe, M.G., Taylor, C.M., Harris, P.P., Weedon, G.P., Ellis, R.J., 2013b. Quantifying
797	land surface temperature variability for two Sahelian mesoscale regions during the wet
798	season. J. Hydrometeor, 14, 1605-1619.
799	
800	Dewar, R., Franklin, O., Mäkelä, A., Mcmurtrie, R., Valentine, H., 2009. Optimal Function
801	Explains Forest Responses to Global Change. Biosci., 59, 127–139.
802	
803	Dickinson, R.E., Shaikh, M., Bryant, R., Graumlich, L., 1998. Interactive canopies for a
804	climate model. J. Clim. 11, 2823–2836.
805	
005	
806	Dietze, M. C., Serbin, S. P., Davidson, C., Desai, A. R., Feng, X., Kelly, R., Kooper,

R., LeBauer, D., Mantooth, J., McHenry, K. Wang, D. 2014, A quantitative assessment of a
terrestrial biosphere model's data needs across North American biomes, J. Geophys. Res.
Biogeosciences, 119, 286–300.

810

Birmeyer, P.A., Gao, X., Zhao, M., Guo, Z.H., Oki, T., Hanasaki, N., 2006a. GSWP-2multimodel analysis and implications for our perception of the land surface. B. Am. Meteorol.
Soc., 87, 1381-1397.

- 814
- 815 Dirmeyer, P. A., Koster, R. D., Guo, Z. 2006b, Do global models properly represent the 816 feedback between land and atmosphere? J. Hydrometeor., 7, 1177-1198.

817

Duursma, R.A., Payton, P., Bange, M.P., Broughton, K.J., Smith, R.A., Medlyn, B.E., Tissue,
D.T., 2013. Near-optimal response of instantaneous transpiration efficiency to vapour
pressure deficit, temperature and [CO2] in cotton (Gossypium hirsutum L.). Agricultural and
Forest Meteorology 168, 168–176

822

- 823
- 824 Egea, G., Verhoef, A., Vidale, P.L., 2011. Towards an improved and more flexible
- 825 representation of water stress in coupled photosynthesis–stomatal conductance models. Agric.

826 For. Meteorol. 151, 1370–1384.

827

- 828 Farquhar, G.D., Sharkey, T.D., 1982. Stomatal conductance and photosynthesis. Annu. Rev.
- 829 Plant Physiol. 33, 317–345.
- 830
- 831 Gallego-Sala, A., Clark, J., House, J., Orr, H., Prentice, I.C., Smith, P., Farewell, T.,
- 832 Chapman, S., 2010. Bioclimatic envelope model of climate change impacts on blanket
- 833 peatland distribution in Great Britain. Clim. Res. 45, 151–162.

835 836 837	Gedney, N., Cox, P., Douville, H., Polcher, J., Valdes, P., 2000. Characterizing GCM land surface schemes to understand their responses to climate change. J. Clim. 13, 3066–3079.
838 839	Gedney, N., Cox, P., Betts, R., Boucher, O., Huntingford, C., Stott, P., 2006. Detection of a direct carbon dioxide effect in continental river runoff records. Nature 439, 835–838.
840841842843	Hari, P., Mäkelä, A., Korpilahti, E., Holmberg, M., 1986. Optimal control of gas exchange. Tree Physiol. 2, 169–175.
844 845	Hasler, N., Avissar, R. 2006. What controls evapotranspiration in the Amazon Basin? J. Hydrometeor, 8, 380–395.
846 847 848 849	Henderson-Sellers, A., McGuffie, K., Gross, C., 1995. Sensitivity of global climate model simulations to increased stomatal resistance and CO ₂ increases. J. Clim. 8, 1738-1756.
850 851 852	Héroult, A., LIN, YS., Bourne, A., Medlyn, B.E., Ellsworth, D.S., 2013. Optimal stomatal conductance in relation to photosynthesis in climatically contrasting Eucalyptus species under drought. Plant Cell Amp Environ. 36, 262–274.
853 854 855	Hunter, J.D., 2007. Matplotlib: A 2D graphics environment. Comput. Sci. Amp Eng. 9, 90–95.
 856 857 858 859 860 	Jarvis, P., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 273, 593–610.
861 862 863	Jarvis, P.G., 1985. Attributes of Trees as Crop Plants, in: Cannell, M.G.R., Jackson, J.E. (Eds.), Attributes of Trees as Crop Plants. Institute of Terrestrial Ecology, pp. 460–480.

864	Jarvis, P., McNaughton, K., 1986. Stomatal control of transpiration: Scaling up from leaf to
865	region. Adv. Ecol. Res. 15, 1–49.

Jasechko, S., Sharp, Z.D., Gibson, J.J., Birks, S.J., Yi, Y., Fawcett, P.J., 2013. Terrestrial
water fluxes dominated by transpiration. Nature 496, 347–350.

869

- 870 Jung, M., Reichstein, M., Bondeau, A., 2009. Towards global empirical upscaling of
- 871 FLUXNET eddy covariance observations: validation of a model tree ensemble approach
- using a biosphere model. Biogeosciences 6, 2001–2013.

873

- Kala, J., Decker, M., Exbrayat, J.-F., Pitman, A.J., Carouge, C., Evans, J.P., Abramowitz, G.,
- 875 Mocko, D., 2014. Influence of Leaf Area Index Prescriptions on Simulations of Heat,
- 876 Moisture, and Carbon Fluxes. J. Hydrometeorol. 15, 489–503.

877

- 878 Katul, G.G., Palmroth, S., Oren, R., 2009. Leaf stomatal responses to vapour pressure deficit
- 879 under current and CO_{a} -enriched atmosphere explained by the economics of gas exchange.
- 880 Plant Cell Environ. 32, 968–979
- 881
- Kerstiens, G., 1996. Cuticular water permeability and its physiological significance. J. Exp.
 Bot. 47, 1813–1832.

884

- 885 Kowalczyk, E.A., Wang, Y.P., Wang, P., Law, R.H., Davies, H.L., 2006. The CSIRO
- 886 Atmosphere Biosphere Land Exchange (CABLE) model for use in climate models and as an
- offline model (No. CSIRO Marine and Atmospheric Research paper 013). CSIRO.

888

Kowalczyk, E. A., Stevens, L., Law, R. M., Dix, M. D., Wang, Y-P., Harman, I. N., Haynes,
K., Srbinovsky, J., Pak, B. and Ziehn, T. (2013) The land surface model component of
ACCESS: description and impact on the simulated surface climatology. Australian
Meteorological and Oceanographic Journal, 63, 65-82.

- 894 Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P.,
- 895 Ciais, P., Sitch, S., Prentice, I.C., 2005. A dynamic global vegetation model for studies of the
- coupled atmosphere-biosphere system. Glob. Biogeochem. Cycles 19, GB1015.

- Launiainen, S.2010. Seasonal and interannual variability of energy exchange above a boreal
 Scots pine foest. Biogeosci. 7, 3921–3940.
- 900
- Lee, X. and Black, T.A. 1993. Atmospheric turbulence within and above a Douglas fir stand.
 Part II: eddy fluxes of sensible heat and water vapour. Boundary Layer Meteorol, 64, 369–
 389.

904

- 905 Leuning, R., 1995. A critical appraisal of a combined stomatal-photosynthesis model for C_3 906 plants. Plant Cell Environ. 18, 339–355.
- 907

908 Lin, Y.-S., Medlyn, B. E., Duursma, R. A., Prentice, I. C., Wang, H., Baig, S., Eamus, D., 909 Resco de Dios, V. Mitchell, P., Ellsworth, D. S., Op de Beeck, M., Wallin, G., Uddling, J., 910 Tarvainen, L., Linderson, M-J., Cernusak, L. A., Nippert, J. B., Ocheltree, T. W., Tissue. D. 911 T., Martin-StPaul, N. K., Rogers, A., Warren, J. M., De Angelis, P., Hikosaka, K., Han, Q., 912 Onoda, Y., Gimeno, T. E., Barton, C. V. M., Bennie, J., Bonal, D., Bosc, A., Löw, M., 913 Macinins-Ng, C., Rey, A., Rowland, L., Setterfield, S. A., Tausz-Posch, S., Zaragoza-Castells, J., Broadmeadow, M. S. J., Drake, J. E., Freeman, M., Ghannoum, O., Hutley, L. B., 914 915 Kelly, J. W., Kikuzawa, K., Kolari, P., Koyama, K., Limousin, J-M., Meir, P., Lola da Costa, 916 A. C., Mikkelsen, T. N., Norma Salinas, Sun, W., 2015. Optimal stomatal behaviour around 917 the world: synthesis of a global stomatal conductance database. Nature Clim. Change, in 918 press.

- 919
- Lloyd J. 1991. Modeling stomatal responses to environment in Macadamia integrifolia. Aust.J. Plant Physiol., 18, 649-660.
- 922

- 923 Lorenz, R., Pitman, A., Donat, M., Hirsch, A., Kala, J., Kowalczyk, E., Law, R., Srbinovsky,
- 924 J., 2014. Representation of climate extreme indices in the ACCESS1. 3b coupled atmosphere-
- 925 land surface model. Geosci. Model Dev. 7, 545–567.
- 926
- 927 Lu, X.J., Wang, Y.P., Ziehn, T. and Dai, Y.J. (2013). An efficient method for global
- 928 parameter sensitivity analysis and its applications to the Australian community land surface
- 929 models (CABLE). Agric. For. Meteorol, 182-183:292-303.
- 930
- McNaughton, K., Jarvis, P., 1991. Effects of spatial scale on stomatal control of transpiration.
 Agric. For. Meteorol. 54, 279–302.
- 933
- Medlyn, B.E., Duursma, R.A., De Kauwe, M.G., Prentice, I.C., 2013. The optimal stomatal
- 935 response to atmospheric CO2 concentration: Alternative solutions, alternative interpretations.
- 936 Agric. For. Meteorol., 182-183, 200-203.
- 937
- 938 Medlyn, B.E., Duursma, R.A., Eamus, D., Ellsworth, D.S., Prentice, I.C., Barton, C.V.M.,
- 939 Crous, K.Y., De Angelis, P., Freeman, M., Wingate, L., 2011. Reconciling the optimal and
- 940 empirical approaches to modelling stomatal conductance. Glob. Change Biol. 17, 2134–2144.
- 941
- Medvigy, D. M., S. C. Wofsy, J. W. Munger, D. Y. Hollinger, and P. R. Moorcroft (2009),
 Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem
 Demography model version 2. J. Geophys. Res., 114, G01002.
- 945

- 948 Meinzer, F., Andrade, J., Goldstein, G., Holbrook, N., Cavelier, J., Jackson, P., 1997. Control
- 949 of transpiration from the upper canopy of a tropical forest: the role of stomatal, boundary
- 950 layer and hydraulic architecture components. Plant Cell Environ. 20, 1242–1252.
- 951

Meinzer, F.C., 1993. Stomatal control of transpiration. Trends Ecol. Amp Evol., 8, 289–294.947

Miralles, D., De Jeu, R., Gash, J., Holmes, T., Dolman, A., 2011. Magnitude and variability
of land evaporation and its components at the global scale. Hydrol. Earth Syst. Sci., 15, 967981.

- 956 Miralles, D., van den Berg, M., Gash, J., Parinussa, R., de Jeu, R., Beck, H., Holmes, D.,
- Jimenez, C., Verhoest, N., Dorigo, W., Teuling, A. J. and Dolman, J. 2014. El Niño-La Niña
- 958 cycle and recent trends in continental evaporation. Nature Clim. Change 4, 122–126
- 959
- Mott, K., Parkhurst, D., 1991. Stomatal responses to humidity in air and helox. Plant Cell
 Environ. 14, 509–515.
- 962
- 963 Mueller, B., Hirschi, M., Jimenez, C., Ciais, P., Dirmeyer, P., Dolman, A., Fisher, J., Jung,
- 964 M., Ludwig, F., Maignan, F., others, 2013. Benchmark products for land evapotranspiration:
- 965 LandFlux-EVAL multi-data set synthesis. Hydrol. Earth Syst. Sci. 17, 3707–3720.
- 966
- 967 Oleson, K.W., Lawrence, D.M., Bonan, G.B., Drewniak, B., Huang, M., Koven, C.D., Levis,
- 968 S., Li, F., Riley, W.J., Subin, Z.M., Swenson, S.C., Thornton, P.E., Bozbiyik, A., Fisher, R.,
- 969 Heald, C.L., Kluzek, E., Lamarque, J.-F., Lawrence, P.J., Leung, L.R., Lipscomb, W.,
- 970 Muszala, S., Ricciuto, D.M., Sacks, W., Sun, Y., Tang, J., Yang, Z.-L., 2013. Technical
- 971 Description of version 4.5 of the Community Land Model (CLM) (NCAR Technical Note No.
- 972 NCAR/TN-503+STR). Citeseer, National Center for Atmospheric Research, P.O. Box 3000,
- 973 Boulder, Colarado.
- 974
- 975 Pitman, A., 2003. The evolution of, and revolution in, land surface schemes designed for
- 976 climate models. Int. J. Clim. 23, 479–510.
- 977
- 978 Pitman, A.J., Avila, F.B., Abramowitz, G., Wang, Y.-P., Phipps, S.J., de Noblet-Ducoudré, N.
- 979 2011, Importance of background climate in determining impact of land-cover change on
- 980 regional climate. Nature Clim. Change, 1, 472–475.
- 981

Pollard, D., Thompson, S.L., 1995. Use of a land-surface-transfer scheme (LSX) in a global
climate model: the response to doubling stomatal resistance. Glob. Planet. Change 10, 129–
161.

985

Prentice, I. C., Dong, N. Gleason, S. M., Maire, V., Wright, I. J. 2014, Balancing the costs of
carbon gain and water transport: testing a new theoretical framework for plant functional
ecology. Ecology Letters, 17, 82-91.

989

990

891 Raupach, M., 1994. Simplified expressions for vegetation roughness length and zero-plane

- displacement as functions of canopy height and area index. Bound.-Layer Meteorol. 71, 211–216.
- 994
- 995 Raupach, M., Finkele, K., Zhang, L., 1997, SCAM (Soil-Canopy-Atmosphere Model):
- 996 Description and comparison with field data. Aspendale Aust. Csiro Cem Tech. Rep. 81.
- 997
- 998 Schymanski, S.J., Sivapalan, M., Roderick, M.L., Hutley, L.B., Beringer, J., 2009. An
- 999 optimality-based model of the dynamic feedbacks between natural vegetation and the water
- 1000 balance. Water Resour. Res. 45, W01412.

- Schlaepfer, W., Ewers, D. R., Shuman, B.E. Williams, B. N, Frank, D. G., Massman, J. M.
 Lauenroth, W. J. 2014, Terrestrial water fluxes dominated by transpiration: Comment.
 Ecosphere 5.
- 1005
- Schlesinger, W.H., Jasechko, S. 2014, Transpiration in the global water cycle. Agric. For.Meteorol. 189, 115–117.
- 1008
- 1009 Sellers, P., Bounoua, L., Collatz, G., Randall, D., Dazlich, D., Los, S., Berry, J., Fung, I.,
- 1010 Tucker, C., Field, C., Jensen, T.G., 1996. Comparison of radiative and physiological effects of
- 1011 doubled atmospheric CO₂ on climate. Science 271, 1402–1406.

1013 Sea, W. B., Choler, P., Beringer, J., Weinmann, R. A., Hutley, L. B., Leuning, R. 2011. 1014 Documenting improvement in leaf area index estimates from MODIS using hemispherical 1015 photos for Australian savannas. Agricultural and Forest Meteorology, 151, 1453–1461. 1016 1017 Serbin, S., Ahl, D. E., Gower, S. T. 2013, Spatial and temporal validation of the MODIS LAI 1018 and FPAR products across a boreal forest wildfire chronosequence. Remote Sens. Environ., 1019 133, 71–84 1020 1021 Shabanov, N. V., Huang, D., Yang, W. Z., Tan, B., Knyazikhin, Y., Myneni, R. B., Ahl, D. 1022 E., Gower, S. T., Huete, A. R., Aragao, L.E.O.C., Shumabukuro, Y. E. 2005. Analysis and 1023 optimization of the MODIS leaf area index algorithm retrievals over broadleaf forests. IEEE 1024 Trans Geosci Remote Sens., 43, 1855–1865 1025 1026 Stoy, P. C., Katul, G., Siqueira, M., Juang, J-Y., Novick, K. A., Uebelherr, J. M., Oren, R. 1027 1028 2006. An evaluation of models for partitioning eddy covariance-measured net ecosystem 1029 exchange into photosynthesis and respiration. Agr. Forest Meteorol., 141, 2-18. 1030 1031 R Core Development Team, 2013. R: A Language and Environment for Statistical 1032 Computing. R Foundation for Statistical Computing, Vienna, Austria. 1033 1034 Wang, Y., Papanatsiou, M., Eisenach, C., Karnik, R., Williams, M., Hills, A., Lew, V.L., 1035 Blatt, M.R., 2012. Systems Dynamic Modeling of a Guard Cell Cl- Channel Mutant Uncovers an Emergent Homeostatic Network Regulating Stomatal Transpiration. Plant 1036 1037 Physiol. 160, 1956–1967. 1038

- 1039 Wang, Y.P., Kowalczyk, E., Leuning, R., Abramowitz, G., Raupach, M.R., Pak, B., van
- 1040 Gorsel, E., Luhar, A., 2011. Diagnosing errors in a land surface model (CABLE) in the time
- 1041 and frequency domains. J. Geophys. Res. Biogeosciences 2005–2012 116.
- 1042
- 1043 Wang, Y.P., Leuning, R., 1998. A two-leaf model for canopy conductance, photosynthesis
- 1044 and partitioning of available energy I: Model description and comparison with a multi-layered
- 1045 model. Agric. For. Meteorol. 91, 89–111.
- 1046
- 1047 Wullschleger, S.D., Meinzer, F., Vertessy, R., 1998. A review of whole-plant water use1048 studies in tree. Tree Physiol. 18, 499–512.
- 1049
- 1050 Walden-Coleman, A.E., Rajcan, I., Earl, H.J., 2013. Dark-adapted leaf conductance, but not
- minimum leaf conductance, predicts water use efficiency of soybean (*Glycine max* L. Merr.).
 Can. J. Plant Sci., 93, 13–22.
- 1053

Williams, M., Rastetter, E.B., Fernandes, D.N., Goulden, M.L., Wofsy, S.C., Shaver, G.R.
and, 1996. Modelling the soil-plant-atmosphere continuum in a Quercus-Acer stand at
Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant
hydraulic properties. Plant Cell Environ. 19, 911–927.

- 1058
- 1059 Zaehle, S., Friend, A., 2010. Carbon and nitrogen cycle dynamics in the O-CN land surface
- 1060 model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates.

1061 Glob. Biogeochem. Cycles 24, GB1005.

1062

Zeppel, M. J. B., Lewis, J. D., Phillips, N., Tissue, D. T. (2014) Consequences of nocturnal
water loss: a synthesis of implications for capacitance, embolism, and use in models. Tree
Physiol., 34, 1047-1055.

1067 1068	Zhang, Q., Pitman, A., Wang, Y., Dai, Y., Lawrence, P., 2013. The impact of nitrogen and phosphorous limitation on the estimated terrestrial carbon balance and warming of land use
1069 1070	change over the last 156 yr. Earth Syst. Dyn. Discuss. 4, 507–539.
1071 1072 1073	Zhou, S., Duursma, R.A., Medlyn, B.E., Kelly, J.W., Prentice, I.C., 2013. How should we model plant responses to drought? An analysis of stomatal and non-stomatal responses to water stress. Agric. For. Meteorol., 182-183, 204-214.
1075 1076 1077	Zhou, S. Medlyn, B., Sabaté, S., Sperlich, D., Prentice, I. C. 2014, Short-term water stress impacts on stomatal, mesophyll and biochemical limitations to photosynthesis differ consistently among tree species from contrasting climates. Tree Physiol, 34, 1035-1046.
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1082	
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1089 Figure Captions

Figure 1: Stomatal sensitivity to increased vapour pressure deficit (*D*). The Leuning model has been parameterised in the same way as the CABLE model, for C3 species: $a_1 = 9.0$, D =1092 1.5 kPa and for C4 plants: $a_1 = 4.0$, $D_0 = 1.5$ kPa. The Medlyn model has been fit to output generated by the Leuning model using least squares for *D* ranging from 0.05 to 3 kPa. The calibrated parameters for the Medlyn model were $g_1 = 3.37$ and $g_1 = 1.09$ for C3 and C4 species, respectively.

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1097 Figure 2: Map showing the plant functional types (PFTs) currently used in CABLE

1098 (Lawrence et al. 2012). CABLE also has C4 crop, wetland and urban PFTs, however these are 1099 currently not operational.

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Figure 3: A comparison of the modelled average seasonal cycle of gross primary productivity (GPP), latent heat flux (LE), transpiration (E) and the observed (OBS) LE flux at 6 FLUXNET sites during approx. daylight hours (8 am – 7 pm). Timeseries have been averaged across all years as described in Table 4 to produce seasonal cycles. Light blue shading indicates the uncertainty in predicted fluxes from the Medlyn model (MED-P), accounting for ± 2 standard errors in the site g_1 parameter value.

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Figure 4: Mean diurnal modelled gross primary productivity (GPP), latent heat flux (LE), transpiration (E) and the observed (OBS) LE flux at the Howard Springs Fluxnet sites during daylight hours (8 am – 7 pm). Timeseries have been averaged across all years as described in Table 2 to produce diurnal seasonal cycles. Light blue shading indicates the uncertainty in predicted fluxes from the Medlyn model (MED-P), accounting for ± 2 standard errors in the site g_1 parameter value.

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1115 Figure 5: Average seasonal cycles of the simulated decoupling coefficient (Ω), total boundary

- 1116 layer conductance $(g_{\rm b})$ and stomatal conductance $(g_{\rm s})$ at 6 Fluxnet sites during daylight hours
- 1117 (8 am 7 pm). Timeseries have been averaged across all years as described in Table 2 to
- 1118 produce seasonal cycles. Light blue shading indicates the uncertainty in predicted fluxes from

1119 the Medlyn model (MED-P), accounting for ± 2 standard errors in the site g_1 parameter value.

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Figure 7: Mean seasonal (December-January-February: DJF and June-July-August: JJA) 1128 1129 difference maps of gross primary productivity (GPP) calculated across the 10 years of the 1130 Global Soil Wetness Project2 (GSWP-2) forcing (1986-1995) period. Panels (a) and (b) show 1131 the difference between the standard CABLE (LEU) model and the Medlyn model fit to the 1132 Leuning model (MED-L), panels (c) and (d) show the difference between the LEU model and the Medlyn model with the g_1 PFT parameterisation (MED-P), and finally, panels (e) and (f) 1133 1134 show the difference between the LEU model and the Medlyn model with the g_1 parameter 1135 predicted as a function of climate indices (MED-C). In total, 126 out of a possible 54,000 1136 pixels have been masked from panels (e) and (f), representing pixels where the temperature 1137 range and moisture index extended outside the range of the synthesis g_s database. at shown 1138 in panels (b), (c), (d), (e), (f) have been clipped, with the maximum ranges extending to (-1.6– 1139 0.36), (-1.28–3.03), (-1.19–3.82), (-1.2–2.9) and (-1.05–3.7) and this affects 1, 64, 34, 42 and 1140 147 pixels, respectively.

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Figure 8: Mean seasonal (December-January-February: DJF and June-July-August: JJA) difference maps of transpiration (E) calculated across the 10 years of the Global Soil Wetness Project2 (GSWP-2) forcing (1986-1995) period. Panels (a) and (b) show the difference between the standard CABLE (LEU) model and the Medlyn model fit to the Leuning model (MED-L), panels (c) and (d) show the difference between the LEU model and the Medlyn model with the g_1 PFT parameterisation (MED-P), and finally, panels (e) and (f) show the difference between the LEU model and the Medlyn model with the g_1 parameter predicted as

- a function of climate indices (MED-C). In total, 126 out of a possible 54,000 pixels have been
- 1150 masked from panels (e) and (f), representing pixels where the temperature range and moisture
- 1151 index extended outside the range of the synthesis g_s database. Data shown in panels (c), (d),
- (e), (f) have been clipped, with the maximum ranges extending to (-0.3-1.12), (-0.33-1.27)
- 1153 0.63–0.84) and (-0.64–1.31) and this affects 36, 251, 8 and 444 pixels, respectively.
- 1154
- 1155 Figure 9: Latitudinal average (December-January-February: DJF and June-July-August: JJA) of mean annual (a,b) gross primary productivity (GPP) and (c,d) evapotranspiration (ET) 1156 1157 predicted by the CABLE model compared to the upscaled FLUXNET and LandFlux-EVAL products. CABLE model simulations are shown are from the standard CABLE (LEU), the 1158 1159 Medlyn model fit to the Leuning model (MED-L), Medlyn model with the g_1 PFT parameterisation (MED-P) and the Medlyn model with the g_1 parameter predicted as a 1160 1161 function of climate indices (MED-C). The shading represents ± 1 standard deviation in the 1162 data product and ± 2 standard errors in the MED-P and MED-C models. Data shown cover the 1163 10 years of the Global Soil Wetness Project2 (GSWP-2) forcing (1986-1995) period. In total, 126 out of a possible 54,000 pixels have been masked from the zonal average of the MED-C 1164 1165 model, which represents pixels where the temperature range and moisture index extended outside the range of the synthesis g_s database. Missing data areas in the both data products 1166 1167 have been also been excluded from any comparisons (for example over the Sahara Desert, see 1168 Zhang et al. 2013).
- 1169
- Figure S1: Global maps showing the uncertainty of the g_1 model parameter. Panel (a) shows 2 standard errors (SE) and (b) + 2 SE for the fitted g_1 for each of CABLE's PFTs. Panel (c) shows –2 standard errors (SE) and (e) + 2 SE for predicted g_1 parameter values considering the influence of climate indices. In total, 126 out of a possible 54,000 pixels have been masked from panels (c) and (d), representing pixels where the temperature range and moisture index extended outside the range of the synthesis g_s database.

- 1177 Figure S2: Minimum measured stomatal conductance (g_s) as a function of corresponding
- 1178 photosynthesis rate, for each dataset in the Lin et al. (2015) synthesis g_s database with
- 1179 minimum photosynthesis rate $< 5 \text{ mol m}^{-2} \text{ s}^{-1}$. Data are separated into C3 (131 datasets) and

- 1180 C4 species (22 datasets). Also shown for comparison are the default g_0 values used in
- 1181 CABLE, as well as average night-time g_0 values for C3 and C4 plants, calculated from Figure
- 1182 2 in a review by Zeppel et al. (2014).

1185 Tables

PFT	g_1 mean (kPa ^{0.5})	g_1 standard error (kPa ^{0.5})
Evergreen needleleaf	2.35	0.25
Evergreen broadleaf	4.12	0.09
Deciduous needleleaf	2.35	0.25
Deciduous broadleaf	4.45	0.36
Shrub	4.70	0.82
C3 grassland	5.25	0.32
C4 grassland	1.62	0.13
Tundra	2.22	0.4
C3 cropland	5.79	0.64

1186 Table 1: Fitted g_1 values based on the CABLE PFTs using data from Lin et al. (2015).

1187

1188 Table 2: Model coefficients used in mixed effects model to predict g_1 from two long-term 1189 average (1960-1990) bioclimatic variables: temperature and a moisture index representing an

PFT	а	b	С	d	е
Evergreen needleleaf	1.32	0.03	0.02	0.01	-0.97
Evergreen broadleaf	1.32	0.03	0.02	0.01	-0.67
Deciduous needleleaf	1.32	0.03	0.02	0.01	-0.97
Deciduous broadleaf	1.32	0.03	0.02	0.01	-0.37
Shrub	1.32	0.03	0.02	0.01	-0.29
C3 grassland	1.32	0.03	0.02	0.01	-0.1
C4 grassland	1.32	0.03	0.02	0.01	-1.35
Tundra	1.32	0.03	0.02	0.01	-0.73

1190 indirect estimate of plant water availability.

C3 cropland	1.32	0.03	0.02	0.01	0.0
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Table 3: A summary of model simulations

Model	Description
Simulation	
LEU	Control experiment, standard CABLE model with the Leuning g_s model.
MED-L	Medlyn model with parameters (g_0 and g_1) calibrated against an offline Leuning model.
MED-P	Medlyn model with the g_1 parameter calibrated by PFT constrained by a global synthesis of stomatal data.
MED-C	Medlyn model with the g_1 parameters predicted from a mixed effects model considering the impacts of temperature and aridity.

Table 4: Summary of flux tower sites.

Site	FLUXNET Vegetation Type	CABLE PFT	Latitude	Longitude	Country	Years	Reference
Bondville	Cropland	C3 Crop	40.00 N	-88.29 W	US	1997-2006	
Cabauw	Grassland	C3 Grass	51.97 N	4.93 E	Holland	2003-2006	
Harvord	Deciduous	Deciduous	42.54 N	72 17 W	US	1004 2001	
Haivaid	broadleaf	broadleaf	42.34 IN	-/2.1/ W	05	1994-2001	
Howard	Woody Savannah	C4 grass	-12.49	131.15 E	Australia	2002-2005	
Springs			S				

Hyytiala	Evergreen	Evergreen	61.85 N	23.29 E	Finland	2001-2004
	needleleaf	needleleaf				
Tumbarumba	Evergreen	Evergreen	-35.66	148.15 E	Australia	2002-2005
	broadleaf	broadleaf	S			

1197 Table 5: Summary statistics of modelled and observed LE at the 6 FLUXNET sites during

1198 daylight hours (9 am – 18 pm) and over the peak-growing season (for Northern hemisphere

1199 sites, from June–July–August and for Southern Hemisphere sites, from December–January–

1200 February).

Site	RMSE			Bias			Index of Agreement		
	LEU	MED-L	MED-P	LEU	MED-L	MED-P	LEU	MED-L	MED-P
Bondville	109.91	102.74	109.78	-12.92	-9.50	-5.80	0.81	0.83	0.84
Cabauw	82.13	78.65	82.76	-13.54	-13.15	-12.75	0.78	0.80	0.79
Harvard	59.17	55.51	58.51	8.35	4.10	7.10	0.94	0.95	0.95
Howard	105.92	105.72	138.57	-4.86	1.16	-61.25	0.83	0.84	0.62
Springs									
Hyytiala	58.90	54.62	47.33	21.00	16.26	-0.24	0.89	0.89	0.89
Tumbarumba	130.91	124.28	124.84	-15.06	-14.30	-13.22	0.76	0.78	0.78

Table 6: Mean and 1 standard deviation difference in annual GPP between the LEU and
MED-L model, the LEU and MED-P models and the LEU-C models for each of CABLE's
PFTs. Where standard deviations are large relative to the mean it suggests large variability
between the LEU and other models within a PFT.

PFT	GPP: LEU – MED-L	GPP: LEU – MED-P	GPP: LEU – MED-C
	$(g C m^{-2} y^{-1})$	$(g C m^{-2} y^{-1})$	$(g C m^{-2} y^{-1})$
Evergreen needleleaf	-3.08 ± 18.39	39.05 ± 34.18	43.45 ± 24.2
Evergreen broadleaf	36.1 ± 51.93	76.12 ± 61.99	73.70 ± 65.08
Deciduous needleleaf	-1.84 ± 5.14	24.06 ± 5.35	34.03 ± 5.75
Deciduous broadleaf	-31.48 ± 57.77	-17.31 ± 38.0	-46.3 ± 69.01

Shrub	-69.28 ± 32.31	-45.46 ± 17.61	-35.39 ± 17.41
C3 grassland	-47.73 ± 46.83	-66.76 ± 41.55	-62.79 ± 50.02
C4 grassland	-93.04 ± 45.95	302.94 ± 113.93	115.53 ± 89.29
Tundra	0.3 ± 12.63	16.61 ± 14.16	13.36 ± 11.02
C3 cropland	-26.85 ± 36.51	-64.93 ± 36.58	-65.45 ± 58.21

1207	Table 7: Mean and 1 standard deviation difference in annual E between the LEU and MED-L
1208	model, the LEU and MED-P models and the LEU-C models for each of CABLE's PFTs.
1209	Where standard deviations are large relative to the mean it suggests large variability between
1210	the LEU and other models within a PFT.

PFT	E: LEU – MED-L	E: LEU – MED-P	E: LEU – MED-C
	$(mm y^{-1})$	$(mm y^{-1})$	$(mm y^{-1})$
Evergreen needleleaf	16.55 ± 9.78	76.27 ± 36.34	81.72 ± 29.36
Evergreen broadleaf	34.34 ± 14.34	27.31 ± 14.7	22.66 ± 48.16
Deciduous needleleaf	10.5 ± 6.18	54.36 ± 17.07	67.03 ± 17.83
Deciduous broadleaf	11.15 ± 13.61	0.56 ± 8.45	-10.16 ± 34.36
Shrub	-11.14 ± 5.2	-4.81 ± 5.51	-1.68 ± 6.21
C3 grassland	0.34 ± 10.68	-17.37 ± 8.63	-15.51 ± 19.63
C4 grassland	-11.99 ± 5.67	107.77 ± 41.88	47.34 ± 32.21
Tundra	5.9 ± 3.87	24.13 ± 14.38	20.96 ± 11.75
C3 cropland	0.8 ± 12.37	-30.07 ± 12.36	-28.56 ± 30.11

	PFT	LEU (JJA; DJF)	MED-P (JJA; DJF)	MED-C (JJA; DJF)				
1214	product and the CABLE model.							
1213	describing the root mean squared error (RMSE) and bias between the FLUXNET-MTE GPP							
1212	Table 8: Summary statistics for December–January–February (DJF) June–July–August (JJA),							

	RMSE	Bias	RMSE	Bias	RMSE	Bias
Evergreen needleleaf	3.23; 0.4	2.73; 0.11	2.98; 0.39	2.42; 0.1	2.92; 0.39	2.37; 0.1
Evergreen broadleaf	2.31; 2.29	1.87; 1.57	2.14; 2.16	1.66; 1.36	2.12; 2.09	1.68; 1.36
Deciduous needleleaf	4.41; 0.00	4.37; 0.00	4.17; 0.00	4.13; 0.00	4.07; 0.00	4.03; 0.00
Deciduous broadleaf	2.33; 1.81	1.75; 1.27	2.33; 1.88	1.78; 1.33	2.35; 1.97	1.82; 1.42
Shrub	0.98; 0.86	0.72; 0.51	1.10; 0.95	0.84; 0.61	1.08; 0.91	0.82; 0.57
C3 grassland	1.86; 1.44	1.37; 0.85	2.09; 1.57	1.67; 0.97	2.06; 1.59	1.61; 0.99
C4 grassland	3.15; 2.36	2.55; 1.73	2.43; 1.67	1.77; 0.94	2.94; 2.16	2.24; 1.43
Tundra	2.48; 0.29	1.79; 0.03	2.31; 0.27	1.62; 0.03	2.34; 0.27	1.66; 0.03
C3 cropland	1.96; 1.25	1.33; 0.83	2.18; 1.39	1.64; 0.94	2.13; 1.43	1.59; 0.96
Table 9: Sur describing the reference.	nmary statistiche root mean	cs for Deceml squared error	per–January–I (RMSE) and	February (DJF bias taking th) June–July–A ne GLEAM E	August (JJA) T product a
PFT	LEU (JJ	(A; DJF)	MED-P ((JJA; DJF)	MED-C (JJA; DJF)
	RMSE	Bias	RMSE	Bias	RMSE	Bias
Evergreen	2.37; 1.83	0.79; 0.24	2.28; 1.83	0.31; 0.23	2.27; 1.83	0.26; 0.23

needleleaf						
Evergreen	2.17; 2.32	-0.05; -	2.18; 2.34	-0.12; -	2.17; 2.32	-0.1; -0.31
broadleaf		0.25		0.32		
Deciduous needleleaf	1.45; 0.69	1.15; -0.02	1.19; 0.69	0.75; -0.02	1.13; 0.69	0.65; -0.0
Deciduous broadleaf	2.69; 2.43	0.79; 0.58	2.69; 2.43	0.77; 0.58	2.69; 2.43	0.78; 0.61
Shrub	1.25; 1.34	0.29; 0.47	1.24; 1.34	0.29; 0.46	1.25; 1.34	0.29; 0.45
C3 grassland	1.66; 1.49	0.53; 0.34	1.67; 1.5	0.55; 0.36	1.67; 1.5	0.54; 0.37
C4 grassland	1.37; 1.38	0.33; 0.29	1.32; 1.35	0.2; 0.09	1.35; 1.35	0.29; 0.2
Tundra	2.35; 1.88	0.74; 0.37	2.31; 1.88	0.55; 0.36	2.31; 1.88	0.57; 0.36
C3 cropland	1.8; 1.38	0.9; 0.29	1.85; 1.39	0.98; 0.3	1.84; 1.39	0.97; 0.3





















Figure S1



Figure S2

