Authors reply to: Interactive comment on “Modeling stomatal conductance in the Earth system: linking leaf water-use efficiency and water transport along the soil-plant-atmosphere continuum” posted by S. Otto

1. The formula of Goudriaan’s G-function approximation $G = \phi_1 + \phi_2 \mu$ is not correct. It holds $G = \phi_1 + \phi_2 |\mu|$

Response: CLM calculates solar zenith angle over the range 0-$\pi/2$ so μ (cosine of solar zenith angle) is equal to $|\mu|$

2. The usage of Goudriaan’s G-function approximation is not the best one in my opinion. There are better approximations of Dickinson and deRidder. Moreover, there are exact formulas of G for various standard leaf normal distributions functions (spherical, uniform, planophile etc.). Why aren’t they applied?

Response: The intent of this study was to investigate alternative stomatal conductance parameterizations for Earth system models, not radiative transfer schemes. However, as clarification we note that CLM uses the two-stream radiative transfer parameterization (developed by Robert Dickinson and Piers Sellers) and also implemented in the SiB series of land surface models by Sellers et al. The function $G = \phi_1 + \phi_2 \mu$ is used to calculate parameters required by the two-stream approximation in addition to direct beam extinction coefficient (average inverse diffuse optical depth per unit leaf area; single scattering albedo).

3. Since the G-function is (not only) part of the solar exponential term of the radiative transfer equation, small deviations (e.g. due to inaccuracies) in G can have a big impact on the transported radiation, photosynthesis calculations and so on. How do both facts influence the results of your work?

Response: The intent of this study was not to investigate radiative transfer schemes. Moreover, many parameters are used by CLM and other such land surface models. Uncertainty in the G-function would need to be investigated as part of a larger study of parameter/parameterization uncertainty in land surface models. Our study clearly demonstrates that error in stomatal conductance response to soil moisture stress has a large impact on model simulations and provides a path forward to implement soil moisture stress.

Authors reply to: Interactive comment on “Modeling stomatal conductance in the Earth system: linking leaf water-use efficiency and water transport along the soil-plant-atmosphere continuum” posted by E. Blyth

This is an excellent paper that needs to be published. The ideas in it are very exciting. We have been waiting a long time to break away from the Ball-Berry method of linking photosynthesis and transpiration and their links to soil water stress. The assumptions in the Ball-Berry method have dominated the Land Surface Models used in climate modelling and depend on a difficult to calibrate link between stoma and humidity deficit that I think is not entirely mechanistic. For such an important aspect of the earth system, it is really important to explore new ways of solving the riddle and this paper describes a very promising avenue. The paper is well written and would allow other researchers to try the ideas out. I urge that the paper is published forthwith.

Response: We thank Eleanor for her endorsement of this manuscript.

Authors reply to: Interactive comment on “Modeling stomatal conductance in the Earth system: linking leaf water-use efficiency and water transport along the soil-plant-atmosphere continuum” posted by M. De Kauwe

We thank Martin for his informative and constructive comments, which have helped improve the manuscript.

1. The authors don’t appear to acknowledge that detlaAn/deltaEl is essentially Cowan and Farquhar. Given this, I am struggling a little with figure 6 and the lack of text afforded this key figure. The Medlyn model is derived from Cowan and Farquhar and so my expectation is that detlaAn/deltaEl would be more similar to this model, however there is clear ordering to the scatter. Do the authors have any thoughts as to why this might be? One suggestion I would have is to ask them what they fit the g1 parameter to, i.e. what range of VPD? I see that the figure caption says 0-2.6 kPa, but is this actually what the model parameter was fit against? Alternatively how is moisture stress accounted for in this plot, is it excluded, apologies if this was made clear but I have missed it.

Response: (a) We do not mean to imply that our dA_n/dE_l optimization is anything but the Cowan-Farquhar optimization. We discuss the Cowan-Farquhar water-use efficiency optimization in the introduction and assumed that the details are commonly known. To clarify that we have indeed implemented a numerical version of this optimization we re-write this text (new text in italics): “This theory assumes that the physiology of stomata has evolved to constrain the rate of water loss (E_l) for a given unit of carbon gain (A_n) (Cowan, 1977; Cowan and Farquhar, 1977). This optimization can be achieved by assuming that g_s varies to maintain water-use efficiency constant over some time period (*formally this means that* $\partial A_n/\partial E_l$ = *constant; note that Cowan (1977) and Cowan and Farquhar (1977) discussed optimization in the context of the marginal water cost of carbon gain so that* $\partial E_l/\partial A_n$ = *constant).*” Additionally, where we contrast the SPA dA_n/dg_s optimization with the dA_n/dE_l optimization we re-write the text to read: “*We additionally tested the Cowan (1977) and Cowan and Farquhar (1977) water-use efficiency optimization (WUE;* $\Delta A_n/\Delta E_l$*, the marginal carbon gain of water loss)*”

(b) With regard to Figure 6: Our intent with this figure was merely to show that the numerical stomatal optimization can reproduce the Ball-Berry and Medlyn stomatal models. We do not believe that the figure should be interpreted to say that the Ball-Berry model (with h_s) is better than the Medlyn model (with $1/\mathrm{sqrt}(D_s)$). Many environmental factors (air temperature, relative humidity, solar radiation, wind speed) varied simultaneously in the data presented in the figure. This does not provide the best basis for comparison (a controlled experimental protocol would likely be more informative). We delete this figure to avoid confusion and to reduce the manuscript length. Instead, we present in the text the correlation coefficient (r), the slope of the regression, and statistical significance.

2. Following on from the above, a question that I feel should be explored in the discussion is “how much of an improvement in model skill makes such an implementation justified”? This is somewhat provocative, but I think it might be worth tackling. I feel figures such as 11 are a little bit of a straw man, though I understand why they exist and don’t have a major issue with the point being made. But the authors are advocating an iterative optimisation framework should be

inserted into a detailed land surface model. How computational expensive is this likely to be? Is the improvement in model skill justified by the expense? Given that models derived from Cowan and Farquhar exist and are by their nature similar to this approach, what is the trade off in not using them? The authors make the valid point that understanding how these simpler models operate with moisture stress and VPD are difficult, but is this alternative approach really a step forward? Certainly work exists to show how such relationships could be derived (see Zhou et al. 2013, AFM).

Response: Referee Duursma and referee De Kauwe both make a similar point with reference to analytical stomatal conductance models derived from water-use efficiency optimization theory, particularly the Medlyn et al stomatal model (Duursma was second author on that manuscript and De Kauwe has authored subsequent studies with Medlyn using the model). In these comments they ask us to justify why we do not use their stomatal conductance model. Our intent was (and still is) to compare the CLM approach with the SPA approach, not to evaluate the merits of the Medlyn stomatal conductance model. A key feature of the SPA stomatal conductance parameterization is the soil moisture control of stomatal conductance. This, not the details of numerical (SPA) or analytical (Medlyn et al.) water-use efficiency optimization, is important for the CLM and SPA comparisons.

Since the referees raise the issue, it is worth pointing out that the Medlyn model is derived from the Farquhar photosynthesis model based on water-use efficiency optimization, but only for RuBP-limited (light-limited) assimilation. They argue that this is appropriate, because much of the canopy is light-limited (see also Medlyn et al. 2013; Agric. Forest Meteorol., 182/183, 200-203). More complex stomatal conductance models are obtained for Rubisco-limited assimilation (Katul et al. 2010; Annals of Botany, 105, 431-442) or co-limited assimilation (Vico et al. 2013; Agric. Forest Meteorol., 182/183, 191-199), and there is some sharp disagreement on the merits of these various stomatal conductance models. Our intent is not to enter this debate, but we clarify our statements with respect to closed-form variants of the Ball-Berry model. We add the text: "*Variants of the model can be derived from the Farquhar et al. (1980) photosynthesis model based on water-use efficiency optimization, after some simplifying assumptions, but the form and complexity of the model varies among Rubisco-limited (Katul et al., 2010), light-limited (Medlyn et al., 2011b), or co-limited (Vico et al., 2013) rates.*"

A second key point is that the numerical solution optimizes photosynthetic carbon gain per unit water loss while also preventing leaf water potential dropping below a critical minimum level. The model is therefore an optimality model with two distinct criteria (water-use efficiency and hydraulic safety) as opposed to implementations of the Cowan & Farquhar concept, which only consider water-use efficiency. It is this latter control of stomatal conductance by leaf water potential that is critical to the numerical optimization. Other approaches use a Ball-Berry style conductance, empirically modified for soil water. Our approach allows us to calculate the soil moisture stress directly from physiological principles.

As for the added computational cost, that is very subjective and varies with computational platform and software engineering. At NCAR, the run time for CLM is less than 5% that of the atmosphere model. Part of the reviewer's concerns over computational costs may have arisen from our description of the stomatal optimization routine, which was described as numerically incrementing stomatal conductance until the optimization is achieved. This gives the impression that the algorithm increments g_s by a fixed amount at each iteration. In fact, numerical techniques (Brent's method) can efficiently find the optimal g_s. We re-write the text and change Fig 2 to clarify this.

We add text to the discussion to address the computational cost:

"*Our approach, as in SPA, numerically optimizes photosynthetic carbon gain per unit water loss while also avoiding desiccation by preventing low leaf water potential. Alternatively, Ball–Berry style stomatal conductance models provide an analytical equation for stomatal functioning and can be combined with an empirical dependence on soil moisture or leaf water potential (Tuzet et al., 2003; Duursma and Medlyn, 2012; Zhou et al., 2013). However, the greater computational cost (and also the benefit) of the model presented here, relative to CLM4.5, is not the numerics of the stomatal optimization but rather resolving gradients within the canopy. Bonan et al. (2012) showed that inexactness in the absorption of diffuse radiation by shaded leaves leads to errors in GPP for a sunlit/shaded big-leaf canopy model relative to a multi-layer canopy model. This error can be decreased with high values for the nitrogen decay coefficient (K_n), but such values are inconsistent with field estimates (Lloyd et al., 2010). A similar inexactness arises due to gradients of leaf water potential within the canopy. One of the outcomes of the SPA stomatal optimization is that leaves in the upper canopy, with high solar radiation and high transpiration rates, close their stomata to avoid desiccation. Non-linear gradients of light, nitrogen, and leaf water potential must be accounted for when formulating theories of canopy optimization (Peltoniemi et al., 2012). Just as multi-layer profiles of soil carbon are being recognized as important for carbon cycle–climate feedbacks (Koven et al., 2013), profiles in the plant canopy may similarly be important for vegetation–atmosphere coupling. Here, we resolve the canopy leaf area profile at high resolution (increments of 0.1 m^2 m^{-2}). Other SPA simulations successfully divide the canopy into fewer layers (e.g., 10 layers with a leaf area index of 3.5 m^2 m^{-2}, Williams et al., 1996).*"

3. Furthermore, if you look at figure 13/15, I could envisage it might be 'cheaper' to implement a alternative moisture stress scalar on the Ball-Berry model, or additionally adjusting the slope of stomatal conductance model and I would suggest this would arrive at a better model-data match from the Ball Berry model, perhaps questioning the necessity for an iterative optimisation scheme?

Response: Yes, this is exactly the point of these figures. With less soil water stress, the CLM Ball-Berry model works fine. Note that the original submission states: "In our simulations, higher β_t improves the Ball-Berry model" in the presentation of the US-Me2 simulations. We reiterate this point in the discussion: "*In our simulations, higher β_t (less soil moisture stress) improves the CLM-BB model (Figure 12), suggesting that the parameterization of soil moisture stress, not the stomatal model per se, is erroneous.*" However, we also note that our approach calculates the soil moisture stress directly from physiological theory whereas soil moisture stress scalars applied to the Ball-Berry model are by nature empirical.

4. 20 figures feels excessive and in my opinion makes the story of the manuscript hard to follow. Often very little text ends up being dedicated to figure discussion. For example, what is the (fig

10) Taylor diagram actually meant to show? The figure caption offers little detail on how to interpret such a diagram. Do we really need net radiation on the figures when assessing model ’improvement’? Does it add anything? Is Figure 20 necessary? Figure 13 and 15 seems excessively detailed (number of panels). I could go on, I think many of these figures could comprise a supplementary section as they currently detract from the message the authors wish to express.

Response: We delete two figures from the original submission (Figs. 6 and 9). We add text to the discussion of the Taylor diagrams to help readers understand the plots. Net radiation is important to include when comparing model simulations with flux tower observations, because net radiation constrains sensible and latent heat flux. It is necessary to show that the model can reasonably simulate observed net radiation.

We agree that 20 figures (reduced to 18) is large. However, we note that the reviewer stated that: “I particularly like the ways the authors have separated estimates at the leaf and canopy scale and the way they have tackled explaining the differences.” Referee Remko Duursma similarly endorsed the leaf- and canopy-scale evaluation with the comment: “The simulations are separated by leaf-scale and canopy-scale, which I find very useful to help understand the differences between models (rather than just showing the full model behaviour as a black box, which is still too common).” In revisions, we have: 3 figures (Figs. 1-3) describing the model formulation; 3 figures documenting leaf-scale simulations (Figs. 4-6); 8 figures (Figs. 7-14) for canopy simulations; and 4 figures (Figs. 15-18) documenting model sensitivity. These last 4 figures are necessary to address parameter sensitivity and why the model gets the correct results.

5. Minor - The literature review appears to miss a key text when discussing the debate over what stomata respond to: Mott ’88. And generally the text seemingly skates over many other important works in this area.

Response: We purposely do not provide a thorough review of stomatal physiology and stomatal models. Our intent with this manuscript is merely to compare the Ball-Berry model (which is commonly used in land surface models) with the SPA numerical optimization model (which has not been widely used). We re-write the introduction to make this intent more obvious.

6. The authors should dedicate more text to what they mean by optimisation, they describe in terms of a ’model time step’. How long is the model time step they are referring to (presumably 30 minutes)? Are the stomata always behaving optimally? Or do they generally behave optimally over the course of day?

Response: We re-write the text (new text in italics): “Stomatal conductance is *numerically solved* at each *model* time step (*30–60 minutes depending on frequency of flux tower data*) such that further opening does not yield a sufficient carbon gain per unit water loss (defined by a stomatal efficiency parameter ι, μmol CO_2 mol^{-1} H_2O) or further opening causes leaf water potential (ψ_l) to decrease below a minimum value (ψ_{lmin}).”

7. Coupling - The authors make the point in section 2.4.1 that they have used a parameterisation that would suggest strong coupling to the atmosphere (roughness length). Is this the only

resistance in the model? Is there also a boundary layer at the leaf surface? This is not clear from the text.

Response: Equations in the appendix show that leaf sensible heat flux, latent heat flux, temperature, and photosynthesis depend on leaf boundary layer conductance. In the original submission we do not give the equations and state simply that: “Leaf boundary layer conductances vary with leaf dimension and wind speed.” In the revision, we provide these equations.

Authors reply to: Interactive comment on “Modeling stomatal conductance in the Earth system: linking leaf water-use efficiency and water transport along the soil-plant-atmosphere continuum” posted by R. A. Duursma

We thank Remko for his informative and constructive comments, which have helped improve the manuscript.

1. The authors present an optimization of dA/dE as an alternative to the dA/dgs optimization currently employed in SPA, but do not admit that this method is identical to the Cowan-Farquhar optimization framework. Instead, the method is presented as an alternative without explanation (e.g. 89-21). That is, no explanation is given as to why we would follow that optimization algorithm. This can be resolved by explaining clearly throughout that the authors have implemented a numerical solution to the Cowan-Farquhar optimization hypothesis, rather than ‘an alternative algorithm’. In fact, the authors do seem to be aware of this in the Discussion (107-24 and onwards), when they discuss the correspondence between lambda (the marginal cost of water in the Cowan-Farquhar framework) and the stomatal efficiency (the ‘iota’ parameter in SPA and this manuscript). This fact should be made much more clear throughout the manuscript.

Response: We do not mean to imply that our dA_n/dE_l optimization is anything but the Cowan-Farquhar optimization. We discuss the Cowan-Farquhar water-use efficiency optimization in the introduction and assumed that the details are commonly known. To clarify that we have indeed implemented a numerical version of this optimization we re-write this text (new text in italics): “This theory assumes that the physiology of stomata has evolved to constrain the rate of water loss (E_l) for a given unit of carbon gain (A_n) (Cowan, 1977; Cowan and Farquhar, 1977). This optimization can be achieved by assuming that g_s varies to maintain water-use efficiency constant over some time period (*formally this means that* $\partial A_n/\partial E_l$ *= constant; note that Cowan (1977) and Cowan and Farquhar (1977) discussed optimization in the context of the marginal water cost of carbon gain so that* $\partial E_l/\partial A_n$ *= constant).*” Additionally, where we contrast the SPA dA_n/dg_s optimization with the dA_n/dE_l optimization we re-write the text to read: “*We additionally tested the Cowan (1977) and Cowan and Farquhar (1977) water-use efficiency optimization (WUE;* $\Delta A_n/\Delta E_l$*, the marginal carbon gain of water loss)*”

2. This leads to my second point. Why is it necessary to implement a full numerical solution to the optimization hypothesis? Medlyn et al (2011) showed that their simplified (Ball-Berry like) equation fits very well to a full numerical solution (their Figure 2). The closed-form equation would save on computing time (as one fewer iterative loop is necessary as shown in Fig. 2). It does raise the question of why the (simplified version of the) Medlyn equation did not compare very well to the dA/dE optimization method (Fig. 6), but this may be due to effects of soil water stress? To resolve this, the authors should explain their motivation for a full numerical solution, also in the context of the added simulation time (which is relevant for a journal like GMD).

Response: Referee Duursma and referee De Kauwe both make a similar point with reference to analytical stomatal conductance models derived from water-use efficiency optimization theory, particularly the Medlyn et al stomatal model (Duursma was second author on that manuscript and De Kauwe has authored subsequent studies with Medlyn using the model). In these comments they ask us to justify why we do not use their stomatal conductance model. Our intent was (and still is) to compare the CLM approach with the SPA approach, not to evaluate the merits of the Medlyn stomatal conductance model. A key feature of the SPA stomatal conductance parameterization is the soil moisture control of stomatal conductance. This, not the details of numerical (SPA) or analytical (Medlyn et al.) water-use efficiency optimization, is important for the CLM and SPA comparisons.

Since the referees raise the issue, it is worth pointing out that the Medlyn model is derived from the Farquhar photosynthesis model based on water-use efficiency optimization, but only for RuBP-limited (light-limited) assimilation. They argue that this is appropriate, because much of the canopy is light-limited (see also Medlyn et al. 2013; Agric. Forest Meteorol., 182/183, 200-203). More complex stomatal conductance models are obtained for Rubisco-limited assimilation (Katul et al. 2010; Annals of Botany, 105, 431-442) or co-limited assimilation (Vico et al. 2013; Agric. Forest Meteorol., 182/183, 191-199), and there is some sharp disagreement on the merits of these various stomatal conductance models. Our intent is not to enter this debate, but we clarify our statements with respect to closed-form variants of the Ball-Berry model. We add the text: "*Variants of the model can be derived from the Farquhar et al. (1980) photosynthesis model based on water-use efficiency optimization, after some simplifying assumptions, but the form and complexity of the model varies among Rubisco-limited (Katul et al., 2010), light-limited (Medlyn et al., 2011b), or co-limited (Vico et al., 2013) rates.*"

A second key point is that the numerical solution optimizes photosynthetic carbon gain per unit water loss while also preventing leaf water potential dropping below a critical minimum level. The model is therefore an optimality model with two distinct criteria (water-use efficiency and hydraulic safety) as opposed to implementations of the Cowan & Farquhar concept, which only consider water-use efficiency. It is this latter control of stomatal conductance by leaf water potential that is critical to the numerical optimization. Other approaches use a Ball-Berry style conductance, empirically modified for soil water. Our approach allows us to calculate the soil moisture stress directly from physiological principles.

As for the added computational cost, that is very subjective and varies with computational platform and software engineering. At NCAR, the run time for CLM is less than 5% that of the atmosphere model. Part of the reviewer's concerns over computational costs may have arisen from our description of the stomatal optimization routine, which was described as numerically incrementing stomatal conductance until the optimization is achieved. This gives the impression that the algorithm increments g_s by a fixed amount at each iteration. In fact, numerical techniques (Brent's method) can efficiently find the optimal g_s. We re-write the text and change Fig 2 to clarify this.

We add text to the discussion to address the computational cost:

"*Our approach, as in SPA, numerically optimizes photosynthetic carbon gain per unit water loss while also avoiding desiccation by preventing low leaf water potential. Alternatively, Ball–Berry style stomatal conductance models provide an analytical equation for stomatal functioning and can be combined with an empirical dependence on soil moisture or leaf water potential (Tuzet et al., 2003; Duursma and Medlyn, 2012; Zhou et al., 2013). However, the greater computational cost (and also the benefit) of the model presented here, relative to CLM4.5, is not the numerics of* *the stomatal optimization but rather resolving gradients within the canopy. Bonan et al. (2012) showed that inexactness in the absorption of diffuse radiation by shaded leaves leads to errors in GPP for a sunlit/shaded big-leaf canopy model relative to a multi-layer canopy model. This error can be decreased with high values for the nitrogen decay coefficient (K_n), but such values are inconsistent with field estimates (Lloyd et al., 2010). A similar inexactness arises due to gradients of leaf water potential within the canopy. One of the outcomes of the SPA stomatal optimization is that leaves in the upper canopy, with high solar radiation and high transpiration rates, close their stomata to avoid desiccation. Non-linear gradients of light, nitrogen, and leaf water potential must be accounted for when formulating theories of canopy optimization (Peltoniemi et al., 2012). Just as multi-layer profiles of soil carbon are being recognized as important for carbon cycle–climate feedbacks (Koven et al., 2013), profiles in the plant canopy may similarly be important for vegetation–atmosphere coupling. Here, we resolve the canopy leaf area profile at high resolution (increments of 0.1 m^2 m^{-2}). Other SPA simulations successfully divide the canopy into fewer layers (e.g., 10 layers with a leaf area index of 3.5 m^2 m^{-2}, Williams et al., 1996).*"

3. The stomatal conductance model includes a full implementation of the energy balance, which is necessary as it affects the leaf-air temperature difference (Tleaf-Tair), which affects leaf-to-air VPD and thus stomatal conductance (gs) itself. However, it would be very helpful to understand the results if the authors would discuss how well coupled the canopy is (that is, values of the boundary layer conductance both at leaf and canopy scales). For example, in Fig. 5, a curvilinear response of A to gs is demonstrated when Vcmax (and I assume Jmax, though this is not stated) was varied across a wide range. If Tleaf=Tair, this relationship should yield a set of straight lines, not curves (as at a given set of environmental drivers, the ratio A/gs will indicate the marginal cost of water. Therefore it is not affected by Vcmax or Jmax). These curves can be explained by the boundary layer : as Vcmax increases, gs increases, which decreases Tleaf, decreases VPD, and allows a higher gs at given A (because lower VPD means lower E at a given gs, which would open the stomata slightly if dA/dE is constant). It would be very helpful if the authors explained this, and other, results in terms of Tleaf-Tair, as currently it is not possible to separate those effects from the assumptions embedded in the optimization hypotheses. At the moment, this pattern is not explained whatsoever, just stated (102-14).

Response: The reviewer raises two points here. (a) Leaf-air coupling in relation to leaf boundary layer and canopy aerodynamic conductance. He makes a similar point in comment #4 (immediately below), and we address this in our response to #4. (b) With regard to Figure 5: The reviewer is correct in explanation of the curvilinear response in Fig 5b. We do not want to elaborate too much on this, because the manuscript is already long and this is not a main point of the manuscript, but add the text: "*The curvilinear response arises from interactions among stomatal conductance, leaf temperature, and vapor pressure deficit.*"

4. Related to the above, the degree of coupling can be expected to be very different for the canopy simulations (canopy+leaf boundary layers) compared to the leaf simulations (leaf boundary layers only). It seems from the main results of the canopy-scale simulations that the different model implementations actually did not have a very large effect on simulations of the latent heat flux (Figs. 9, 11, 14 and possibly the Taylor diagrams but those confuse me I have to confess). This could be the case if canopy latent heat flux is mostly energy limited (poorly

coupled), but the authors have not presented the information necessary to evaluate this. Also, net radiation simulations are only relevant in the context of modeling Tleaf-Tair, but this is not discussed nor presented. I find a thorough discussion of the boundary layer conductances and their effects on gas exchange simulations crucial to understand the results in this manuscript.

Response: The reviewer makes several points here. (a) The reviewer is correct in noting that the canopy simulations include the leaf boundary layer and aerodynamic conductances while the leaf simulations include only the leaf boundary layer conductance. It is beyond the scope of this manuscript to evaluate these differences (and the manuscript is already quite long). We have additional CLM development that investigates alternative above- and within-canopy aerodynamics and turbulence parameterizations (which have been a weakness in land surface models). The leaf-air coupling should be addressed in that context. (b) Net radiation is important to include when comparing model simulations with flux tower observations, because net radiation constrains sensible and latent heat flux at the canopy scale. (c) We add the leaf boundary layer conductance equations to the model appendix and give representative values.

5. In the Abstract and elsewhere, ‘the Ball-Berry model’ is confused with the actual implementation in CLM, especially in reference to drought stress. In CLM, drought stress effect is only on g0 and A, not on g1 (as many others have done, which is admitted in the manuscript). So, a statement like “The SPA-WUE optimization performs significantly better than the Ball–Berry model when there is soil moisture stress” (106-19) cannot refer to the Ball-Berry model (since that does not include any soil water stress effect), but only to the particularly strange implementation in CLM. This should be carefully worded throughout the manuscript. It also raises the question why the authors did not try a simple soil moisture stress effect on g1 in the Ball-Berry model as an alternative to the full complex numerical simulation?

Response: (a) We now distinguish between the “Ball–Berry” model and the Ball-Berry model as implemented in CLM. The CLM implementation is denoted by “CLM Ball–Berry”, abbreviated as “CLM-BB”. (b) Yes, we make exactly this point in our analysis of US-Me2 (with drought stress). With less soil water stress, the CLM Ball-Berry model works fine. Note that the original submission states: “In our simulations, higher β_t improves the Ball–Berry model” in the presentation of the US-Me2 simulations. We reiterate this point in the discussion: “*In our simulations, higher β_t (less soil moisture stress) improves the CLM-BB model (Figure 12), suggesting that the parameterization of soil moisture stress, not the stomatal model per se, is erroneous.*” However, we also note that our approach calculates the soil moisture stress directly from physiological theory whereas soil moisture stress scalars applied to the Ball-Berry model are by nature empirical.

6. The authors have implemented a hydraulic maximum on transpiration rate, which is a useful way to include soil water stress effects on gs. However, it should be made more clear that we really have two models here : an optimization algorithm (either dA/dgs or dA/dE), coupled with a maximum transpiration rate framework. When E = Emax, the optimization framework is not relevant, since transpiration will simply follow the maximum allowable E, given soil water stress and components of the soil-plant water transport pathway. A lot of the results could be better understood if it is shown whether the gs predictions are from optimization or the hydraulic constraint. For example, in Figures 8 and 14, in which of the timesteps was LWP = minLWP?

This could be shown with two different colours of the symbols. At the moment it is unclear whether the improvements are due to the optimization criterion, or due to the inclusion of a hydraulic maximum transpiration rate.

Response: We performed additional simulations in which the minLWP control of g_s was removed (so that g_s depends only on the water-use efficiency optimization algorithm). We present these simulations in the results section with the following text. We do not add new figures, because the manuscript is already long.

"The importance of soil moisture stress for the flux tower simulations is further highlighted by SPA-iWUE and SPA-WUE simulations that eliminated stomatal closure when leaf water potential (ψ_l*) decreased below* ψ_{lmin} *(this removes stomatal dependence on soil moisture). In these simulations, stomatal conductance is only regulated by the stomatal efficiency parameter. The greatest difference in these simulations compared with the full model is seen in latent heat flux and GPP on sites that are drought stressed. At US-Me2 during the July 2002 drought, for example, latent heat flux in the SPA-WUE simulation is overestimated with removal of* ψ_{lmin}*, and the model skill declines from 0.92 to 0.81. GPP is similarly overestimated, and the skill declines from 0.91 to 0.86. Sensible heat flux skill is unchanged. Similar results are seen in July 2005. The reduction in model skill is greater for the SPA-iWUE optimization, for which the decline in* ψ_l *with high transpiration rates is a key regulator of stomatal conductance. At US-Me2 during the July 2002 drought, the latent heat flux skill decreases from 0.86 to 0.42, GPP skill decreases from 0.92 to 0.69, and sensible heat flux skill decreases from 0.96 to 0.79 with removal of soil moisture stress. At other flux tower sites, where soil water stress is less important, the skill of the model is not greatly affected when soil water stress is neglected (i.e.,* ψ_{lmin} *is removed)."*

SPECIFIC COMMENTS AND TECHNICAL CORRECTIONS

87-16 : 'vapor pressure deficit term', this is confusing because VPD has not been mentioned yet. To resolve, write the Ball-Berry model in the paragraph above with an f(VPD) term instead of hs.

Response: We use the standard notation for the Ball-Berry model, with humidity (h_s) instead of vapor pressure deficit (D_s). We then show the relationship between h_s and D_s. We replace "vapor pressure deficit term" with "*vapor pressure deficit*".

87-24 : Oren et al. did not demonstrate a D**-0.5 dependence of gs (though the ln(D) response is similar).

Response: We delete the reference to Oren et al. (1999).

88-4 : Other methods have used both, and this seems to be quite successful (see Zhou et al. 2013 10.1016/j.agrformet.2013.05.009).

Response: We add the sentence: "*Some evidence suggests that both diffusive and biochemical limitations must be considered (Zhou et al., 2013).*"

88-6 : ‘alternative approach’. Alternative to what? The previous paragraph already mentioned optimization, and the approach described in this paragraph does not account for soil water stress either.

Response: We replace “alternative approach” with “*An alternative to the Ball–Berry model of stomatal conductance…*”

89-5 : What about Hickler et al. 2006 (10.1111/j.1466-8238.2006.00254.x)? They included a hydraulic framework into LPJ, this should be cited and discussed here.

Response: Our intent is not to provide a thorough review of this class of model. We state: “Many models of plant hydraulic architecture exist that explicitly represent the movement of water to and from the leaf (McDowell et al., 2013).” We believe that this review is a good starting point into the literature. And our statement refers specifically to the “land surface models used with Earth system models”. LPJ is not one of those land surface models.

89-21 : The SPA algorithm has no inherent stomatal response to VPD, but this does emerge as a result of the minimum leaf water potential (minLWP) assumption. Once this minLWP is reached, a further increase in D would decrease gs at a rate 1/D (so as to keep LWP constant). This is not described well in this manuscript (and Fig. 3 implies there is no VPD response, but this result is only for when LWP > minLWP). It would also be relevant to cite Misson et al. 2004 in this context (TreePhys 24, 529-541).

Response: We agree that our text is misleading. We rephrase the text to read: “*In that approach, stomatal response to D_s emerges from stomatal closure with low leaf water potential.*”

91-25 : “The Ball–Berry model requires an iterative calculation of gs and An”. Actually Ci may be calculated without iteration, as the intersection between supply curve (diffusion constraint) and demand (the Farquhar A-Ci model) can be written as a quadratic and solved (as is done in Maestra/Maespa, see https: //bitbucket.org/remkoduursma/maespa/src, file physiol.f90, subroutine PHOTOSYN). This may be worth considering for the implementation of CLM, as again it may yield a decrease in simulation time.

Response: The specific solution for C_i that the reviewer refers to is for C3 plants. CLM is a global model and also simulates C4 plants, for which that solution is not valid. Other versions of CLM use a product-limited rate and co-limitation among the three photosynthetic rates (for both C3 and C4 plants). The C_i iteration (shown in Fig 2) is a general approach that maintains flexibility among the various implementations of the Farquhar model and among C3 and C4 plants. The greatest portion of the iteration in the CLM implementation is with respect to leaf temperature, independent of how C_i is calculated. We clarify this by new text (in italics): “…requires an iterative calculation of g_s and A_n, *because photosynthetic parameters vary with leaf temperature and leaf temperature varies with transpiration rate* (Figure 2a).

91-28 : StomataL conductance

Response: Corrected

92-3 : decrease

Response: Corrected

93-3 : ‘can be observed directly’, What does this mean? Actually the minimum leaf water potential is very difficult to measure; when do we know it really is the minimum value? Even Choat et al. 2012 (there cited) uses the lowest value ever recorded for that species, hardly a direct measurement.

Response: We delete this sentence.

94-6 : I don’t understand the relevance of the detailed discussion of the components of the plant hydraulic conductance, as the only value really needed is the whole-plant leaf-specific hydraulic conductance (94-25 onwards)? The latter is normally estimated from the nearly straight relationship between E and LWP-LWPpredawn.

Response: The purpose of this section is to constrain the leaf-specific stem hydraulic conductance (k_p) based on observations. As mentioned in the first paragraph of the section, several previous implementations of SPA used a value that varied by a factor of 30 among various papers. We show that our value is consistent with literature estimates. To clarify this, we add new text (in italics): “we used a leaf-specific stem hydraulic conductance k_p = 4 mmol H_2O m^{-2} leaf area s^{-1} MPa^{-1}, estimated from stem, root, and whole-plant conductance reported in the literature *as follows below*.” In the paragraph detailing observational estimates of k_p, we add the sentence: “*Our value for k_p is consistent with observational estimates.*” We delete the discussion on the root component to whole-plant conductance, except to justify the assumption of equal root and shoot conductance. With this assumption, we show that our stem conductance (k_p) is consistent with observational estimates of whole-plant conductance (k_L).

94-12 : It is not possible to convert hydraulic conductivity (measured on shoots by Tyree) to whole trees when only considering the path length. As vessels taper (and to a differing degree), whole-stem conductance does not simply follow from shoot hydraulic conductivity.

Response: We delete this sentence.

95-15 : Explain here in detail that stomatal efficiency is the inverse of lambda (for the dA/dE algorithm)

Response: We revise the text to clarify that $\Delta A_n/\Delta g_s$ is from SPA and the $\Delta A_n/\Delta E_l$ is from Cowan (1977) and Cowan and Farquhar (1977). We add a sentence: “*This latter approach follows Cowan (1977) and Cowan and Farquhar (1977), with ι the inverse of their optimization parameter lambda (based on $\partial E_l/\partial A_n$, the marginal water cost of carbon gain).*”

95-19 : This is very tentative, as Glopnet likely includes a wide range of VPD (not just very low; many of the measurements are taken around midday). How different are the estimates of iota when you assume, say, a VPD of 1.5 or 2kPa?

Response: We revise this text to say that our estimate of ι is consistent with, not estimated from, the Glopnet leaf trait database. The new text is: "*These values give maximum* A_n *and* g_s *that are consistent with observations from the Glopnet leaf trait database (Wright et al., 2004) and that minimize root mean square error in canopy-scale simulations.*" See also our response to comment 102-2 (below).

96-11 : It is not clearly described why an estimate of the root hydraulic resistivity is needed here. It affects the total plant kL, but does it matter otherwise? Please explain.

Response: We add the text: "*The root-to-stem conductance* (k_r) *requires a root hydraulic resistivity* (R_r^*)*.*"

97-7 : For which year were the simulations performed (CO2 = 367ppm is quite low).

Response: Simulation years vary among tower sites and are given in Table 1. The value of 367 ppm is used in CLM4.5, and we used the same value here to allow comparisons with CLM4.5

98-9 : This section is not clear to me. What do the 'random errors' represent and why is this approach useful?

Response: We add two sentences to this discussion: "*Flux measurement errors arise from systematic bias and random errors (Richardson et al., 2012)*" and "*Random errors in flux measurements occur because of sampling errors, errors in the instrument system, and other factors and can be large (Richardson et al., 2012)*"

98-20 : Why was g0 varied to include even very large values (0.1 mol m-2 s-1)?

Response: Other studies report a value as high as 0.06, and Melanie Zeppel (in a visit to NCAR) mentioned g0 as high as 0.1 mol/m2/s. However, the parameter sensitivity studies clearly select for a value < ~0.045. The very high values do not produce results consistent with the flux tower measurements and are discarded from further analysis.

98-21 : It should be mentioned that the SPA routines implicitly assume that g0 =0 (unless this was added as a minimum conductance, but this is not mentioned).

Response: SPA does have a minimum conductance. We add this to the appendix, in our description of the SPA stomatal conductance optimization.

98-25 : Why vary the four components of the belowground conductance, not just the total hydraulic conductance? The four components are varied by different orders of magnitude (MT 2.5 fold, rr 5 fold, rd 2.5 fold and Rr 50 fold). It is then no surprise that "Root resistivity [Rr] explains 85

Response: Each of the four parameters is required to calculate belowground conductance. We assess which of these parameters is most important for matching the flux tower data. The range of parameter values is based on observations of the four different properties reported in literature. One strength of the model is that total root resistance can be related to these observations. We added the sentence: "*The range of parameter values reflects the range of values reported in literature and previous modeling studies.*"

100-12 : Was Jmax co-varied with Vcmax?

Response: Yes. We add the text: "*The photosynthetic parameters* J_{max25} *and* R_{d25} *are proportional to* V_{cmax25} *and so also varied.*" We add these equations in the model description (appendix).

100-22 : This is the further simplified form of the Medlyn 2011 model (mention that here). It is useful because it can be used as an index for illustration (unlike the 1+ form of the equation).

Response: Our intent here is to perform a similar analysis as Medlyn et al (2011), Fig. 3 and Table 2 using the index $A_n/c_s/\mathrm{sqrt}(D_s)$. We cite Medlyn et al. (2011) as the reference.

101-16 : As mentioned above, this misses the point that if LWP = minLWP, gs responds steeply to VPD in the dA/dgs algorithm.

Response: We delete this text.

101-20 : Why is this analysis presented here, how is it relevant to the manuscript? As the number of figures is far too large anyway, perhaps this is not necessary. This issue was already discussed by Katul et al. (2009), to which nothing new is added here.

Response: Yes, Katul et al. (2009) discussed this (which we acknowledge and cite). We feel that this is a necessary verification of the numerical stomatal optimization model. We return to this point in the discussion.

102-2 : Please admit here that Glopnet is not very well suited at all to testing stomatal conductance models, in fact I would advocate removing that entire comparison as Glopnet does not even include fundamental drivers (VPD, Tair, CO2). It is a useful dataset to study broad plant trait patterns, not detailed gas exchange models.

Response: The relationship between maximum A_n and g_s has been a hallmark in developing theories of stomatal functioning across plant functional types (especially during the 1980s and 1990s). We think it is important to show that the stomatal efficiency parameters (ι_* and ι) affect the simulated relationship between A_n and g_s. We agree that matching the Glopnet database (because of its uncertainty) does not show that the model is correct. We re-write this paragraph in the results to better emphasize this point: "*With iWUE and WUE optimization,* A_n *increases as* g_s *increases (Figure 5). This is consistent with the range of observations of maximum* A_n-g_s *from the Glopnet leaf trait database, but direct comparisons are not possible because of uncertainties in the conditions for which the measurements were obtained.*" In our discussion of stomatal efficiency in the discussion section, we state: "*The stomatal efficiency determines the relationship between maximum* g_s *and* A_n *seen in leaf trait databases (Figure 5).*"

102-20 : This should be no surprise, given that Medlyn et al. 2011 already demonstrated that these stomatal indices fit well to the full numerical solution, because they are based on the same principles. However it is unclear (as mentioned above) why panel 6d shows such a poor correlation. Can you explain the reason for this? Was it inadvertently switched with 6c (the Ball-Berry model surely should give a worse comparison, since it uses relative humidity).

Response: Our intent with this figure was merely to show that the numerical stomatal optimization can reproduce the Ball-Berry and Medlyn stomatal models. We do not believe that the figure should be interpreted to say that the Ball-Berry model (with h_s) is better than the Medlyn model (with 1/sqrt(D_s)). Many environmental factors (air temperature, relative humidity, solar radiation, wind speed) varied simultaneously in the data presented in the figure. This does not provide the best basis for comparison (a controlled experimental protocol would likely be more informative). We delete this figure to avoid confusion and to reduce the manuscript length. Instead, we present in the text the correlation coefficient (r), the slope of the regression, and statistical significance.

105-13 : 'to some extent' is vague.

Response: We delete this phrase.

105-21 : This is not unexpected, but it is useful to discuss Barnard Bauerle 2013 (10.1002/jgrg.20112) in this context, who did not take into account this strong correlation in a sensitivity analysis (and thus wrongly concluded g0 is very important).

Response: This is a minor point in our analysis. Given the already long manuscript, we do not want to expand upon the point, but we add the sentence: "*Analyses that vary only g_0 or g_1 may erroneously produce acceptable simulations.*"

106-2 and Abstract : as commented above, the only reason Rr seems important is because it was varied 50-fold. Also, the Abstract focuses exclusively on this parameter but it is not demonstrated that the model fit could only be improved by varying Rr (and not other parameters related to belowground hydraulics).

Response: The large range of parameter values reflects the large uncertainty of this parameter (see response to 98-25 above). We agree that, given their multiplicative impacts on total root resistance, soil hydraulic parameters could also be important, but that is beyond the scope of this model documentation.

107-15 : This is correct, but only when T is constant. In field conditions D and T are strongly correlated, which actually gives a different effective relationship between gs and D (see Duursma et al. 2014 (10.1016/j.agrformet.2013.12.007). This point is often overlooked.

Response: We clarify our discussion of this by adding text to the leaf-scale results section: "*In these simulations, air temperature was held constant (T_{ref} = 22.6 °C) and relative humidity* *varied from 5–100% so that D_s varied from 0.8 to 2.7 kPa. Leaf temperature was nearly constant, but decreased from 29.1 °C to 27.0 °C as D_s increased.*"

Conclusion – though well written, I find the conclusions to be much too general compared to the current study. Perhaps this can be focussed to be more relevant to the current study.

Response: We wrote the discussion section to address specific points raised in this study. We wrote the conclusion to be a general summary.

Fig. 9 – the modelled diurnals are obscured by the measurements. Use of transparent colors would resolve this.

Response: We delete this figure to reduce the length of the manuscript.

Fig. 10 and 12 – what does REF mean?

Response: REF refers to a value of 1.0. We change the graphs to show this.