



Ideas and perspectives: How coupled is the vegetation to the boundary layer?

Martin G. De Kauwe¹, Belinda E. Medlyn², Jürgen Knauer³, and Christopher A. Williams⁴

¹Department of Biological Science, Macquarie University, North Ryde NSW 2109 Australia

²Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith NSW 2751 Australia

³Department of Biogeochemical Integration, Max Planck Institute for Biogeochemistry, 07745 Jena, Germany

⁴Graduate School of Geography, Clark University, 950 Main Street, Worcester, MA01602 USA

Correspondence to: Martin De Kauwe (mdekauwe@gmail.com)

Abstract. Understanding the sensitivity of transpiration to stomatal conductance is critical to simulating the water cycle. This sensitivity is a function of the degree of coupling between the vegetation and the atmosphere, and is commonly expressed by the decoupling factor. The level of decoupling assumed by models varies considerably and has previously been shown to be a major cause for model disagreement when simulating changes in transpiration in response to elevated CO₂. The degree of coupling also offers us insight into how different vegetation types control transpiration fluxes, fundamental to our understanding of land–atmosphere interactions. To explore this issue, we estimated the decoupling factor from FLUXNET data, finding notable departures from values previously reported in single site studies. Evergreen needleleaf forests appear to be on the whole more decoupled than the literature suggests, whilst evergreen broadleaved forests and shrubs were considerably more coupled than is suggested in the literature or than would be predicted based on leaf size and plant stature. We found that the assumption that grasses would be strongly decoupled (due to vegetation stature) was only true for high precipitation sites. These results were robust to assumptions about aerodynamic conductance and energy balance closure. Thus, these data form a benchmarking metric against which to test model assumptions about coupling. Our results identify a clear need to improve the quantification of the processes involved in scaling from the leaf to the whole ecosystem. Progress could be made with targeted measurement campaigns at flux sites, as well as more site characteristic information across the FLUXNET network.

15 1 Introduction

Predicting the response of transpiration to global change and the subsequent feedback to climate remains a major challenge for Earth system models (Zhu et al., 2017). Improving our understanding of how stomatal controls on transpiration vary between vegetation types is fundamental to simulating land–atmosphere interactions. Experimental evidence strongly indicates that stomatal conductance (G_s) is generally reduced in response to elevated CO₂ (Morison, 1985; Medlyn et al., 2001; Ainsworth and Rogers, 2007). In models, incorporating this leaf-level reduction in G_s commonly results in predictions of decreased transpiration and increased runoff at global scales (Gedney et al., 2006; Betts et al., 2007; Cao et al., 2010). However, the magnitude of this effect varies strongly among models, because the sensitivity of transpiration to a change in G_s depends on the assumption made about the strength of coupling of the vegetation to the surrounding boundary layer (Jarvis and McNaughton,



1986; McNaughton and Jarvis, 1991; Jacobs and De Bruin, 1992). De Kauwe et al. (2013) identified differences in the degree of coupling to be a major cause of disagreement among 11 model predictions of transpiration in response to elevated CO₂ at two forest Free-Air CO₂ Enrichment (FACE) experiments in the USA. Consequently, resolving this discrepancy among models in their assumptions of vegetation-atmosphere coupling is key to reducing model uncertainty in future predictions of changes in transpiration.

The degree of coupling between vegetation and the atmosphere is commonly expressed by the decoupling factor (Ω ; Jarvis and McNaughton, 1986). If the decoupling factor is high, transpiration is more strongly controlled by incoming radiation and less by changes in G_s . Low stature-canopies, and species with large leaves, are expected to be more decoupled (high Ω), than tall-stature canopies, and species with small leaves. Values given in the literature for coniferous forests are typically low, $\Omega = \sim 0.1-0.2$ (Whitehead et al., 1984; Jarvis, 1985; Lee and Black, 1993; Meinzer et al., 1993), although Launiainen (2010) reported a higher summertime value (0.32) at the Hyytiälä site in Finland. Values are typically higher for deciduous broadleaved: $\Omega = 0.2-0.4$ (Magnani et al., 1998; Wullschleger et al., 2000), evergreen broadleaved species: $\Omega = 0.4-0.9$ (Meinzer et al., 1997; Wullschleger et al., 1998; Cienciala et al., 2000), grasses: $\Omega = 0.8$ (McNaughton and Jarvis, 1983), and crops: $\Omega = 0.2-0.9$ (Black et al., 1970; Brown, 1976; Meinzer et al., 1993; Mielke et al., 1999). These literature estimates of the degree of decoupling are wide and thus, do not offer a clear constraint to models. Furthermore, methods to estimate Ω often differ across studies, which complicates interpretations about variation across plant functional types. Single studies, that have employed a consistent method to estimate Ω across multiple species are rare (e.g. Stoy et al., 2006).

There has been considerable recent effort to develop better global datasets of stomatal behaviour for use by the modelling community (Lin et al., 2015; Miner et al., 2017). However, constraining the coupling between stomatal conductance and transpiration is equally important. For example, De Kauwe et al. (2015) demonstrated modest changes in transpiration when using the Lin et al. (2015) dataset to constrain the parameterisation of G_s in the Community Atmosphere Biosphere Land Exchange (CABLE) land surface model. The CABLE model assumes a relatively high level of decoupling (De Kauwe et al., 2013). It is likely that models that assume stronger coupling (e.g. the Joint UK Land Environment Simulator, JULES; Best et al., 2011) would obtain different results.

To shed new light on this important question of vegetation-atmosphere coupling, we used eddy-covariance data from FLUXNET to estimate the Ω coefficient for different plant functional types (PFTs). We aimed to: (i) examine if decoupling coefficients estimated from FLUXNET were consistent with literature values; and (ii) develop a benchmark metric against which to test model assumptions about coupling.



2 Materials and Methods

2.1 Flux Data

Half-hourly eddy covariance measurements of the exchange of carbon dioxide, energy and water vapour were obtained from the FLUXNET “La Thuile” Free and Fair dataset (<http://www.fluxdata.org>). We estimated the degree of decoupling (Jarvis and McNaughton, 1986) as:

$$\Omega = \frac{1 + \epsilon}{1 + \epsilon + \frac{G_a}{G_s}} \quad (1)$$

where $\epsilon = s / \gamma$, s is the slope of the saturation vapour pressure curve at air temperature (Pa K^{-1}), γ is the psychrometric constant (Pa K^{-1}) and λ is the latent heat of water vapour (J mol^{-1}).

We estimated values of G_s by inverting the Penman-Monteith equation using measured latent heat (LE) flux for all datasets where the net radiation (R_n ; W m^{-2}) and the frictional velocity (u_* ; m s^{-1}) where available:

$$G_s = \frac{G_a \gamma \lambda E}{s(R_n - G) - (s + \gamma)\lambda E + G_a M_a c_p D} \quad (2)$$

where G_a ($\text{mol m}^{-2} \text{s}^{-1}$) is the canopy aerodynamic conductance, E ($\text{mol m}^{-2} \text{s}^{-1}$) is the canopy transpiration, γ is the psychrometric constant (Pa K^{-1}), D (Pa) is the vapour pressure deficit, G (W m^{-2}) is the soil heat flux, M_a (kg mol^{-1}) is molar mass of air, c_p is the heat capacity of air ($\text{J kg}^{-1} \text{K}^{-1}$). At sites where values of G were not available, G was set to zero.

G_a was calculated following Thom (1975):

$$G_a = \frac{c}{\frac{u}{u_*^2} + 6.2u_*^{-\frac{2}{3}}} \quad (3)$$

where $c = P / (R_{\text{gas}} T_k)$ is a conversion factor from units of m s^{-1} to $\text{mol m}^{-2} \text{s}^{-1}$, P is atmospheric pressure (Pa), R_{gas} is the gas constant ($\text{J mol}^{-1} \text{K}^{-1}$), T_k is the air temperature in Kelvin, and u (m s^{-1}) is the wind speed.

The approach we have taken (similar to Jarvis and McNaughton, 1986) ignores differences between canopy and air temperature (radiative coupling) within the canopy (see Martin, 1989). However, correcting for the longwave radiative conductance (G_r) most impacts vegetation with the weakest control on transpiration the most and as a result, this assumption has little impact on the decoupling range for forest species, but may be a factor for other species.

Flux data were first screened as follows: (i) data flagged as “good”; (ii) data from the three most productive months, to account for the different timing of summer in the Northern and Southern hemispheres; (iii) daylight hours between 8 am and 4 pm; (iv) half-hours with precipitation, and the subsequent 48 half-hours, were excluded; and (v) data with a $u_* < 0.25$ were excluded to avoid conditions of low turbulence (Sánchez et al., 2010).



Pressure was estimated using the hypsometric equation based on site elevation data. Where site elevation information was missing, values were gap-filled using the 30-arc second (~1 km) global digital elevation model GTOPO30 data from the United States Geological Survey (USGS). After filtering, 175 sites and 634 site-years remained.

We also tested the sensitivity of estimated values to: (i) errors in G_a ; and (ii) errors due to a lack of energy balance closure. First, we increased/decreased estimated values of G_a by 30% to examine the sensitivity of G_s values inverted from the Penman-Monteith equation. Secondly, following recommendations by Wohlfahrt et al. (2009), we tested the sensitivity of our results to energy balance closure, by correcting the Bowen-ratio (each half-hourly LE and H flux) based on the available energy ($R_n - G$) on a longer time scale (three most productive months).

2.2 Results

Broadly speaking, estimated decoupling coefficients differed among PFTs in line with previous literature values (Fig. 1) and in line with expectations related to vegetation roughness and/or stature. Evergreen needleleaf forests (ENF), which have small leaves, were tightly coupled (low Ω), while deciduous broadleaved forests and tropical rain forest (large leaves), and C_3 grasses and crops (small stature), had greater levels of decoupling (higher Ω). However, the low decoupling coefficient for evergreen broadleaf forests (despite their large leaves and rough canopy structure), as well as the range of decoupling coefficients for C_3 grasses, were surprising. The high level of coupling from sites with shrubs was also unexpected, given the expectation that shorter stature vegetation would be more decoupled. Across PFTs, the range of decoupling factors was less than that typically cited in the literature. The median value for ENF is above 0.2, in contrast to the range suggested by Jarvis (1985) (0.1–0.2), while the median value for broadleaf forests and crops is below 0.5, which is towards the lower end of previously quoted ranges (0.2–0.9) (Meinzer et al., 1993, 1997; Wullschleger et al., 1998; Cienciala et al., 2000).

Among ENF sites, the range in estimated values shown in Fig. 1 was striking, extending from ~0.05 to ~0.4. To attempt to better understand this range better, we first separated ENF sites into: (a) sites with a low inter-annual coefficient of variation (20%), indicating consistent year-to-year estimates of decoupling; (ii) sites with a coefficient of variation > 20%, indicating sites with year-to-year variability in coupling; and (iii) sites with only two years of data. This separation was intended to rule out sampling issues. Figure 2 shows that the variability in estimated decoupling coefficient cannot be explained by sampling bias, with significant site-to-site variability, irrespective of the inter-annual variability.

We then probed these results for relationships with site variables, by testing to see if: (i) sites with higher precipitation (in the three most productive months) were more decoupled, where precipitation was assumed to be a proxy for leaf area index (LAI)/productivity; or (ii) windy sites were more coupled. For C_3 grasses we found a significant relationship between the degree of decoupling and precipitation (Fig. 3). The data suggest that in more open grasslands (i.e. sites with a low precipitation) the vegetation is very coupled to the atmosphere, with a high level of stomatal control. This relationship between decoupling and precipitation ($r=0.77$) explains the high variability in estimated decoupling coefficients for C_3 grasses shown in Fig. 1. The prediction that grasses would be strongly decoupled due to small vegetation stature only holds true at sites with high 3-month precipitation, which are presumably sites with high LAI. We also found a significant relationship for ENF sites ($r=0.46$), and deciduous broadleaved forests ($r=0.63$) suggesting that decoupling increased with canopy density. We also found evidence of a



weak negative relationship ($r=-0.21$) between wind speed and the degree of coupling for forest sites, i.e. windier sites tended to be more coupled (Fig 4).

Finally, we examined sensitivity of our results to potential errors. We tested whether our results were sensitive to different estimates of G_a and whether our estimates of G_s were sensitive to energy imbalance. We found that the broad pattern of our results in Fig. 1 was insensitive to errors in G_a . Increasing or decreasing G_a by 30%, led to the median decoupling coefficient increasing or decreasing by roughly 0.05 for evergreen broadleaf forest (EBF) sites for example. However, we did find that our results were sensitive to a correction for the lack of energy balance closure. Figure S1 shows that attempting to correct for a lack of closure leads to sites becoming more decoupled, but does not shift the between-PFT differences in decoupling. The largest changes were for C3 crops (Ω changed from ~ 0.4 to ~ 0.6) and shrubs (Ω changed from ~ 0.2 to ~ 0.3).

10 2.3 Discussion

Correctly characterising the sensitivity of transpiration to G_s is critical for simulating the water cycle, particularly for future projections of the terrestrial biosphere where it is widely expected that G_s will decrease in response to increasing atmospheric CO_2 . The parameterisation of this crucial link between leaf- and canopy-scale water fluxes has been largely ignored in model studies addressing the impact of elevated CO_2 (Betts et al., 2007; Cao et al., 2010; Zhu et al., 2017). Resulting projections of changes in transpiration and associated fluxes (e.g. runoff, precipitation) are likely to be model-specific, with large uncertainty among models (De Kauwe et al., 2013). Model studies rarely provide information about the degree of decoupling assumed within the model. The range of assumptions commonly incorporated in models include: (i) coupling is a function of roughness length (determined by vegetation height), e.g. JULES; (ii) coupling is a function of leaf size, e.g. CLM (the Community Land Model; Oleson et al., 2013); (iii) coupling is affected by within canopy turbulence, e.g. CABLE (Raupach et al., 1997; Kowalczyk et al., 2006); (iv) some combination of all three, e.g. CABLE/CLM (v) coupling is not sensitive to low wind speeds (i.e. wind speed is fixed), e.g. SDGVM (Sheffield dynamic vegetation model; Woodward et al., 1995); or (vi) models that use an alternative to the Penman-Monteith equation, e.g. LPJ (Lund-Potsdam-Jena family of models; Sitch et al., 2003). This family of models use an empirically calibrated hyperbolic function of canopy conductance (Huntingford and Monteith, 1998) and the implied level of coupling depends on how this function is parameterised.

Understandably, the pioneering work of Jarvis and colleagues (e.g. Jarvis and McNaughton, 1986) is widely cited when issues of coupling are discussed in the literature. However, many of the earlier estimates of coupling are taken from single sites and thus do not necessarily reflect the diversity of global vegetation. In this study we have leveraged data from FLUXNET to estimate decoupling factors across a wide range of sites. Unlike previous studies that have collated estimates of coupling across studies (e.g. Jarvis and McNaughton, 1986), in which methods to estimate coupling may have differed, we have applied a consistent methodology across all the FLUXNET sites. For forest species, our results point to a greater level of decoupling than is often assumed. Notably, ENF species were found to be less coupled across the FLUXNET network than work by Jarvis and others suggested. We found that the often assumed high degree of decoupling for grasses is likely to only be true for high precipitation (and presumably high LAI) sites; low precipitation sites were strongly coupled. A further plausible explanation is that these drier sites are limited by available soil moisture, with lower G_s resulting in a high degree of coupling. We could



not easily explain the coupling values estimated for evergreen broadleaf forests, which were estimated to be more coupled than evergreen needleleaf forests; a break from theoretical understanding developed from vegetation roughness and/or stature. Finally, grouping the data by PFTs also highlighted marked within-PFT variation in the degree of coupling.

As land models move towards more realistic representations of the variability of stomatal conductance, informed by leaf-level syntheses (Lin et al., 2015; Miner et al., 2017; De Kauwe et al., 2015), it is also important that they accurately simulate the coupling between vegetation and the atmosphere. Without this focus, any efforts to improve the realism at the leaf-scale will not be reflected in improvements in simulated transpiration at the canopy scale.

2.3.1 Caveats

One criticism of the approach taken here is that we have assumed a big-leaf approximation to estimate vegetation decoupling (see Raupach and Finnigan, 1988). It is of course likely that variation within a canopy in terms of micro-climate (i.e. vapour pressure deficit, irradiance, temperature), as well as how stomata respond, may invalidate this approach. Use of a big-leaf approximation could be a possible explanation for the surprisingly low level of decoupling found in evergreen broadleaf forests, although it would appear unlikely given the higher level of decoupling found for deciduous broadleaved and tropical rainforest species.

We found high variation in the estimated decoupling factor both across sites and within sites. Two assumptions we make with respect to the flux data could explain this variation. Firstly, we excluded data for 24 hours after rainfall (Law et al., 2002; Groenendijk et al., 2011; Dekker et al., 2016) to minimise the effects of soil evaporation. Clearly, if soil evaporation is still a component of the LE flux after this point it would introduce error to our estimates. Secondly, flux towers commonly do not close the energy balance (Foken, 2008; Wilson et al., 2002). Our use of the inverted Penman-Monteith equation implies that we are attributing any errors due to energy imbalance to the sensible heat flux. Additionally, where data on the soil heat flux were missing, we assumed there was no storage. Correcting for these issues is not straightforward as it requires determining which flux is the source of the error (see Wohlfahrt et al., 2009, for a detailed discussion). We followed recommendations by Wohlfahrt et al. (2009) and tested the sensitivity of our results to energy balance closure, by correcting the Bowen-ratio based on the available energy ($R_n - G$). Whilst we did find some sensitivity in our results (particularly for C3 crops and shrubs), it did not change the ordering of decoupling factors between PFTs, or explain the unexpected high level of decoupling for EBF sites.

Finally, we estimated the canopy aerodynamic conductance (G_a) using an empirical equation following Thom (1975). Knauer et al. (in review) tested the impact on different methods of estimating G_a from flux data on estimates of the stomatal slope parameter (the sensitivity of stomatal conductance to assimilation). They found that correcting G_a for atmospheric instabilities only led to small increases in estimates of G_a during daytime growing conditions. They also found that a more physically-based representation of G_a (Su et al., 2001), led to lower estimate of G_a at two EBF flux sites, and higher estimates of G_a at another EBF and a deciduous broadleaved site. We tested the sensitivity of our results to a change in G_a of the order shown by Knauer et al. and found that the patterns in decoupling to be robust across PFTs.



2.3.2 Route forward

Estimates of decoupling from ecosystem scale flux data are directly relevant for models. We previously speculated (De Kauwe et al., 2013) that discrepancies among models in decoupling might be resolved by examining eddy covariance data. The range in decoupling factors we have estimated from the FLUXNET data provides an overall constraint on the level of decoupling that should be assumed in models, as well as an indication of the appropriate degree of variability in decoupling across PFTs and rainfall regimes.

Our results also identify a clear need to better understand leaf-to-atmosphere coupling. We need to better understand why decoupling factors vary within PFTs. There are a number of plausible explanations, such as drought, diversity of vegetation within a flux footprint, data issues, and it is likely that more detailed site-specific insight will be required to move forward. To assist in better understanding patterns, we will need greater detail in terms of ancillary data from FLUXNET sites. We attempted to probe our results with respect to canopy height and LAI, but for many sites this information was not available. Other potentially useful information would include leaf size, stem density and crown length, and whether canopy height is static or increasing. These data would facilitate more sophisticated approaches to be explored, for example stability corrections and/or estimates of G_a based on leaf size (Su et al., 2001). A more fundamental process understanding will require targeted G_s measurements throughout the canopy, alongside corresponding sap flux measurements in forests and chamber measurements in grasslands. Targeted measurements campaigns at flux sites could lead to new knowledge, which would advance our understanding of the processes involved in scaling from the leaf to the canopy.

Code availability. All code is freely available from: https://github.com/mdekauwe/flux_decoupling

Data availability. All Eddy covariance data are available from: <http://fluxnet.fluxdata.org/data/la-thuille-dataset/>

20 *Competing interests.* The authors declare no competing financial interests.

Acknowledgements. This work used eddy covariance data acquired by the FLUXNET community and in particular by the following networks: AmeriFlux (U.S. Department of Energy, Biological and Environmental Research, Terrestrial Carbon Program (DE-FG02-04ER63917 and DE-FG02-04ER63911)), AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, CarboItaly, CarboMont, ChinaFlux, Fluxnet-Canada (supported by CFCAS, NSERC, BIOCAP, Environment Canada, and NRCan), GreenGrass, KoFlux, LBA, NECC, OzFlux, TCOS-Siberia, USCCC. We acknowledge the financial support to the eddy covariance data harmonization provided by CarboEuropeIP, FAO-GTOS-TCO, iLEAPS, Max Planck Institute for Biogeochemistry, National Science Foundation, University of Tuscia, Université Laval and Environment

Biogeosciences Discuss., doi:10.5194/bg-2017-182, 2017

Manuscript under review for journal Biogeosciences

Discussion started: 17 May 2017

© Author(s) 2017. CC-BY 3.0 License.



Canada and US Department of Energy and the database development and technical support from Berkeley Water Center, Lawrence Berkeley National Laboratory, Microsoft Research eScience, Oak Ridge National Laboratory, University of California, University of Virginia.



References

- Ainsworth, E. and Rogers, A.: The response of photosynthesis and stomatal conductance to rising [CO₂]: mechanisms and environmental interactions, *Plant, Cell and Environment*, 30, 258–270, doi:10.1111/j.1365-3040.2007.01641.x, 2007.
- 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, O., Cox, P. M., Grimmond, C. S. B., and Harding, R. J.: The Joint UK Land Environment Simulator (JULES), model description – Part 1: Energy and water fluxes, *Geoscientific Model Discussions*, 4, 677–699, 2011.
- 5 Betts, R., Boucher, O., Collins, M., Cox, P., Falloon, P., Gedney, N., Hemming, D., Huntingford, C., Jones, C., Sexton, D., and Webb, M. J.: Projected increase in continental runoff due to plant responses to increasing carbon dioxide, *Nature*, 448, 1037–1041, 2007.
- Black, T. A., Tanner, C., and Gardner, W.: Evapotranspiration from a snap bean crop, *Agronomy Journal*, 62, 66–69, 1970.
- 10 Brown, K. W.: *Vegetation and the Atmosphere*, chap. Sugar beet and potatoes, Academic Press, London, 1976.
- Cao, L., Bala, G., Caldeira, K., Nemani, R., and Ban-Weiss, G.: Importance of carbon dioxide physiological forcing to future climate change, *PNAS*, 107, 9513–9518, doi:10.1073/pnas.0913000107, 2010.
- Cienciala, E., Kučera, J., and Malmer, A.: Tree sap flow and stand transpiration of two *Acacia mangium* plantations in Sabah, Borneo, *Journal of Hydrology*, 236, 109–120, 2000.
- 15 De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Hickler, T., Jain, A. K., Luo, Y., Parton, W. J., Prentice, I. C., Smith, B., Thornton, P. E., Wang, S., Wang, Y.-P., Wårlind, D., Weng, E., Crous, K. Y., Ellsworth, D. S., Hanson, P. J., Seok Kim, H., Warren, J. M., Oren, R., and Norby, R. J.: Forest water use and water use efficiency at elevated CO₂: a model-data intercomparison at two contrasting temperate forest FACE sites, *Global Change Biology*, 19, 1759–1779, doi:10.1111/gcb.12164, 2013.
- De Kauwe, M. G., Kala, J., Lin, Y.-S., Pitman, A. J., Medlyn, B. E., Duursma, R. A., Abramowitz, G., Wang, Y.-P., and Miralles, D. G.: A test of an optimal stomatal conductance scheme within the CABLE land surface model, *Geoscientific Model Development*, 8, 431–452, doi:10.5194/gmd-8-431-2015, 2015.
- 20 Dekker, S. C., Groenendijk, M., Booth, B. B. B., Huntingford, C., and Cox, P. M.: Spatial and temporal variations in plant water-use efficiency inferred from tree-ring, eddy covariance and atmospheric observations, *Earth System Dynamics*, 7, 525–533, 2016.
- Foken, T.: The energy balance closure problem: an overview, *Ecological Applications*, 18, 1351–1367, 2008.
- 25 Gedney, N., Cox, P., Betts, R., Boucher, O., Huntingford, C., and Stott, P.: Detection of a direct carbon dioxide effect in continental river runoff records, *Nature*, 439, 835–838, doi:10.1038/nature04504, 2006.
- Groenendijk, M., Dolman, A., van der Molen, M., Leuning, R., Arneth, A., Delpierre, N., Gash, J., Lindroth, A., Richardson, A., Verbeeck, H., et al.: Assessing parameter variability in a photosynthesis model within and between plant functional types using global Fluxnet eddy covariance data, *Agricultural and Forest Meteorology*, 151, 22–38, 2011.
- 30 Huntingford, C. and Monteith, J.: The behaviour of a mixed-layer model of the convective boundary layer coupled to a big leaf model of surface energy partitioning, *Boundary-Layer Meteorology*, 88, 87–101, 1998.
- Jacobs, C. and De Bruin, H.: The sensitivity of regional transpiration to land-surface characteristics: significance of feedback, *Journal of Climate*, 5, 683–698, 1992.
- Jarvis, P. and McNaughton, K.: Stomatal control of transpiration: Scaling up from leaf to region, *Advances in Ecological Research*, 15, 1–49, 1986.
- 35 Jarvis, P. G.: Attributes of Trees as Crop Plants, chap. Transpiration and assimilation of tree and agricultural crops: the omega factor, pp. 460–480, Institute of Terrestrial Ecology, 1985.



- Kowalczyk, E. A., Wang, Y. P., Wang, P., Law, R. H., and Davies, H. L.: The CSIRO Atmosphere Biosphere Land Exchange (CABLE) model for use in climate models and as an offline model, Tech. Rep. CSIRO Marine and Atmospheric Research paper 013, CSIRO, CABLE model, 2006.
- Launiainen, S.: Seasonal and inter-annual variability of energy exchange above a boreal Scots pine forest, *Biogeosciences*, 7, 3921–3940, 5 2010.
- Law, B., Falge, E., Gu, L. v., Baldocchi, D., Bakwin, P., Berbigier, P., Davis, K., Dolman, A., Falk, M., Fuentes, J., et al.: Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation, *Agricultural and Forest Meteorology*, 113, 97–120, 2002.
- Lee, X. and Black, T. A.: Atmospheric turbulence within and above a Douglas-fir stand. Part II: Eddy fluxes of sensible heat and water vapour, *Boundary-Layer Meteorology*, 64, 369–389, 1993.
- 10 Lin, Y.-S., Medlyn, B. E., Duursma, R. A., Prentice, I. C., Wang, H., Baig, S., Eamus, D., de Dios, V. R., Mitchell, P., Ellsworth, D. S., de Beeck, M. O., Wallin, G., Uddling, J., Tarvainen, L., Linderson, M.-L., Cernusak, L. A., Nippert, J. B., Ocheltree, T. W., Tissue, D. T., Martin-StPaul, N. K., Rogers, A., Warren, J. M., De Angelis, P., Hikosaka, K., Han, Q., Onoda, Y., Gimeno, T. E., Barton, C. V. M., Bennie, J., Bonal, D., Bosc, A., Low, M., 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., Kelly, J. W., Kikuzawa, K., Kolari, P., Koyama, K.,
- 15 Limousin, J.-M., Meir, P., Lola da Costa, A. C., Mikkelsen, T. N., Salinas, N., Sun, W., and Wingate, L.: Optimal stomatal behaviour around the world, *Nature Climate Change*, 5, 459–464, 2015.
- Magnani, F., Leonardi, S., Tognetti, R., Grace, J., and Borghetti, M.: Modelling the surface conductance of a broad-leaf canopy: effects of partial decoupling from the atmosphere, *Plant, Cell & Environment*, 21, 867–879, 1998.
- Martin, P.: The significance of radiative coupling between vegetation and the atmosphere, *Agricultural and Forest Meteorology*, 49, 45–53, 20 1989.
- McNaughton, K. and Jarvis, P.: *Water Deficits and Plant Growth*, vol. 7, chap. Predicting effects of vegetation changes on transpiration and evaporation, pp. 1–47, Academic Press, New York, 1983.
- McNaughton, K. and Jarvis, P.: Effects of spatial scale on stomatal control of transpiration, *Agricultural and Forest Meteorology*, 54, 279–302, 1991.
- 25 Medlyn, B., Barton, C., Broadmeadow, M., Ceulemans, R., De Angelis, P., Forstreuter, M., Freeman, M., Jackson, S., Kellomaki, S., Laitat, E., Rey, A., Roberntz, P., Sigurdsson, B., Strassmeyer, J., Wang, K., Curtis, P., and Jarvis, P.: Stomatal conductance of forest species after long-term exposure to elevated CO₂ concentration: a synthesis, *New Phytologist*, 149, 247–264, 2001.
- Meinzer, F., Goldstein, G., Holbrook, N., Jackson, P., and Cavellier, J.: Stomatal and environmental control of transpiration in a lowland tropical forest tree, *Plant, Cell & Environment*, 16, 429–436, 1993.
- 30 Meinzer, F., Andrade, J., Goldstein, G., Holbrook, N., Cavellier, J., and Jackson, P.: Control of transpiration from the upper canopy of a tropical forest: the role of stomatal, boundary layer and hydraulic architecture components, *Plant, Cell & Environment*, 20, 1242–1252, 1997.
- Mielke, M. S., Oliva, M., de Barros, N. F., Penchel, R. M., Martinez, C. A., and de Almeida, A. C.: Stomatal control of transpiration in the canopy of a clonal *Eucalyptus grandis* plantation, *Trees-Structure and Function*, 13, 152–160, 1999.
- 35 Miner, G. L., Bauerle, W. L., and Baldocchi, D. D.: Estimating the sensitivity of stomatal conductance to photosynthesis: A review, *Plant, Cell & Environment*, 2017.
- Morison, J. I. L.: Sensitivity of stomata and water use efficiency to high CO₂, *Plant, Cell & Environment*, 8, 467–474, 1985.



- Oleson, K. W., Lawrence, D. M., Bonan, G. B., Drewniak, B., Huang, M., Koven, C. D., Levis, S., Li, F., Riley, W. J., Subin, Z. M., Swenson, S. C., Thornton, P. E., Bozbiyik, A., Fisher, R., Heald, C. L., Kluzek, E., Lamarque, J.-F., Lawrence, P. J., Leung, L. R., Lipscomb, W., Muszala, S., Ricciuto, D. M., Sacks, W., Sun, Y., Tang, J., and Yang, Z.-L.: Technical Description of version 4.5 of the Community Land Model (CLM), NCAR Technical Note NCAR/TN-503+STR, National Center for Atmospheric Research. Climate and Global Dynamics Division, National Center for Atmospheric Research, P.O. Box 3000, Boulder, Colorado, 2013.
- 5 Raupach, M. and Finnigan, J.: 'Single-layer models of evaporation from plant canopies are incorrect but useful, whereas multilayer models are correct but useless': *Discuss, Functional Plant Biology*, 15, 705–716, 1988.
- Raupach, M., Finkele, K., and Zhang, L.: SCAM (Soil-Canopy-Atmosphere Model): Description and comparison with field data, Aspendale, Australia: CSIRO CEM Technical Report, p. 81, 1997.
- 10 Sánchez, J., Caselles, V., and Rubio, E.: Analysis of the energy balance closure over a FLUXNET boreal forest in Finland, *Hydrology and Earth System Sciences*, 14, 1487–1497, 2010.
- Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J., Levis, S., Lucht, W., Sykes, M., Thonicke, K., and Venevski, S.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Vegetation Model, *Global Change Biology*, 9, 161–185, 2003.
- 15 Stoy, P., Katul, G., SIQUEIRA, M., JUANG, J., Novick, K., McCARTHY, H., Christopher Oishi, A., Uebelherr, J., KIM, H., and Oren, R.: Separating the effects of climate and vegetation on evapotranspiration along a successional chronosequence in the southeastern US, *Global Change Biology*, 12, 2115–2135, 2006.
- Su, Z., Schmugge, T., Kustas, W., and Massman, W.: An evaluation of two models for estimation of the roughness height for heat transfer between the land surface and the atmosphere, *Journal of Applied Meteorology*, 40, 1933–1951, 2001.
- 20 Thom, A. S.: *Vegetation and the Atmosphere*, chap. Momentum, Mass and Heat Exchange of Plant Communities, pp. 57–109, Academic Press, London, 1975.
- Whitehead, D., Jarvis, P. G., and Waring, R. H.: Stomatal conductance, transpiration, and resistance to water uptake in a *Pinus sylvestris* spacing experiment, *Canadian Journal of Forest Research*, 14, 692–700, 1984.
- Wilson, K., Goldstein, A., Falge, E., Aubinet, M., Baldocchi, D., Berbigier, P., Bernhofer, C., Ceulemans, R., Dolman, H., Field, C., et al.: Energy balance closure at FLUXNET sites, *Agricultural and Forest Meteorology*, 113, 223–243, 2002.
- 25 Wohlfahrt, G., Haslwanter, A., Hörtnagl, L., Jasoni, R. L., Fenstermaker, L. F., Arnone, J. A., and Hammerle, A.: On the consequences of the energy imbalance for calculating surface conductance to water vapour, *Agricultural and forest meteorology*, 149, 1556–1559, 2009.
- Woodward, F. I., Smith, T. M., and Emanuel, W. R.: A global land primary productivity and phytogeography model, *Global Biogeochemical Cycles*, 9, 471–490, 1995.
- 30 Wullschleger, S. D., Meinzer, F., and Vertessy, R.: A review of whole-plant water use studies in tree, *Tree physiology*, 18, 499–512, 1998.
- Wullschleger, S. D., Wilson, K. B., and Hanson, P. J.: Environmental control of whole-plant transpiration, canopy conductance and estimates of the decoupling coefficient for large red maple trees, *Agricultural and Forest Meteorology*, 104, 157–168, 2000.
- Zhu, P., Zhuang, Q., Ciais, P., Welp, L., Li, W., and Xin, Q.: Elevated atmospheric CO₂ negatively impacts photosynthesis through radiative forcing and physiology-mediated climate feedback, *Geophysical Research Letters*, 2017.

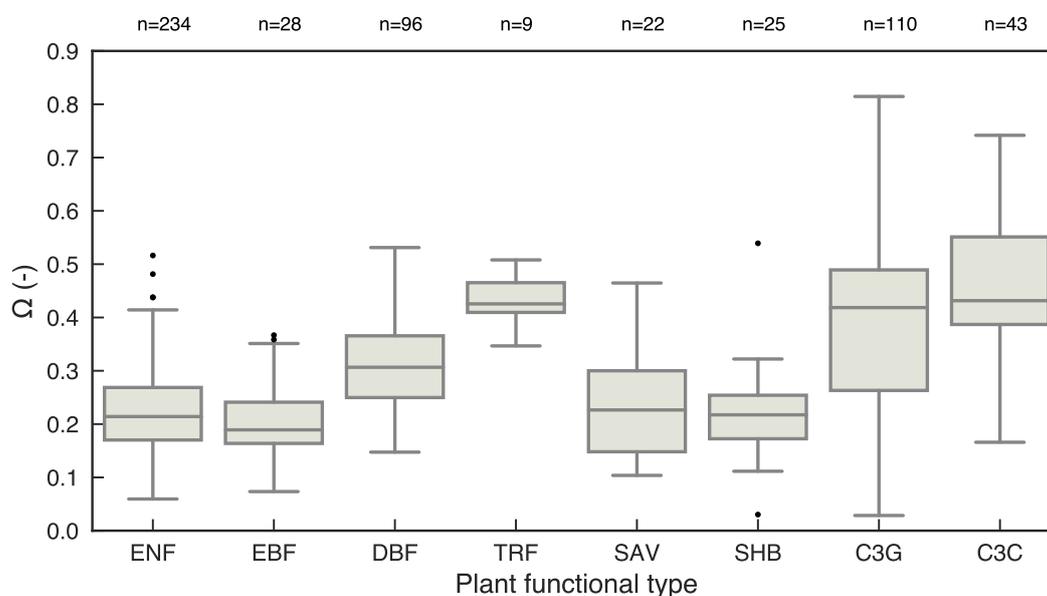


Figure 1. Box and whisker plot (line, median; box, inter-quartile range) showing the estimated decoupling coefficient (Ω) from FLUXNET data, grouped by plant functional type. Whiskers extend to 1.5 times the inter-quartile range, with dots outside of the whiskers showing outliers. Plant functional types are defined as: ENF - evergreen needle leaved forest, EBF - evergreen broadleaved forest, DBF - deciduous broadleaved forest, TRF - tropical rain forest, SAV - savanna, SHB - shrub, C3G - C₃ grass, C4G - C₄ grass, C3C - C₃ crops, C4C - C₄ crops. Values of n indicate the number of site-years for FLUXNET.

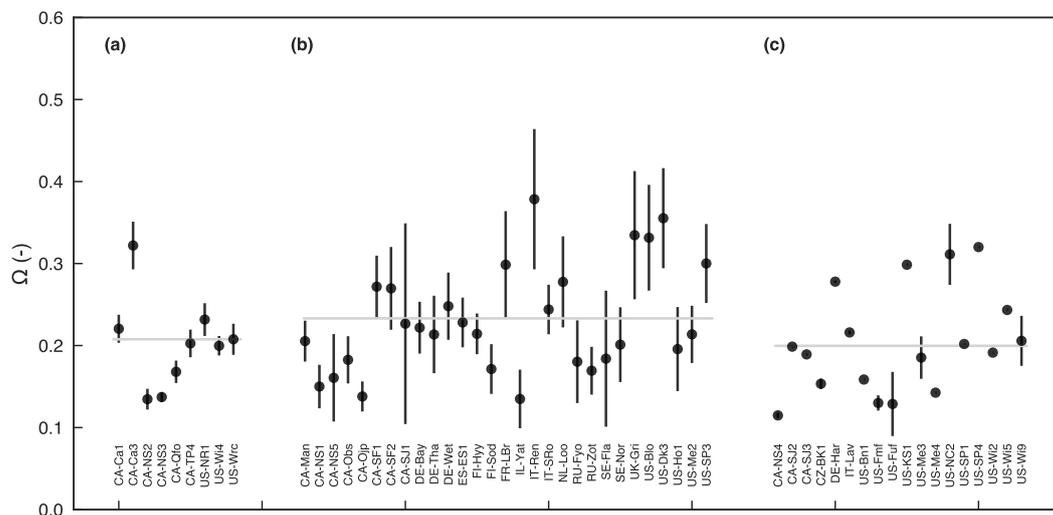


Figure 2. Values of decoupling coefficient (Ω) for site from the evergreen needleleaf forests (ENF) plant functional type. Estimated values of Ω have been split into: (a) sites where the coefficient of variation (COV) is < 20%; (b) sites where the COV is > 20%; and (c) sites with only two years of data. Grey lines show overall mean decoupling coefficients.

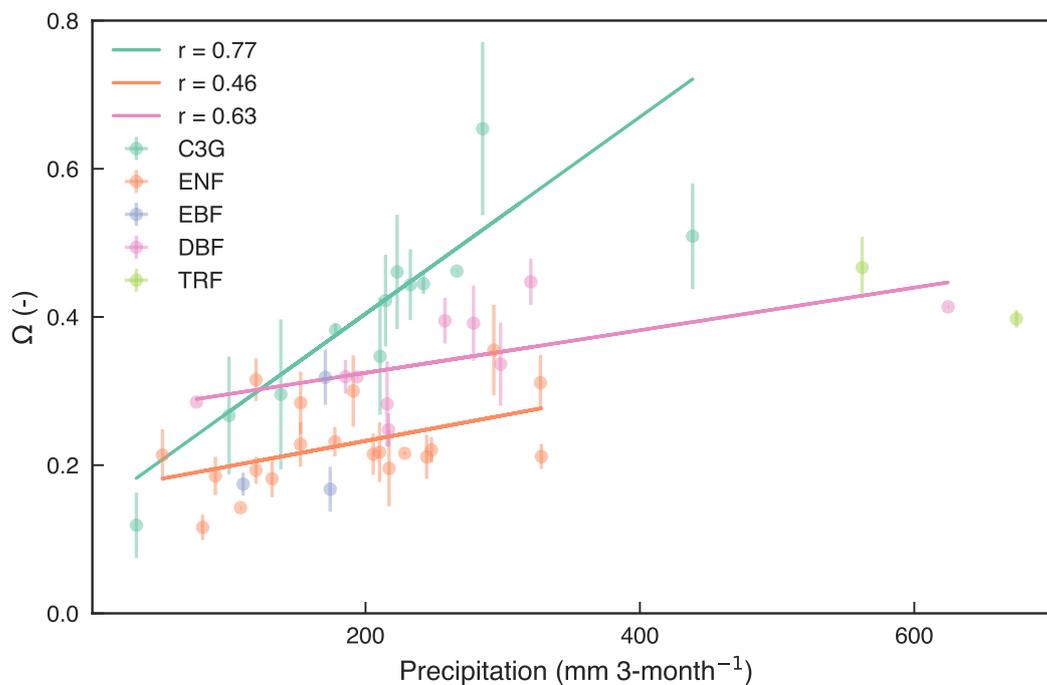


Figure 3. Values of the estimated decoupling coefficient (Ω) for forest (ENF, EBF, DBF, TRF) vegetation and C₃ grasses as a function of precipitation in the three most productive months. Lines indicate statistically significant regression ($P < 0.05$). Plant functional types are defined as: C3G - C₃ grass, ENF - evergreen needle leaved forest, EBF - evergreen broadleaved forest, DBF - deciduous broadleaved forest and TRF - tropical rain forest.

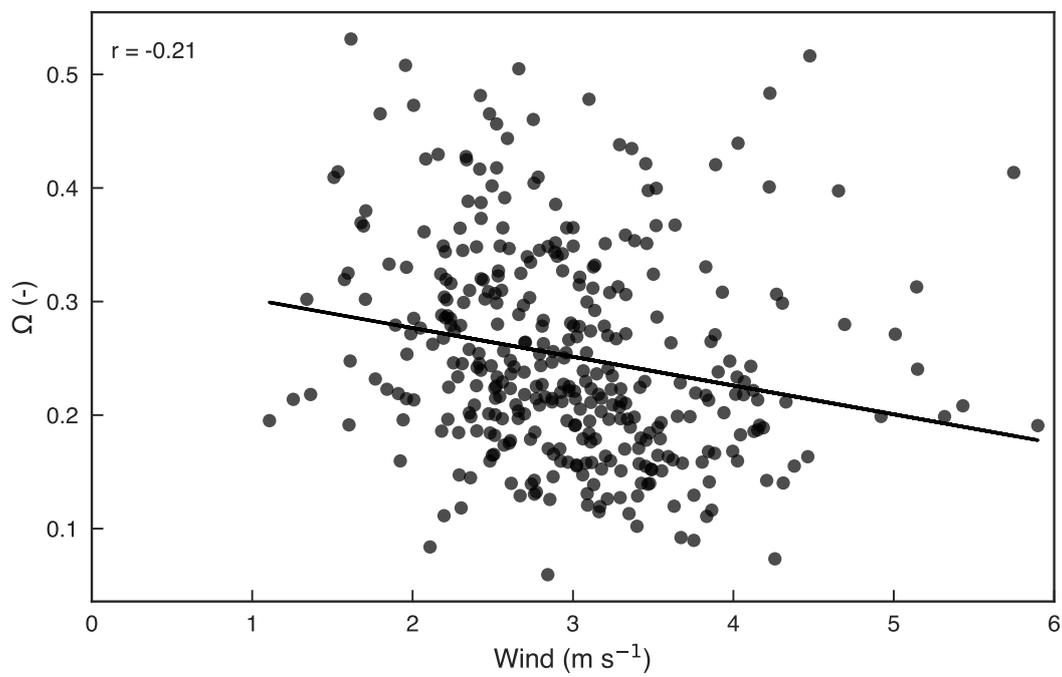


Figure 4. Values of the estimated decoupling coefficient (Ω) for forest (ENF, EBF, DBF, TRF) vegetation as a function of wind speed. Line indicates statistically significant regression ($P < 0.05$), r is the correlation coefficient. Plant functional types are defined as: ENF - evergreen needle leaved forest, EBF - evergreen broadleaved forest, DBF - deciduous broadleaved forest, TRF - tropical rain forest.



Appendix A

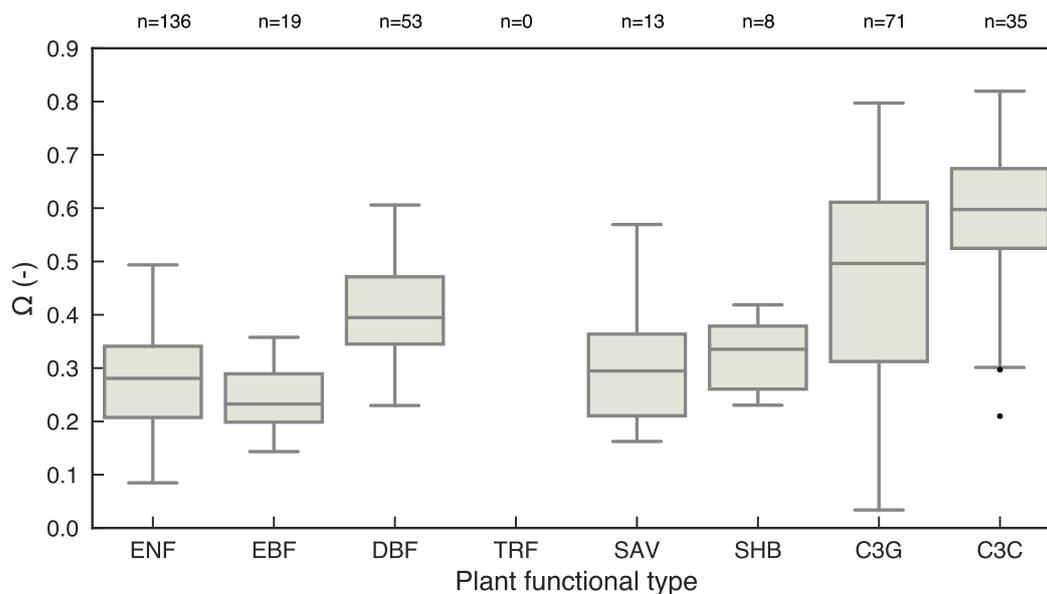


Figure A1. Box and whisker plot (line, median; box, inter-quartile range) showing the estimated decoupling coefficient (Ω) from FLUXNET data, grouped by plant functional type. These data have been corrected for energy imbalance, adjusting the Bowen-ratio by the imbalance across the three most productive months. Whiskers extend to 1.5 times the inter-quartile range, with dots outside of the whiskers showing outliers. Plant functional types are defined as: ENF - evergreen needle leaved forest, EBF - evergreen broadleaved forest, DBF - deciduous broadleaved forest, TRF - tropical rain forest, SAV - savanna, SHB - shrub, C3G - C₃ grass, C4G - C₄ grass, C3C - C₃ crops, C4C - C₄ crops. Values of n indicate the number of site-years for FLUXNET.