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Examining the evidence for sustained transpiration during heat extremes

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Abstract. Recent experimental evidence suggests that during heat extremes, wooded ecosystems may decouple photosynthesis and transpiration: reducing photosynthesis to near zero but increasing transpiration into the boundary layer. This feedback may act to dampen, rather than amplify, heat extremes in wooded ecosystems. We examined eddy-covariance databases (OzFlux and FLUXNET2015) to identify whether there was field-based evidence to support these experimental findings. We focused on two types of heat extremes: (i) the three days leading up to a temperature extreme, defined as including a daily maximum temperature > 37°C (similar to the widely used TXx metric) and (ii) heatwaves, defined as three or more consecutive days above 35°C. When focussing on (i), we found some evidence of reduced photosynthesis and sustained or increased latent heat fluxes in seven Australian evergreen wooded flux sites. However, when considering the role of vapour pressure deficit and focusing on (ii), we were unable to conclusively disentangle the decoupling between photosynthesis and latent heat flux from the effect of increasing vapour pressure deficit. Outside of Australia, the Tier-1 FLUXNET2015 database provided limited scope to tackle this issue as it does not sample sufficient high temperature events with which to probe the physiological response of trees to extreme heat. Thus, further work is required to determine whether this photosynthetic decoupling occurs widely, ideally by matching experimental species with those found at eddy-covariance towers sites. Such measurements would allow this decoupling mechanism to be probed experimentally and at the ecosystem scale. Transpiration during heatwaves remains a key issue to resolve, as no land surface model includes a decoupling mechanism, and any potential dampening of the land-atmosphere amplification is thus not included in climate model projections.

1 Introduction

In response to a warming climate, heatwaves have increased in frequency, magnitude and duration (Alexander et al., 2006; Perkins et al., 2012). Coupled climate models from the Coupled Model Intercomparison Project (CMIP5) project a marked increase in the frequency and severity of these heat extremes (Coumou and Robinson, 2013, Sillmann et al. 2013), highlighting the urgent need to understand the underlying driving mechanisms. Whilst heatwaves are commonly associated with large-scale, high-pressure synoptic systems (anticyclones) (Perkins, 2015), there is increasing evidence of the role of the land-surface in the amplification of heat extremes (Fischer et al., 2007; Teuling et al., 2010; Miralles et al., 2012; Kala et al., 2016; Donat et al. 2017). This land-atmosphere feedback is driven by drying soils and an increase in the sensible heat flux which further warms the boundary layer (Lorenz et al., 2010; Seneviratne et al., 2006). The combination of heat advection and heat storage in the boundary layer is recycled back to the surface over successive days and can lead to increasingly intense heatwaves, including "mega-heatwaves" (Miralles et al., 2014).

A number of studies have highlighted the contrasting functional traits of grasslands and forests as important controls on the role of the land surface in the amplification of heatwaves (Teuling et al. 2010; van Heerwaarden and Teuling, 2014). Grasses often have shallow root profiles and a relatively small reduction in soil moisture can stress a grassland, resulting in decreased transpiration (either directly via reduced stomatal conductance and/or indirectly via reduced leaf area), leading to a repartitioning of the available (radiant) energy towards sensible heat. Heatwaves also affect forests, but the deeper root profiles that characterise forests may make surface drying less likely to influence the surface energy balance. However, whilst this slower soil water depletion may buffer the transition to increased sensible heat flux, ultimately the decline in soil moisture may still result in heatwave intensification during prolonged dry spells (Teuling et al., 2010).

On the other hand, recent experimental evidence has highlighted a previously overlooked vegetation-atmosphere feedback that may in fact dampen, rather than amplify, heat extremes. A number of heatwave experiments carried out in well-watered, potted plants, have suggested that during temperature extremes, photosynthesis and stomatal conductance (g_s) become decoupled, such that photosynthesis is reduced to near zero, but transpiration is maintained (Ameye et al. 2012; von Caemmerer and Evans, 2015; Urban et al. 2017). For example, in a growth chamber study, Urban et al. (2017) found that g_s increased with rising temperature despite photosynthetic activity shutting down for both *Pinus taeda* and *Populus deltoides* x *nigra*. This result was also confirmed in a field-based whole tree-chamber study by Drake et al. (2018), who reported that transpiration was increased and decoupled from photosynthesis in 6-m tall *Eucalyptus parramattensis* trees during an imposed heatwave of four consecutive days with temperatures exceeding 43°C. Crucially, in the Drake et al. (2018) study, the plants were not well-watered. Instead, these trees had been subject to an imposed one-month drought prior to the experiment to reduce soil water stores. Evidence that transpiration increases during a heatwave, resulting in a cooler canopy temperature, would be consistent with an active mechanism (Trewavas et al. 2009) by trees to cool their canopies. Such a response to heat extremes would increase the latent heat flux into the boundary layer and have two major negative feedbacks on heat extremes: first, the increase in latent heat flux would be at the cost of the sensible heat flux, and a reduction in sensible heat flux would potentially reduce any land amplification on heatwaves over forested regions. Second, by moistening the boundary layer, the chance of clouds being formed would increase, leading to a decrease in solar radiation at the surface and a consequent cooling effect.

In climate models, including CMIP5 models, the land surface is represented by modules that assume photosynthesis and g_s (and consequently transpiration) are inherently coupled (De Kauwe et al., 2013). At high temperatures, models assume that photosynthesis is reduced due to: (i) the direct impairment of the photosynthetic biochemistry; (ii) increased respiration; and (iii) reduced g_s due to the associated high vapour pressure deficit. Finding additional evidence of a decoupling between photosynthesis and g_s at high temperatures would therefore require revisiting existing assumptions embedded in all climate models and have important implications for model-based assessments of the role of the land surface in the amplification of heat extremes. In this paper we therefore explore eddy-covariance measurements to examine whether there is widespread field-based evidence that during heat extremes, trees decouple photosynthesis and g_s, leading to increased transpiration. We chose to focus on wooded ecosystems as the capacity to maintain transpiration throughout a heat extreme most likely requires deep soil water access and is in line with previous experimental evidence from trees (Drake et al., 2018; Urban et al., 2017).

2 Materials and Methods

2.1 Evidence of photosynthesis-canopy conductance decoupling

A range of definitions currently exist to identify an extreme temperature event (see Perkins et al. 2014 for a review). Most of these are defined from the context of the climate and may not reflect the physiological adaptations of the vegetation. Given this lack of a single unifying definition, we tested two approaches on the eddy-covariance measurements: (1) the change in GPP and latent heat flux during the preceding three days leading up to and including a temperature extreme (i.e. four days in total). A temperature extreme was defined as being a day when the daily maximum temperature exceeded 37°C; and (2) the change in GPP and latent heat flux during a heatwave, defined as at least three consecutive days where the maximum daily temperature exceeded 35°C. The first approach can be viewed as analogous to the behaviour leading up to the hottest day of the year (commonly defined as TXx; Klein et al. 2009) and the imposed lower boundary of 37°C similar to selecting a number of "hot" days by using a percentile from the TXx but defined from a more physiological standpoint. This temperature threshold was selected to ensure the events were hot enough to stress the vegetation (Curtis et al. 2016; O'sullivan et al. 2017; Zhu et al. 2018). For the Australian sites, 37°C was consistent with a site's climate-of-origin + threshold (mean summer maximum temperature; Tmax + 10°C) (Drake et al. 2017).

For each of these events we recorded the maximum daytime temperature, the mean daytime (6am – 8 pm) latent heat flux (LE), and the daytime summed gross primary productivity (GPP). We hypothesised that evidence of decoupling would present itself as a reduction in GPP and an increase LE as air temperatures increased. It is important to clarify that decoupling does not mean that g_s will increase as GPP declines, only that it will decline *less strongly* than current theory would predict if photosynthesis and g_s remained coupled. As temperature increases, vapour pressure deficit (D) also increases, which will drive an increase in LE unless there is stomatal closure, but this effect is unrelated to the decoupling mechanism we seek to find. To disentangle the potentially contributing role of D, we also estimated GPP x $D^{0.5}$ in line with the theoretical expectation of the effect of D on g_s (Lloyd et al. 1991; Medlyn et al. 2011).

To test for evidence of decoupling in the flux behaviour we fitted a linear regression to the fluxes from each event leading up to a day where the maximum temperature exceeded 37°C (i.e. approach 1 above), showing events where the fitted slope was negative for GPP and positive for LE. We do not necessarily expect the response of GPP or LE to be linear with respect to increasing temperature, but selecting events based on their fitted (positive/negative) slopes allows us to identify patterns in the data. We do not seek to draw inference from the fitted slope being significant or not, given the small number of samples (n=4) in each event. We simply use this distinction to identify stronger positive or negative trends in these data. To probe the effect of D during heatwaves (i.e. approach 2) we plot LE expressed as evapotranspiration (mm day^{-1}), as a function of GPP x $D^{0.5}$.

2.2 Flux data

Half-hourly eddy covariance measurements of the exchange of carbon dioxide, energy, and water vapour were obtained from the OzFlux (http://www.ozflux.org.au/) and FLUXNET2015 (http://fluxnet.fluxdata.org/data/fluxnet2015-dataset) and releases. We confined our FLUXNET2015 analysis to sites classified as wooded according to the International Geosphere–Biosphere Programme, namely: evergreen needleleaf forest; evergreen broadleaved forest; and deciduous broadleaved forest (albeit noting that these names have an inherently Northern Hemisphere bias, and would be better classified as evergreen coniferous, evergreen angiosperm, and deciduous angiosperm forest, respectively). We excluded sites classified as savanna due to the associated complication of needing to attribute the total transpiration flux to grasses and trees; however, we do acknowledge that many of the Australian sites are also relatively open (see screening step below). We also excluded sites classified as mixed forest from our analysis, or those that did not meet our physiological threshold of a daily maximum temperature that exceeded 37°C. We also excluded sites that experienced burning. A total of nine sites met these criteria in the Tier 1 (freely available) FLUXNET 2015 database. FLUXNET data were pre-processed using the FluxnetLSM R package (Ukkola et al., 2017). For OzFlux, we used Level 6 gap-filled data following Isaac et al. (2017). These data were then screened to only keep measured and good-quality gap filled data. Events were ignored if a rainfall event greater than 0.5 mm day^{-1} was observed during, or in the two days prior to a heat event in the eddy covariance data as this could bias the LE flux by leading to an increase in LE not associated with the mechanism we wished to identify (i.e. due to soil/canopy evaporation).

2.3 Accumulated heat stress

To characterise a measure of the annual heat accumulated stress experienced by the vegetation we calculated the average number of growing degree days above our upper threshold of 37°C per year (GDD_{37}). We used surface air temperature from the 6-hourly, re-analysis by the Global Soil Wetness Project Phase 3 (GSWP3; http://hydro.iis.u-tokyo.ac.jp/GSWP3 and Dirmeyer et al. 2006) dataset during the period of 1970-2015 at a 0.5° spatial resolution. We opted to use this coarser dataset to estimate GDD_{37} rather than the observed flux record due to the longer temporal record, which is likely to be more reflective of longer-term conditions.

2.4 Analysis code

All analysis code is freely available from: https://github.com/mdekauwe/heat_extremes_decoupling.

3 Results & Discussion

We first focus on the Australian sites as these experienced more temperature extremes due to the warm climate. We found significant evidence of thermal heat stress (Table 1), with 85.8 GDD_{37} at Alice Springs, 85.1 GDD_{37} at Great Western Woodlands, 68.3 at Calperum, 31.7 at Gingin, 13.5 at Cumberland Plains, 13.4 at Whroo and 3.1 at Wombat.

Figure 1 shows a consistent reduction in the flux-derived GPP with increasing daily maximum temperature for each of the events (4-day events, where the maximum temperature > 37°C). We emphasise (see methods) that one should only interpret differences between significant negative slopes (dark blue lines) and negative slopes (dark green lines) as indicative of (possibly) stronger or more consistent reductions in GPP as a function of temperature. This reduction in GPP follows theory related to biochemical, respiratory and stomatal drivers (Lin et al., 2012). With the exception of the Whroo site, GPP was reduced to close to zero at temperatures greater than 40°C. Figure S1 shows the limited occurrences where the fitted slopes indicated a positive (or arguably flat) response with increasing temperature.

Evidence for the hypothesised decoupling between photosynthesis and g_s, which would lead to an increase in LE with temperature (but a concomitant decline in GPP, Fig. 1), is shown in Fig. 2. Despite variability in the measured data, at each of the seven sites, LE is found to increase or be sustained as the temperature increases in the lead up to the maximum temperature of each heat event. This increase is steepest at the Wombat State Forest site but is based on only one GDD_{37} event (Table S1). At the other sites, the magnitude of the increase is smaller. However, it is clear that the LE flux is not reduced in line with GPP (Fig. 1) and instead remains sustained with temperature throughout the extreme events. Figure S2 shows the occurrences where the fitted slopes indicated a negative response with increasing temperature. In many cases these events were broadly flat in response to increasing temperature, again indicating a sustained LE flux. Taken together, Figs. 1, 2 and S2 provide consistent evidence of a decoupling between photosynthesis and transpiration during significant heat extremes across a range of Australian wooded ecosystems.

We now seek to explore the strength of this apparent decoupling in more detail by looking at the ratio of positive to negative fitted slopes shown in Figs 1 and 2 and Figs S1 and S2. Figures 3 and 4 shows the distribution of fitted positive and negative slopes as a function of temperature across the Australian sites for GPP and LE, respectively. Whilst the fitted slopes for GPP are predominately negative (Figure 3), there does not appear to be a consistent pattern in the frequency of positive vs. negative fitted LE slopes, with some sites having more positive slopes (e.g. Gingin, Great Western Woodlands) and some registering more negative slopes (Calperum, Whroo), while others are about even (Alice Springs, Cumberland Plains) (Figure 4). This result is not surprising given our hypothesis that significant transpiration during a heatwave is dependent upon the available supply of soil moisture. As soil water supply becomes limiting, we would expect to find more frequent negative slopes. Consistent with this link to soil moisture, there is a small drop in the proportion of positive slopes (i.e. increased LE) towards the end of summer, which is coincident with an increase in the frequency of negative slopes (Fig S3).

Evidence for an increase in LE with temperature and for photosynthetic decoupling during heat extremes was much weaker across the seven FLUXNET2015 sites (excluding Australian sites; Fig. S4 and S5) that exceeded our 37°C threshold. The number of concomitant negative GPP slopes (Fig. S4) and positive LE slopes (Fig. S5) was noticeably lower when compared to Australian sites, making it harder to draw clear inferences. On the one hand, the weaker evidence from across the larger FLUXNET2015 dataset may point to this decoupling behaviour being species or climatic zone specific (i.e. located in very hot environments). However, we would caution against that interpretation as it is as likely to also point to the lack of representation of FLUXNET sites in regions, other than Australia, that experience very hot temperature extremes (e.g. the average GDD_{37} for the non-Australian sites was >1 at only two sites, Table 1). Given the limited signal in the results obtained from FLUXNET2015 sites, we continue to focus our analysis on Australian sites. However, given the extremely hot summer experienced across Europe in 2018, future studies may wish to revisit this analysis as these updated flux data become available.

Increasing temperature also usually leads to increasing D and as a result, even with perfect coupling between photosynthesis and g_s, we would still expect to see transpiration changing as a function of GPP x $D^{0.5}$. Figure 5 shows this relationship for consecutive heatwave and non-heatwave days (note Wombat State Forest was excluded from this analysis as there were insufficient consecutive days > 35°C.) If the change in transpiration was being driven by a decoupling of g_s from the response of photosynthesis, we might expect to see increasing transpiration for a given GPP x $D^{0.5}$, i.e. a spread in points vertically for heatwave days. If the change was being driven by increasing water use efficiency, we might expect to see increased GPP x $D^{0.5}$ for a given unit of transpiration, i.e. a spread horizontally for heatwave days. Across the sites there was not a clear difference in the behavior for heatwave vs. non-heatwave days. At Calperum, Cumberland Plains and Whroo the relationship between GPP x $D^{0.5}$ and transpiration was fairly constant, whereas at Great Western Woodlands, transpiration for a given GPP x $D^{0.5}$ on heatwave days was slightly higher than on non-heatwave days and at Alice Springs and Gingin, slightly lower. At Alice Springs and Gingin, this seems to fit with our expectation of increasing D driving increasing water use efficiency, i.e. not the decoupling mechanism. At Great Western Woodlands, there is some indication the data spread vertically, which may be consistent with our expectation outlined for decoupling, but the pattern is not conclusive.

Recent experimental studies (Drake et al., 2018; Urban et al., 2017) have identified that at very high temperatures (> 40°C), plant decouple photosynthesis and g_s and instead increase transpiration in an apparent active process to cool their canopies. Our results from across seven wooded ecosystems located in Australia were inconclusive. We found some indication (Figs. 1-4) that LE was increased or sustained as GPP decreased when exploring the behavior in the lead up to the hottest days of the year. However, when we focused on heatwave events (i.e. consecutive days > 35°C; Fig. 5) and considered the role of D (i.e. as a driver of increased LE), rather than specifically a decoupling to increase the transpiration flux to cool the canopy (i.e. in response to leaf temperature), we found little clear support for photosynthetic decoupling. Using data from FLUXNET to isolate the experimental result found in Drake et al. (2018) is complicated. Their analysis inferred the photosynthetic decoupling by demonstrating that the observed decline in g_s was weaker than predicted by a coupled leaf A-g_s model, which was specifically calibrated to the experimental data. However, this approach is not viable across multiple sites as it necessitates detailed site measurements that are often prohibited by the tall canopy height of mature stands. Applying such a coupled model (e.g. a land surface model) to these site data simply demonstrates that the model is not able to capture the observed site responses (not shown). As a result, we could not reliably infer that the divergence from the model behaviour points to decoupling, as opposed to, for example, poor parameterization associated with leaf area index or root zone soil moisture.

Our analysis also relies on GPP which is not directly observed but is instead modelled using assumptions related to the extrapolation of night-time respiration (ER) and measured net ecosystem exchange. It is debatable whether these assumptions hold at very high temperatures, and examining these modelled GPP estimate estimates at high temperatures warrants further investigation, particular as researchers leverage these data to explore the responses of the vegetation to temperature extremes. Our analysis is limited by the number of extreme events recorded in the existing record and the clear bias in these data towards Australian sites is due to the lack of representation of sites within the FLUXNET data collection that sample locations in extreme environments outside of Australia. In our analysis we focused on hot days and heatwaves with a very hot temperature range, i.e. consecutive days > 35°C, hence a fair criticism of our approach is that a lower threshold might be also relevant for different environments and species. Any choice of threshold is arguably arbitrary; we chose ours to ensure we were focusing on the vegetation response to a threshold that would lead to a degree of physiological limitation and is line with studies that suggest this occur at temperatures above our chosen thresholds (Curtis et al. 2016; O'sullivan et al. 2017; Zhu et al. 2018).

In conclusion, our analysis did not find conclusive evidence either way from eddy-covariance data for the experimentally observed photosynthetic decoupling. The role of transpiration during heatwaves remains an important issue to resolve. The implications for modelling studies that focus on heat extremes are clear, particularly for studies in Australia. None of the current generation of land surface models has the capacity to decouple transpiration from the down-regulation of photosynthesis with increasing temperature. Instead models assume photosynthesis and g_s (and consequently transpiration) remain coupled at all times. As a result, climate models will underestimate the capacity of the vegetation to dampen heat extremes in simulations for Australia. This underestimation has potential relevance for planning strategies focused on which species to plant in “green cities” to help mitigate future climate extremes. It is clear that further experimental results will be required to resolve this issue and these studies will need to be able to more clearly separate the decoupling mechanism from the response to D. Aligning these experiments with matching species as those found at flux tower sites would be extremely desirable as they would allow further work to test whether this mechanism scales to the ecosystem.

Author contributions. MDK conceived and designed the study based on discussions involving MDK, BEM and JED. MDK wrote the code and analysed the results. AU assembled and processed the eddy covariance data. All authors contributed to writing of the paper.

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

Data availability. All Eddy covariance data are available from: http://www.ozflux.org.au/ and http://fluxnet.fluxdata.org/data/fluxnet2015-dataset

Competing interests. The authors declare no competing financial interests.

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References

Alexander, L., Zhang, X., Peterson, T., Caesar, J., Gleason, B., Klein Tank, A., et al.: Global observed changes in daily climate extremes of temperature and precipitation. Journal of Geophysical Research: Atmospheres, 111(D5), 2006.

Ameye, M., Wertin, T. M., Bauweraerts, I., McGuire, M. A., Teskey, R. O., & Steppe, K.: The effect of induced heat waves on *Pinus taeda* and *Quercus rubra* seedlings in ambient and elevated CO_2 atmospheres. New Phytologist, 196, 448–461. 2012.

Berbigier, P., Bonnefond, J.-M. and Mellmann, P.: CO_2 and water vapour fluxes for 2 years above Euroflux forest site. Agricultural and Forest Meteorology, 108, 183–197, 2001.

Beringer, J., Hutley, L. B., Hacker, J. M., Neininger, B. and Kyaw Tha Paw U.: Patterns and processes of carbon, water and energy cycles across northern Australian landscapes: From point to region. Agricultural and Forest Meteorology, 151, 1409–1416, 2011.

Cleverly, J., Boulain, N., Villalobos-Vega, R., Grant, N., Faux, R., Wood, C., Cook, P. G., Yu, Q., Leigh, A. and Eamus, D.: Dynamics of component carbon fluxes in a semi-arid Acacia woodland, central Australia, Journal of Geophysical Research: Biogeosciences, 118, 1168–1185, 2013.

Coumou, D. and Robinson, A.: Historic and future increase in the global land area affected by monthly heat extremes, Environmental Research Letters, 8, 034018, 2013.

Curtis, E. M., Gollan, J., Murray, B. R. and Leigh, A.: Native microhabitats better predict tolerance to warming than latitudinal macro-climatic variables in arid-zone plants. Journal of Biogeography, 43, 1156-1165, 2016.

De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Hickler, T. et al.: Forest water use and water use efficiency at elevated CO_2: A model-data intercomparison at two contrasting temperate forest FACE sites. Global Change Biology, 19, 1759–1779, 2013.

Dirmeyer, P. A., Gao, X., Zhao, M., Guo, Z. H., Oki, T., and Hanasaki, N.: GSWP-2-multimodel analysis and implications for our perception of the land surface. Bulletin of the American Meteorological Society, 87, 1381–1397, 2006.

Donat, M. G., A. J. Pitman, and S. I. Seneviratne.: Regional warming of hot extremes accelerated by surface energy fluxes, Geophysical Research Letters, 44, 7011-7019, 2017.

Drake, J. E., Vårhammar, A., Kumarathunge, D. et al. A common thermal niche among geographically diverse populations of the widely distributed tree species *Eucalyptus tereticornis*: No evidence for adaptation to climate-of-origin. Global Change Biology, 23, 5069–5082, 2017.

Drake, J. E., Tjoelker, M. G., Vårhammar, A., Medlyn, B. E., Reich, P. B., Leigh, A., et al.: Trees tolerate an extreme heatwave via sustained transpirational cooling and increased leaf thermal tolerance. Global Change Biology, 24, 2390-2402, 2018.

Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B. and Otero-Casal, C.: Hydrologic regulation of plant rooting depth. Proceedings of the National Academy of Sciences, 114, 10572-10577, 2017.

Fischer, E., Seneviratne, S., Lüthi, D. and Schär, C.: Contribution of land-atmosphere coupling to recent European summer heat waves. Geophysical Research Letters, 34, L06707, 2007.

Griebel, A., Bennett, L. T., Metzen, D., Cleverly, J., Burba, G., & Arndt, S. K.: Effects of inhomogeneities within the flux footprint on the interpretation of seasonal, annual, and interannual ecosystem carbon exchange. Agricultural and Forest Meteorology, 221, 50-60, 2016.

Isaac, P., Cleverly, J., McHugh, I., van Gorsel, E., Ewenz, C., & Beringer, J.: OzFlux data: network integration from collection to curation. Biogeosciences, 14, 2903-2928, 2017.

Kala, J., De Kauwe, M. G., Pitman, A. J., Medlyn, B. E., Wang, Y.-P., Lorenz, R, et al.: Impact of the representation of stomatal conductance on model projections of heatwave intensity. Scientific Reports, 6, 1–7, 2016.

Klein Tank, A. M. G., Zwiers, F. W. and Zhang, X.: Guidelines on Analysis of extremes in a changing climate in support of informed decisions for adaptation, Geneva, Switzerland, 2009.

Lin, Y.-S., Medlyn, B. E. and Ellsworth, D. S.: Temperature responses of leaf net photosynthesis: The role of component processes. Tree Physiology, 32, 219–231, 2012.

Lloyd, J. Modeling stomatal responses to environment in Macadamia integrifolia. Australian Journal of Plant Physiology, 18, 649–660, 1991.

Lorenz, R., Jaeger, E. B. and Seneviratne, S. I.: Persistence of heat waves and its link to soil moisture memory. Geophysical Research Letters, 37, L09703, 2010.

Macfarlane, C.: Great Western Woodlands OzFlux: Australian and New Zealand Flux Research and Monitoring hdl: 102.100.100/14226, 2013.

Mao, J., Pitman, A. J., Phipps, S. J., Abramowitz, G. and Wang, Y: Global and regional coupled climate sensitivity to the parameterization of rainfall interception. Climate Dynamics, 37, 171–186, 2011.

McHugh, I. D., Beringer, J., Cunningham, S. C., Baker, P. J., Cavagnaro, T. R., Mac Nally, R. et al.: Interactions between nocturnal turbulent flux, storage and advection at an ideal eucalypt woodland site. Biogeosciences, 14, 3027., 2017.

Medlyn, B. E., Duursma, R. A., Eamus, D. , Ellsworth, D. S., Prentice, I. C., Barton, C. V., Crous, K. Y., De Angelis, P. , Freeman, M. And Wingate, L.: Reconciling the optimal and empirical approaches to modelling stomatal conductance. Global Change Biology, 17: 2134-2144, 2011.

Medlyn, B. E., De Kauwe, M. G., Lin, Y., Knauer, J., Duursma, R. A., Williams, C. A., Arneth, A., Clement, R., Isaac, P., Limousin, J., Linderson, M., Meir, P., Martin-StPaul, N. and Wingate, L.: How do leaf and ecosystem measures of water-use efficiency compare? New Phytologist, 216, 758-770, 2017.

Merbold, L., Ardö, J., Arneth, A., Scholes, R., Nouvellon, Y., De Grandcourt, A., et al.: Precipitation as driver of carbon fluxes in 11 African ecosystems, Biogeosciences, 6, 1027–1041, 2009.

Meyer, W., Kondrlovà, E. and Koerber, G.: Evaporation of perennial semi-arid woodland in southeastern Australia is adapted for irregular but common dry periods. Hydrological Processes, 29, 3714–3726, 2015.

Miralles, D., Berg, M. van den, Teuling, A. and Jeu, R. de: Soil moisture-temperature coupling: A multiscale observational analysis. Geophysical Research Letters, 39, L21707, 2012.

Miralles, D. G., Teuling, A. J., Van Heerwaarden, C. C. and Arellano, J. V.-G. de: Mega-heatwave temperatures due to combined soil desiccation and atmospheric heat accumulation. Nature Geoscience, 7, 345-349, 2014.

O'sullivan, O. S., Heskel, M. A., Reich, P. B., Tjoelker, M. G., Weerasinghe, L. K., Penillard, A. , Zhu, L. , Egerton, J. J., Bloomfield, K. J., Creek, D. , Bahar, N. H., Griffin, K. L., Hurry, V. , Meir, P. , Turnbull, M. H. and Atkin, O. K.: Thermal limits of leaf metabolism across biomes. Glob Change Biology, 23: 209-223, 2017.

Perkins, S., Alexander, L. and Nairn, J.: Increasing frequency, intensity and duration of observed global heatwaves and warm spells. Geophysical Research Letters, 39, L20714, 2012.

Perkins, S. E.: A review on the scientific understanding of heatwaves—their measurement, driving mechanisms, and changes at the global scale. Atmospheric Research, 164, 242–267, 2015.

Pitman, A., Avila, F., Abramowitz, G., Wang, Y., Phipps, S. and Noblet-Ducoudré, N. de: Importance of background climate in determining impact of land-cover change on regional climate. Nature Climate Change, 1, 472–475, 2011.

Rambal, S., Joffre, R., Ourcival, J., Cavender-Bares, J. and Rocheteau, A.: The growth respiration component in eddy co2 flux from a quercus ilex mediterranean forest. Global Change Biology, 10, 1460–1469, 2004.

Raupach, M.: Simplified expressions for vegetation roughness length and zero-plane displacement as functions of canopy height and area index. Boundary-Layer Meteorology, 71, 211–216., 1994.

Raupach, M., Finkele, K. and Zhang, L.: SCAM (Soil-Canopy-Atmosphere Model): Description and comparison with field data, Aspendale, Australia: CSIRO CEM Technical Report, 132, 81, 1997.

Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P. G. and Valentini, R.: Annual variation in soil respiration and its components in a coppice oak forest in central Italy. Global Change Biology, 8, 851–866, 2002.

Sabbatini, S., Arriga, N., Bertolini, T., Castaldi, S., Chiti, T., Consalvo, C., et al.: Greenhouse gas balance of cropland conversion to bioenergy poplar short-rotation coppice. Biogeosciences, 13, 95, 2016.

Schmid, H. P., Grimmond, C. S. B., Cropley, F., Offerle, B. and Su, H.-B.: Measurements of CO_2 and energy fluxes over a mixed hardwood forest in the mid-western United States. Agricultural and Forest Meteorology, 103, 357 – 374, 2000

Seneviratne, S. I., Luethi, D., Litschi, M. and Schaer, C.: Land-atmosphere coupling and climate change in Europe. Nature, 443, 205–209, 2006.

Silberstein, R.; Gingin OzFlux: Australian and New Zealand Flux Research and Monitoring hdl: 102.100.100/22677, 2015.

Sillmann, J., V. V. Kharin, F. W. Zwiers, X. Zhang, and D. Bronaugh (2013), Climate extremes indices in the CMIP5 multimodel ensemble: Part 2. Future climate projections, Journal of Geophysical Research: Atmospheres, 118, 2473–2493

Teuling, A. J., Seneviratne, S. I., Stöckli, R., Reichstein, M., Moors, E., Ciais, P., et al: Contrasting response of European forest and grassland energy exchange to heatwaves. Nature Geoscience, 3, 722-727, 2010.

Trewavas, A.: What is plant behaviour? Plant, Cell & Environment, 32: 606-616, 2009.

Ukkola, A. M., Pitman, A. J., Decker, M., De Kauwe, M. G., Abramowitz, G., Kala, J., et al.: Modelling evapotranspiration during precipitation deficits: Identifying critical processes in a land surface model. Hydrology and Earth System Sciences, 20, 2403–2419, 2016.

Ukkola, A. M. and Haughton, N. and De Kauwe, M. G. and Abramowitz, G. and Pitman, A. J.: FluxnetLSM R package (v1.0): a community tool for processing FLUXNET data for use in land surface modelling. Geoscientific Model Development, 10, 3379-3390, 2017.

Urban, J., Ingwers, M. W., McGuire, M. A. and Teskey, R. O.: Increase in leaf temperature opens stomata and decouples net photosynthesis from stomatal conductance in pinus taeda and populus deltoides x nigra. Journal of Experimental Botany, 68, 1757–1767, 2017

Van Gorsel, E., Wolf, S., Cleverly, J., Isaac, P., Haverd, V., Ewenz, C., et al.: Carbon uptake and water use in woodlands and forests in southern australia during an extreme heat wave event in the angry summer of 2012/2013. Biogeosciences, 13, 5947, 2016.

van Heerwaarden, C. C. and Teuling, A. J.: Disentangling the response of forest and grassland energy exchange to heatwaves under idealized land–atmosphere coupling. Biogeosciences, 11, 6159-6171, 2014.

von Caemmerer, S., & Evans, J. R.: Temperature responses of mesophyll conductance differ greatly between species. Plant, Cell & Environment, 38, 629–637, 2015.

Yu, G.-R., Wen, X.-F., Sun, X.-M., Tanner, B. D., Lee, X. and Chen, J.-Y.: Overview of Chinaflux and evaluation of its eddy covariance measurement. Agricultural and Forest Meteorology, 137, 125–137, 2006.

Zhu L, Bloomfield KJ, Hocart CH, et al.: Plasticity of photosynthetic heat tolerance in plants adapted to thermally contrasting biomes. Plant, Cell & Environment,18, 1251-1262, 2018.

Figures

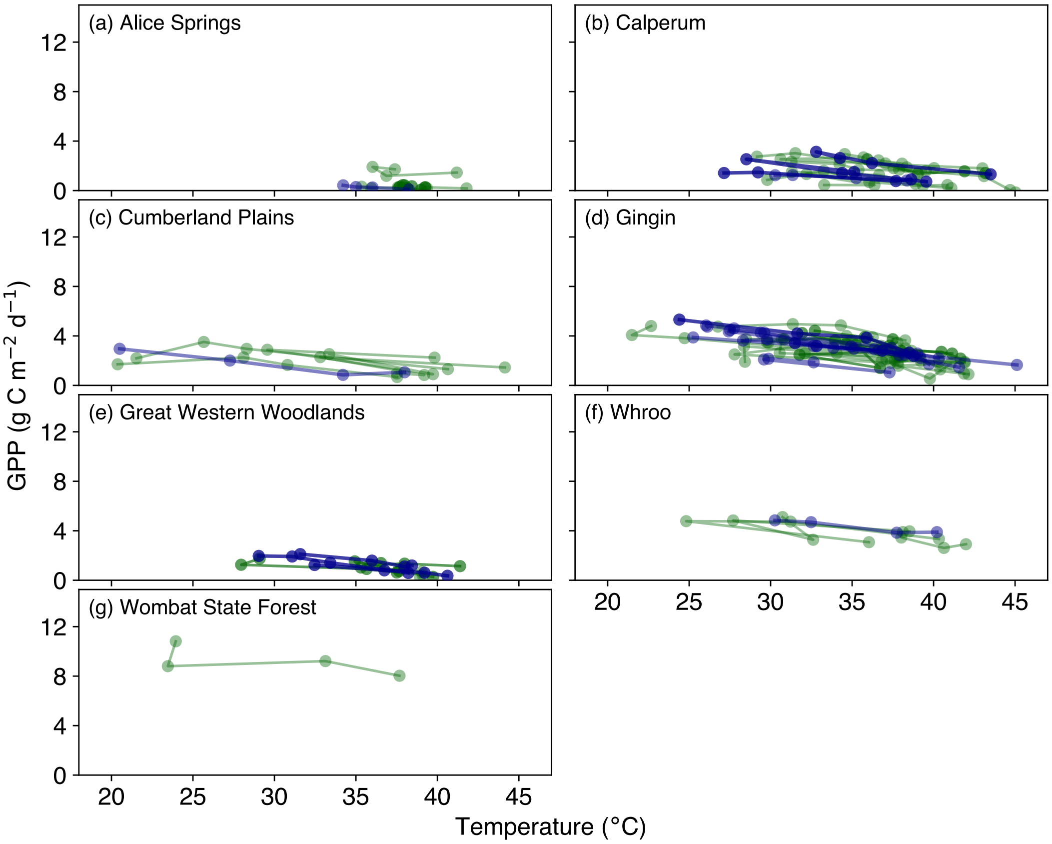

Figure 1: Evolution of GPP in the three days prior to and including a hot temperature extreme (daily maximum temperature exceeded 37°C). Dark blue lines represent events in which a fitted linear regression indicated a significant negative slope, 5 whilst dark green lines represent events where the fitted slope was negative but not significant. Events where the fitted slope was positive are shown in Figure S1.

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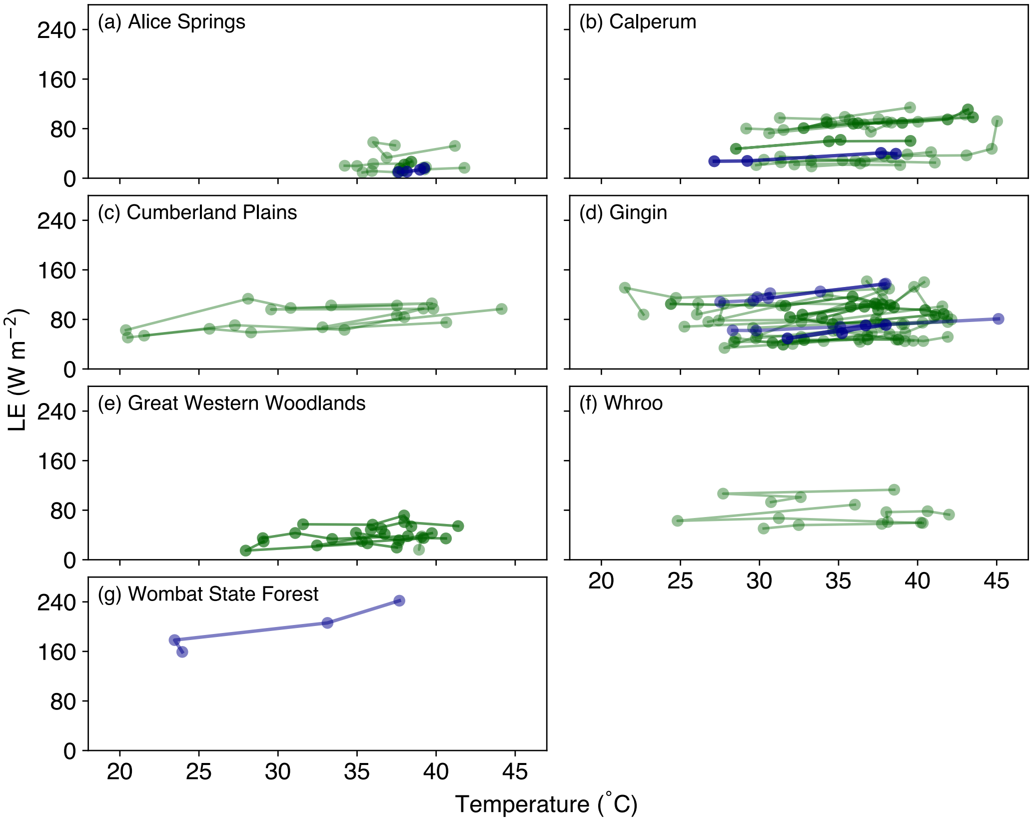

Figure 2: Evolution of LE in the three days prior to and including a hot temperature extreme (daily maximum temperature exceeded 37˚C). Dark blue lines represent events in which a fitted linear regression indicated a significant positive slope, whilst dark green lines represent events where the fitted slope was positive but not significant. Events where the fitted slope 5 was negative are shown in Figure S2.

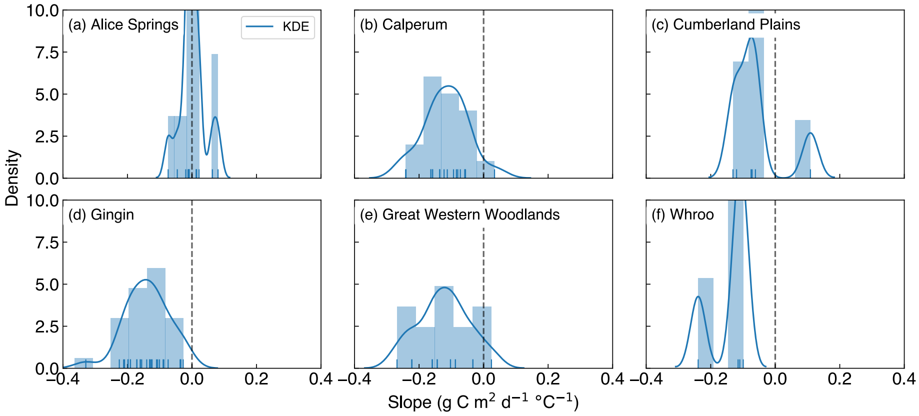

Figure 3: Density and histogram showing the distribution of fitted positive and negative GPP slopes across the OzFlux sites. The dark blue curve shows the fitted kernel density estimate (KDE) and the vertical blue lines along the x-axis are "rugs",

which represent the individual occurrence of fitted slopes. Data from Wombat State Forest has been omitted from the graph as there was only one slope.

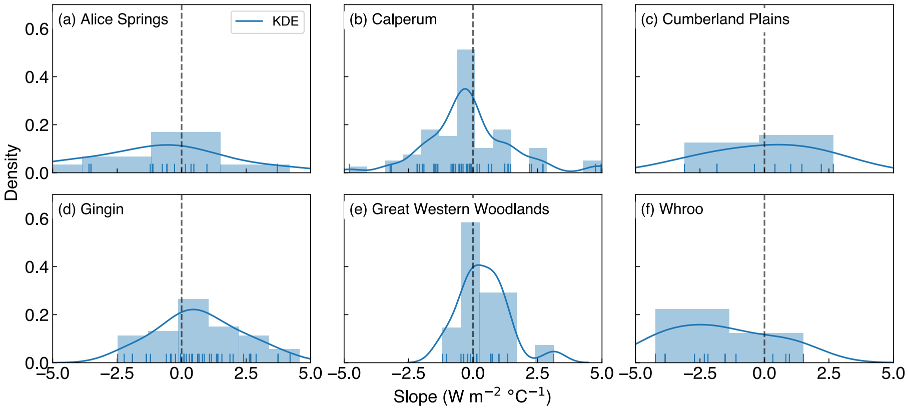

Figure 4: Density and histogram showing the distribution of fitted positive and negative LE slopes across the OzFlux sites. The dark blue curve shows the fitted kernel density estimate (KDE) and the vertical blue lines along the x-axis are "rugs", which represent the individual occurrence of fitted slopes. Data from Wombat State Forest has been omitted from the graph as there was only one slope.

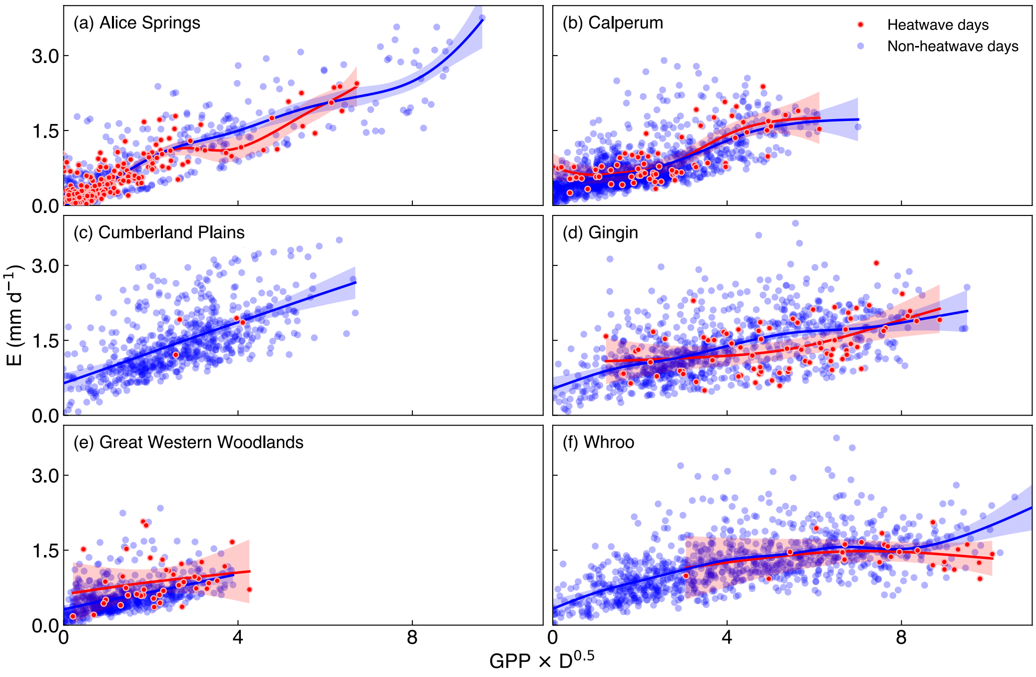

Figure 5: E as a function of GPP x $D^{0.5}$ on heatwave and non-heatwave days. The solid lines are smoothed time series using a generalized additive model (with a 95% confidence intervals). Note the generalized additive model was not fit to the heatwave days at Cumberland Plains due to the limited data.

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Tables

Table 1. OzFlux and FLUXNET2015 site information. GDD_{37} is the average number of growing degree days above our threshold of 37°C. Plant Functional types (PFT) were: ENF - evergreen needleleaf forest; EBF - evergreen broadleaved forest; and DBF - deciduous broadleaved forest. Note the FLUXNET sites Castel d'Asso 1 and 3 and Roccarespampani 1 and 2 have been combined in the table.

Site	Latitude	Longitude	GDD_{37}	Dominant Species	Years	Reference
OzFlux sites						
Alice Springs	-22.28	133.25	85.8	*Acacia aneura*	2010-2013	
Calperum	-34.00	140.59	68.3	Mallee	2011-14	Meyer et al. (2015)
Cumberland Plains	-33.61	150.72	13.5	*Eucalyptus moluccana* and *Eucalyptus fibrosa*	2013-14	Renchon et al. (2018)
Gingin	-31.37	115.71	31.7	*Banksia*	2012-14	Silberstein (2015)
Great Western Woodlands	-30.19	120.65	85.1	*Eucalyptus salmonophloia*	2013-15	Macfarlane (2013)
Whroo	-36.67	145.03	13.4	*Eucalyptus microcarpa* and *Eucalyptus leucoxylon*	2012-14	McHugh et al. (2017)
Wombat State Forest	-37.42	144.09	3.1	*Eucalyptus obliqua, Eucalyptus radiata* and *Eucalyptus rubida*	2011-14	Griebal et al. (2016)
***FLUXNET2015* sites**						
Castel d'Asso	42.38	12.02	0.1	Poplar species	2011-14	Sabbatini et al. (2016)
Le Bray	44.71	-0.77	0.5	*Pinus pinaster*	1996-08	Berbigier et al. (2001)
Mongu	-15.44	23.25	52.6	*Brachystegia bakeriana* and *Brachystegia spiciformis*	2000-09	Merbold et al. (2009)
Morgan Monroe State Forest	39.32	-86.41	21.5	*Acer saccharum, Liriodendron tulipifera, Sassafras albidum, Quercus alba and Quercus nigra*	1999-2014	Schmid et al. (2000)
Puechabon	43.74	3.60	0.4	*Quercus ilex*	2000-14	Rambal et al. (2004)
Qianyanzhou	26.74	115.05	20.9	*Pinus elliottii* and *Pinus massoniana*	2003-05	Yu et al. (2006)

Roccarespampani	42.39	11.92	0.2	*Quercus Cerris L.*	2000-12	Rey et al. (2002)