We would like to thank both reviewers for the positive and constructive comments. Their suggestions have helped improve our study. Our responses are listed below in blue and italic.

Response to reviewer 1

Overall Review

The article presents a detailed exercise of upscaling photosynthesis from the leaf scale to the stand level for the climatic conditions and vegetation distribution corresponding to the EucFACE experiment (forest stand dominated by Eucalyptos tereticornis) and thus it includes ambient and elevated CO2 (eCO2) scenarios. Upscaling leaf-level response to tree and forest stand scale is a long-standing problem in biogeoscience and while it has been tackled in various ways in the literature, the study presented here is innovative for the thoroughness and level of detail included in the analysis. Furthermore, the analysis is carried out for ambient and eCO2 conditions using a terrestrial biosphere model (MAESPA) that represents explicitly each tree and solve the canopy using multiple layers and accounts in each layer for multiple points representing radial variability in incoming light. The study also accounts for the acclimation response of photosynthesis and it is strongly constrained by observations, which is rarely the case in other similar studies. The study convincingly shows that a strong increase in leaflevel light-saturated photosynthesis (+33%) under eCO2 reflects in a minor increase in stand level GPP (10%) because of the prevalence of electron transport limitations in photosynthesis and to a minor extent downregulation of photosynthetic capacity due to the leaf acclimation to eCO2. Results also show a large uncertainty in computing GPP at the stand level when a small area (corresponding to a CO2 enrichment ring) is considered. While upscaling photosynthesis at the forest stand scale is not a new task, the way this problem is solved here, represents a scientific advancement because it is presented in the context of a FACE experiment and provide a number of interesting discussion points on mechanistic model parameterization and uncertainties (e.g., the role of the curvature for electron transport, the Jc,max/Vc,max ratio, photosynthesis acclimation, forest stand heterogeneity). It is clearly shown that translating leaf-level responses of CO2 effects to the ecosystem scale is very misleading and most important the study provides mechanistic explanations for the differences. The search for the reasons and the clear explanations provided concerning subcomponents of the photosynthesis model (e.g., Rubisco vs. electron transport limited, or acclimation of photosynthetic capacity) represents an innovative approach, which I did not see before in the literature. For these reasons, beyond the importance of estimating GPP in ambient and eCO2 conditions that will serve future studies in the context of the EucFACE experiment, the article represents an important piece of work for the mechanistic understanding of ecosystem responses to elevated CO2.

The article is overall very well written and presented. In summary, I think the manuscript is making an important contribution to the field and I sincerely congratulate the authors for this nice piece of work. In the following, I just have a number of minor comments that can be helpful to improve further the presentation of this work.

Sincerely,

Simone Fatichi

*Response: We would like to thank the reviewer for his detailed and positive evaluation of our work. We have modified the manuscript according to his comments.*

Minor comments

P.2 Line 34-37. The difference between canopy scale "direct response" of +11% and the mean actual response of 6%, while very clear in the manuscript, it is not so clear at the abstract level. Maybe introducing the concept of "uncertainty" associated with the variability across rings or something associated to the "actual field response" according to the experimental configuration may help.

*Response: We have changed the text to read:*

*'After taking in account the baseline variability in leaf area index across plots, we estimated a field GPP response to $eC_a$ of 6% with a 95% confidence interval (-2, 14%).'*

P.3 Line 51. The "hence" here is out of place, because the causality is not straightforward. An increase in carbon uptake does not necessarily lead to an increase in the amount of carbon stored in the ecosystem. The authors are well aware of this. Something like "which in turn could potentially increase. . ." will be more correct.

*Response: We have changed this line to read:*

*''These physiological responses at the leaf scale can increase ecosystem carbon uptake, which in turn may result in increased carbon storage in the ecosystem, mitigating against the rise in $C_a$.''*

P.3. Line 57. A short overview of main disagreements between various studies is provided in Fatichi et al. 2019.

*Response: We thank the reviewer for bringing the paper to our attention. The citation is now added to the paper.*

P.3. Line 57-68. I think this paragraph would benefit from referring to the estimates of global terrestrial C sink. While the attribution of the land C-sink is still debated, an average C-sink of 20–30 g C year-1 m-2 over vegetated land in the last decades is not

a detail in the overall story about eCO2.

*Response: We have referred to the land carbon sink in the text:*

*'Similarly, the global carbon budget indicates a strong sink for carbon on land (Le Quéré et al., 2018).'*

P. 4. Line 80. While, practically, I would agree in defining the response of GPP to eCO2 an upper bound. Theoretically, this is not a limit, if for some reason, plants in eCO2 conditions will be able to do maintenance with half of the respiration costs, then the NPP response could be larger than the GPP response. I think a "reference value" is more correct than an "upper-bound".

*Response: We have modified the line to read:*

*"The response of GPP is important because it provides a reference point against which to compare the response of other components of ecosystem carbon balance, such as above-ground growth."*

P.4. Line 115 and P.6 Line 161 and 166. Yang et al. 2019 is missing from the reference list, overall, I would avoid referring to papers, which are not published.

*Response: The paper is now accepted at Tree Physiology (https://doi.org/10.1093/treephys/tpz103). We have added the reference to the list.*

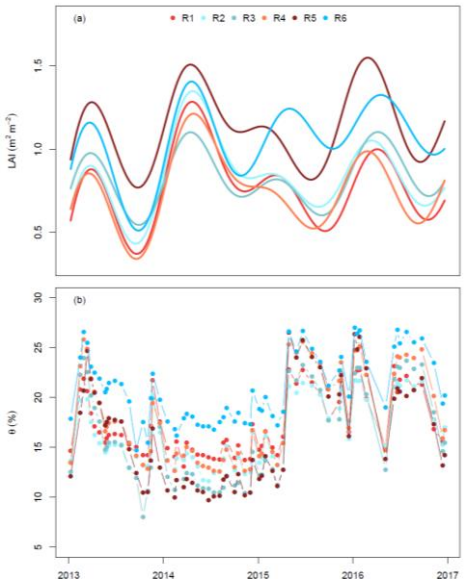
P.4 Line 116 and P.6 Line 170-171. I would not mix the "meteorological forcing" with the "model parameterization". The two aspects are different from a modeling perspective, one represents the inputs to the model, the other (e.g., physiological and structural attributes) represents model parameters, or prognostic variables if these are time dynamics and computed in the model. One can use the same model parameterization with different meteorological inputs and the other way around.

*We agree with the reviewer and deleted 'meteorological' in the sentence.*

P.6 L.173. Figure 2b. I am strongly encouraging to avoid using a linear interpolation

for soil moisture values at least in its graphical representation. Soil moisture temporal dynamics have a fast and strong response to rainfall events. Linearly interpolating biweekly value is creating a misleading perception of the real temporal dynamics of soil moisture. I would prefer to have just the points when the soil moisture values have been collected rather than the current representation where raising and descending soil moisture dynamics are often unrealistic.

*Response: We have adapted the suggestion by plotting the soil wwater content as dots and revised the figure legend. Thank you for this suggestion. We experimented with removing the lines from this plot as suggested but it is hard to see anything without the lines.*




P.7. Line 220. Just a suggestion. Maybe the Fig. S1 could be included in the main manuscript.

*Response: We are glad to see that the reviewer likes fig s1. The fig works well as a conceptual figure showing how the model works but does not related directly to the inputs and results of the model. We thus decide to leave it in the supplementary material.*

P.9 Line Table 1. I know that in literature it is quite typical to report µmol only. However, this is not very precise, especially when we are dealing with photosynthesis. I would suggest to explicitly say µmol of what, e.g., µmol-CO2, µmol-H20, µmol-electrons or better µmol-Eq. as in the original Farquhar et al. 1980.

*We have revised the table as suggested:*

*Table 1. Summary table of parameter definitions, units, and sources used in this study.*

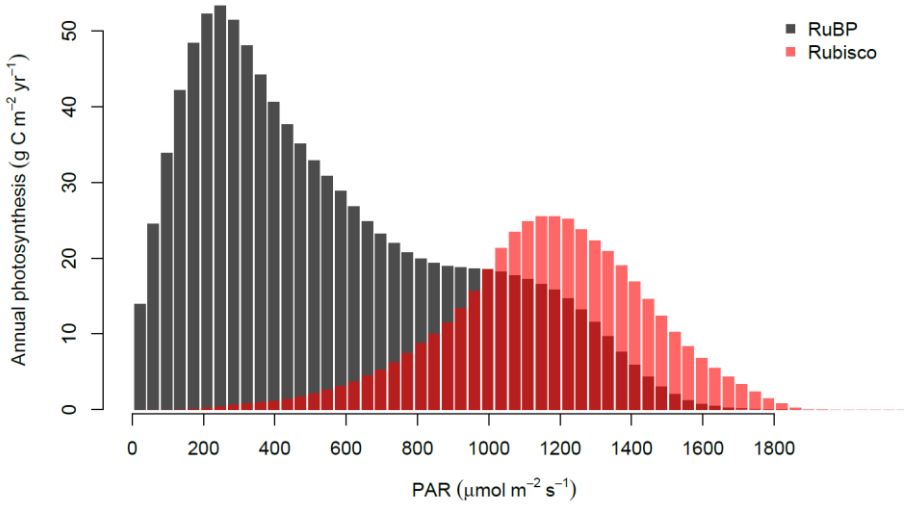
| Parameters | Definitions | Units | Values | Eqn. |
|---|---|---|---|---|
| $\alpha_J$ | Quantum yield of electron transport rate | µmol electron µmol$^{-1}$ photon | 0.30 | S7 |
| $a$ | Fitted slope of LA and DBH | m$^2$ m$^{-1}$ | 492.6 | 4 |
| $a_{abs}$ | Absorptance of PAR | fraction | 0.825 | S4 |
| $b$ | Fitted index of LA and DBH | - | 1.8 | 4 |
| $c_D$ | Slope of $V_{cmax}$ to $D$ | kPa$^{-1}$ | 0.14 | 3 |
| $\Delta S$ | Entropy factor | J mol$^{-1}$ K$^{-1}$ | 639.60 ($V_{cmax}$); 638.06 ($J_{max}$) | S5 |
| $E_a$ | Activation energy | J mol$^{-1}$ | 66386 ($V_{cmax}$); 32292 ($J_{max}$) | S5 |
| $g_{1.max}$ | Maximum $g_1$ value | kPa$^{0.5}$ | 5.0 | 2 |
| $H_d$ | Deactivation energy | J mol$^{-1}$ | 200000 | S5 |
| $\theta_J$ | Convexity of electron transport rate to $Q_{APAR}$ | - | 0.48 | S8 |
| $\theta_{max}$ | Upper limit of soil water content above which $g_1$ is maximum | - | 0.240 | 2 |
| $\theta_{min}$ | Lower limit of soil water content below which $g_1$ is zero | - | 0.106 | 2 |
| $J_{max.25}$ | Value of $J_{max}$ at 25ºC | µmol electron m$^{-2}$ s$^{-1}$ | 159 | 3 |
| $k_T$ | Sensitivity of $R_{dark}$ to temperature | ºC$^{-1}$ | 0.078 | S6 |
| $q$ | The non-linearity of the $g_1$ dependence of $\theta$ | - | 0.425 | 2 |
| $R_{day.25}$ | Light respiration rate | µmol C m$^{-2}$ s$^{-1}$ | 0.9 | S6 |
| $R_{dark.25}$ | Dark respiration rate | µmol C m$^{-2}$ s$^{-1}$ | 1.3 | S6 |
| $R_{gas}$ | Gas constant | J mol$^{-1}$ K$^{-1}$ | 8.314 | S5 |
| $V_{cmax.25}$ | Value of $V_{cmax}$ at 25ºC | µmol C m$^{-2}$ s$^{-1}$ | 91 (ambient); 83 (elevated) | 3 |

P.10. Line 286-290. Did you check if with MAESPA you get the same +33% of leaflevel photosynthesis if you simulated the same environmental conditions of the 600 A-Ci curves? Very likely, yes, because these are used to estimate the photosynthesis parameters, but just as a double check.

*Response: The leaf gas exchange model in MAESPA is the same leaf-scale model as the 'photosyn' function implemented in the 'plantecophys' R package. We did not check the full MAESPA model but checked the leaf gas exchange model in the R package, which can reproduce the 33% value depending on parameterisation.*

P.10 Figure 6 and 7. In Fig.7 is reported incident PAR and in Fig. 6 absorbed PAR, even though one refer to the stand scale and the other to the leaf-level, I think it would have been better to use either absorbed or incident PAR in both of them for comparison.

*Response: We have changed Fig 6 to PAR so that both figures are directly comparable.*




P. 11. Line 318. From the Supp. Material, the curvature for electron transport θj is also used as curvature and for overall photosynthesis (Eq. S8). These two values are typically different in models (e.g., Bonan et al 2011). This needs to be specified in the manuscript as well. The reference θj =0.85 is typically assumed for the curvature and for the overall photosynthesis, rather than for the curvature of electron transport, which is typically lower in some models (0.7, Bonan et al 2011, Fatichi et al 2016). This needs to be discussed.

*Response: We have modified L320-321 to read:*

*"We explored this effect by investigating the effect of varying the convexity, $\theta_J$, which is assumed to be the same as the convexity of overall photosynthesis."*

*and L422-423 to read:*

*"The parameter value we fitted to data measured in situ ($\theta_J$ = 0.48) is lower than the value commonly assumed in the models (e.g., 0.7 in Bonan et al., 2011). Note that some model studies assume that $\theta_J$ to be lower than the convexity of overall photosynthesis (typically over 0.8; e.g., 0.9 in Medlyn et al., 2002; 0.85 in Haverd et al., 2018). Here we assumed that the convexity of electron transport rate and overall photosynthesis are the same (see Supplementary Text S1 for details)."*

*We added justifications in Supplementary Text S1:*

*'The assumptions of the quantum yield and convexity being the same between J and overall photosynthesis are further explored by comparing the photosynthesis predicted by 'photosyn' function with the fitted $\alpha_A$, and $\theta_J$ to the measured light response curve. There's good agreement with a root mean square error of 2.3 μmol $m^{-2}$ $s^{-1}$ and a $R^2$ of 0.92, suggesting the assumptions are appropriate in our site. '*

P. 12. Line 377. I am honestly impressed by the inter-ring differences in GPP. I think these are mostly related to the relative small size of the rings. Or better, the size is quite large in comparison to experimental capabilities but relative small to average forest stand heterogeneities.

*Response: Despite the relatively consistent overstorey vegetation, this mature forest has remained unmanaged for at least over 90 years, subject to native and variable environmental fluctuations. We therefore believe that spatial heterogeneity is the major driver of the inter-ring variability in GPP.*

P.12 Line 388. Renchon et al 2018 is not in the reference list.

*Response: We have added the paper to the reference list.*

Eq (S3) The denominator should be Ci+2Γ rather than Ci+ Γ (e.g., Wang and Leuning, 1998, Dai et. 2004, Bonan et al 2011);

*Response: Thanks, the equation has been corrected.*

**Response to reviewer 2**

This manuscript syntheses a large amount of data from the EucFACE project to examine the effects of Rubisco- versus RuBP limitation on photosynthesis under elevated CO2. The authors present leaf-level measurements, leaf-level modeling, and canopy scale modeling of ambient versus elevated CO2 conditions to illustrate that current projections of GPP under elevated CO2 are overestimated in mature forests due to biases towards light-saturated leaves. This work is scientifically relevant and pedantic. I want to commend the authors on their efforts and have minor suggestions to improve the presentation and make the work clearer to a wider audience.

The introduction is extremely well written and provides appropriate context for the work being conducted within the manuscript. The methodology is thoughtfully presented, and justification was given for parameter choices in the model. The amount of data used to represent the system is commendable and I appreciate the attention to detail. I find the presentation of soil moisture to be the weakest element of the methodology and would recommend a little more attention paid to it as it is one of the few varying parameters between the replicates. The presentation of the results would be strengthened by more clearly delineating measurements vs. leaf scale modeling vs. canopy scale modeling. I would personally be very interested in seeing some of the rawer data forms (e.g., timeseries of canopy model) in addition to the synthesized percent changes. While this may be a question of style, I found the figure captions to contain relevant information that was missing from the text. I would include more of that information in the text for clarity. Figures are adequate, but the figure legends are not descriptive (esp. Fig 2 and 4-7) and the long captions make it difficult to distinguish between the different replicates, responses, etc.

Overall well done and I'm excited to see this work published!

*Response: We appreciate the reviewer's detailed and positive evaluation of our work. We would like to thank the reviewer and have modified the manuscript according to the comments.*

INTRODUCTION

L94 -95 Can you please give an example of the ranges of Jmax:Vmax ratio found in these cited works to show how much it deviates from the normally adopted ratio of 2?

*Response: We have changed the text to read:*

*'However, recent studies have suggested the $J_{max}$:$V_{cmax}$ ratio varies systematically across forest ecosystems and can range from 1 to 3 (Kattge and Knorr, 2007; Ellsworth et al., 2012; Kumarathunge et al., 2018)'*

METHODS

L132: Is the repo unchanged or should the reader be directed to a certain commit version?

*Response: The repo will remain unchanged. Further development of the model will be through other branches of the repo.*

L162: You do not introduce the variable D until line 172 and do not provide units.

*Response: We thank the reviewer for highlighting this, we have introduced D on line 155.*

L164: Can you please clarify the choice between Jmax and Vcmax here in the Vmax, t parameter?

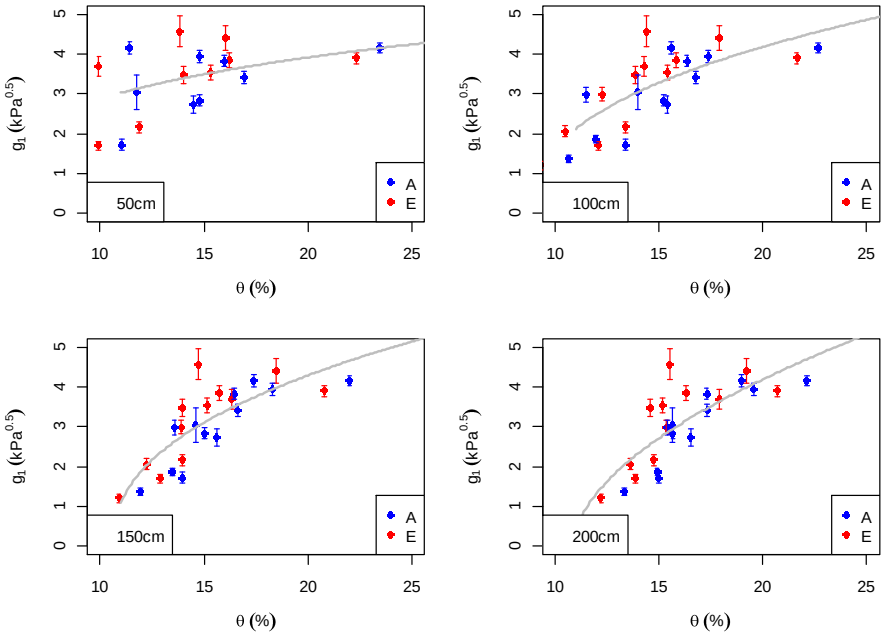
*Response: There are measurements on Jmax25, Vcmax25, and their temperature dependence. We correct Jmax25 and Vcmax25 based on the leaf temperature to derive Jmax and Vcmax following Eqn S5. These values of Jmax and Vcmax are then reduced by VPD (a bit more explanation….). We added reference to Text S1 in the manuscript.*

L175-177: I would introduce the equipment and measurement heights before the frequency, but this is a minor point.

*Response: We have changed the ordering as suggested.*

L186: In Fig 2 you present that you use 150cm neutron probe measurements that were conducted biweekly and linearly interpolated, but here you say these measurements were not gap-filled? While I do not think this would majorly affect your results, averaging the soil moisture over the entire 150 cm profile seems problematic as you are giving equal weight to regions that are likely to contain significantly less root biomass. Would it not be more fitting to use a weighted average based on the below-ground biomass distribution to represent the soil moisture that the tree actually "feels"? Would this have changed your g1?

Response: We did not account for root distribution. Instead, we tested the g1 - SWC relationship using SWC averaged over different depths and found that 150cm has the best fit. This result is not shown in the paper but is as below.




L202: Minor point of convention – normally see DBH represented in [cm]. I assume you used DBH in [cm] in your allometry in Eq 4?

*Response: That was a typo and we have now fixed the unit to be cm, thanks.*

L214-215: Fit statistics of this allometry?

*Response: We have modified the sentence to read:*

*'The values obtained via fitting for a and b were 492.6 and 1.8 respectively, with a root mean square error of 14.4 $m^2$ and $R^2$ of 0.83'*

L225: No, no to citing an "in prep" when you seem to be presenting this data in this work.

*Response: We replaced the "in prep" citation with Ellsworth et al. (2017) who also use these data. A much more detailed manuscript is in preparation and we had hoped to be able to cite that, but the 2017 citation is also appropriate.*

L278 Misspelling of ntheta_min

*Response: Thanks, this has been fixed.*

L246: Please expand up on the statement "within two weeks without rain" – was there some selection of points that happened based on this? I'm bit confused with the g1 and soil moisture match up.

*Response: We have modified the text to read:*

*'The $g_1$ values were related to the nearest measurements of $\theta$ (within two weeks). In all cases, there has been no rainfall between $g_1$ and $\theta$ measurement dates. '*

L255: Missing commas.

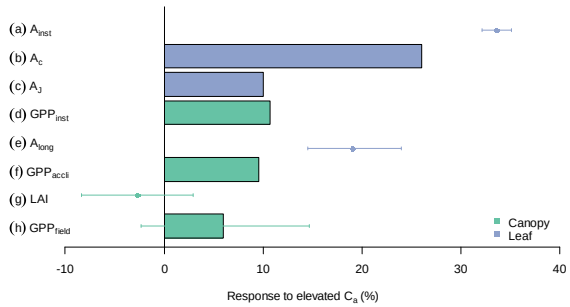
*Response: It was not clear to us what the reviewer is referring to.*

RESULTS

The results presentation is somewhat difficult to follow given the large number of simulations and measurements spanning scales. Figure 4's mix of bar and point measurements is difficult to follow. Separating data measurements from modeled responses could help the reader follow better what is derived from models and what was an actual measured response. I appreciate the color coding between leaf and canopy measurements. Also, making a clearer distinction between the leaf-level models using the R package and the canopy scaled measures made using MAESPA would be helpful.

*Response: We have changed the bottom row in fig4. Now all modelled results are in bars and observations in points. We have further clarified this in the caption. This should also help separate the results from leaf and canopy models.*

*'The bars represent model outputs while points represent observations.'*




‘

DISCUSSION

L397-398: I would love to see the timeseries that illustrates this stomatal closure at the canopy scale.

*Response: These data were originally presented by Gimeno et al. (2016), who show a timeseries in their Figure 2. The data themselves are also publicly available so that the reader can make their own plots. See also Yang et al. (2019) who explore the relationship with VPD.*

L405-418: Ah ha! This was the presentation of J:V ratio ranges that I was waiting for. I would still suggest adding in a range to the introduction so that the reader is primed to consider how variability in J:V could impact these modeled responses to eCa.

*Response: We have addressed this comment above.*

*‘However, recent studies have suggested the $J_{max}$:$V_{cmax}$ ratio varies systematically across forest ecosystems and can range from 1 to 3 (Kattge and Knorr, 2007; Ellsworth et al., 2012; Kumarathunge et al., 2018) ’*

L420: Yes, but would how would the way you averaged your soil moisture values affect this value?

*Response: We think that the reviewer may have confused the convexity parameter $\theta_J$ with soil moisture content $\theta$. Unfortunately, $\theta$ is the most commonly used symbol for the terms in both fields. We edited the definition of the terms in Table 1 to clarify that values of theta, theta max and theta min refer to soil moisture content.*

L449-451 I agree with this statement, but can you be more clear about what “uncertainty” you are referring to? Are you talking about uncertainty in our forcing variables for models; structural uncertainty in the models; both?

*Response: Here we specifically focused on the variability in the measurements (i.e., inter-ring variability in this study). We clarified this further in the text:*

*‘Secondly, the inherent ring-to-ring variation in this natural forest stand is even higher than the GPP response, which highlights the importance of considering both the effect size and uncertainty in the observations than to focus on statistical significance.’*

L462-463 Falsify those model simulations? Should we just throw the models in the trash or can we focus on an improvement in the model structure in order to capture these transitions between Rubisco limitation and RuBP regeneration? Or could it be also that there are other structural differences between those models and the explicit canopy structure of MAESPA?
*Response: As the reviewer highlights, we are falsifying model assumptions, not the model as a whole. Thus, we do not advocate trashing the models, but rather we aim to identify ways forward for model improvement. We modified the text to read:*
*'With our results, it is possible to falsify some of the assumptions made in these model simulations and identify directions for model improvement.'*

FIGURES
L708-711 Fig 2: You give no clear indication about what the different line colors mean. I assume these are replicates, but I am not clear about if these are elevated or control plots. You briefly mention ring numbers in text, but the figure would be improved if you make this distinction more visually apparent.
*Response: We apologise for the confusion. These details were inadvertently omitted from the caption. We now added*
*'Each line colour marks a different plot. Red colours show elevated $CO_2$ plots (treatment), while blue colours show ambient $CO_2$ plots (control).'*

L714: "error bars represent standard error of fitted values" I'm a bit confused by this statement.
*Response: The observations were grouped by date and treatment before fitting. Only one g1 was fitted to each group of data (as stated in the method section 23.3). As a result, the fitting has an uncertainty or error. We used standard error from each fitting to quantify the uncertainty. We added the following to the figure caption:*
*"g1 parameter values are fitted to data grouped by month and treatment."*

L717: This figure is especially hard to follow and the mix of bar and points is difficult. I would suggest adding further groups to help identify measurements vs. leaf scale modeling vs. canopy scale modeling.
*Response: We have addressed this in the earlier comment from the reviewer. Now the bars represent model and points represent observations. We further clarified this in the caption.*

**Low sensitivity of gross primary production to elevated $CO_2$ in a mature Eucalypt woodland**

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**Abstract**

The response of mature forest ecosystems to rising atmospheric carbon dioxide concentration ($C_a$) is a major uncertainty in projecting the future trajectory of the Earth's climate. Although leaf-level net photosynthesis is typically stimulated by exposure to elevated $C_a$ ($eC_a$), it is unclear how this stimulation translates into carbon cycle responses at whole-ecosystem scale. Here we estimate a key component of the carbon cycle, the gross primary productivity (GPP), of a mature native Eucalypt forest exposed to Free Air $CO_2$ Enrichment (the EucFACE experiment). In this experiment, light-saturated leaf photosynthesis increased by 19% in response to a 38% increase in $C_a$. We used the process-based forest canopy model, MAESPA, to upscale these leaf-level measurements of photosynthesis with canopy structure to estimate ~~Gross Primary Production (~~GPP~~)~~ and its response to $eC_a$. We assessed the direct impact of $eC_a$, as well as the indirect effect of photosynthetic acclimation to $eC_a$ and variability among treatment plots via different model scenarios.

At the canopy scale, MAESPA estimated a GPP of 1574 g C $m^{-2}$ $yr^{-1}$ under ambient conditions across four years and a direct increase in GPP of +11% in response to $eC_a$. The smaller canopy-scale response simulated by the model, as compared to the leaf-level response, could be attributed to the prevalence of RuBP-regeneration limitation of leaf photosynthesis within the canopy. Photosynthetic acclimation reduced this estimated response to 10%. After taking in account the baseline variability in leaf area index across plots, we estimated a field GPP response to $eC_a$ of 6% with a 95% confidence interval (-2, 14%). These findings highlight that the GPP response of mature forests to $eC_a$ is likely to be considerably lower than the response of light-saturated leaf photosynthesis. Our results provide an important context for interpreting $eC_a$ responses of other components of the ecosystem carbon cycle.

## 1. Introduction

Forests represent the largest long-term terrestrial carbon storage (Bonan, 2008; Pan et al., 2011). Atmospheric carbon dioxide concentration ($C_a$) has increased significantly since the beginning of the industrial era (Joos and Spahni, 2008), but the increase would have been considerably larger without forest carbon sequestration, which is estimated to have offset 25-33% of recent anthropogenic $CO_2$ emissions (Le Quéré et al. 2017). $C_a$ is projected to continue to increase by 1-5 μmol $mol^{-1}$ per year into the future (IPCC, 2014), but the rate of this rise depends on the magnitude of the forest feedback on $C_a$. At the leaf scale, the direct physiological effects of rising $C_a$ are well understood: elevated $C_a$ ($eC_a$) stimulates plant photosynthesis (Kimball et al. 1993; Ellsworth et al. 2012) and reduces stomatal conductance (Morison, 1985, Saxe et al. 1998), which together increase leaf water-use efficiency (De Kauwe et al. 2014). These physiological responses at the leaf scale can increase ecosystem carbon uptake, which in turn may result in increased carbon storage in the ecosystem, mitigating against the rise in $C_a$. However, projecting the response of the terrestrial carbon sink to future increases in $C_a$ is a major uncertainty in models (Friedlingstein et al. 2014), highlighting an urgent need to make greater use of data from manipulative experiments at leaf scale to inform terrestrial biosphere models (Medlyn et al., 2015).

Our understanding of ecosystem responses to $eC_a$ relies on both experiments and observations. However, results from different types of studies show some important areas of disagreement (Fatichi et al., 2019). At the global scale, satellite data provide evidence of a strong greening trend over the last 20 years, indicating an increase in leaf area and/or above-ground biomass, which has been attributed to the gradual increase in $CO_2$ (Donohue et al., 2009; Donohue et al., 2013; Yang et al., 2016; Zhu et al., 2016). A positive response of carbon uptake/greenness is also found in manipulative $eC_a$ open-top chamber experiments with young trees (Eamus and Jarvis, 1989; Curtis and Wang 1998; Saxe et al. 1998; Medlyn et al., 1999) and ecosystem-scale FACE experiments in young, aggrading forest stands (Ainsworth and Long, 2005; Norby et al., 2005; , Ellsworth et al. 2012; Walker et al. 2019). In contrast, individual-tree experiments with mature trees (>30 years old) have found relatively small responses of tree growth to $eC_a$ despite an apparent increase in leaf photosynthesis (Dawes et al., 2011; Sigurdsson et al., 2013; Klein et al., 2016). Also, tree-ring studies indicate an apparent lack of stimulation of vegetation growth in mature forests over the last century (Peñuelas et al. 2011; Silva and Anand, 2013; van der Sleen et al. 2014). These studies raise important questions about how mature ecosystems will respond to $eC_a$.

The Eucalyptus FACE experiment (EucFACE; Australia) is the first replicated, ecosystem-scale experiment where a mature native forest has been experimentally subjected to $eC_a$ and provides a valuable case study to assess the response of a mature forest response to $eC_a$ under field conditions (Ellsworth et al. 2017). Results from the first five years (2013-2018) of leaf gas exchange measurements showed a consistent stimulation of leaf-level light-saturated net photosynthesis ($A$) of 19% (Ellsworth et al., 2017; Wujeska-Klause et al., 2019). Nevertheless, the increase in $A$ did not lead to a detectable change in above-ground growth (Ellsworth et al., 2017). These experimental results are consistent with empirical evidence arising from tree-ring studies (Peñuelas et al. 2011; Silva and Anand, 2013; van der Sleen et al. 2014) and also with experimental evidence from individual mature trees (Körner et al., 2005; Dawes et al., 2011; Klein et al., 2016).

As a first step towards reconciling the e$C_a$ responses of leaf photosynthesis and above-ground growth in this experiment, here we quantify how the whole canopy carbon uptake, or gross primary productivity (GPP) was increased under e$C_a$. The response of GPP is important because it provides ~~an upper bound~~ a reference point ~~and possibly the upper bound on~~against which to compare the ~~potential~~ response of other components of ecosystem carbon balance, such as above-ground growth. It needs to be quantified explicitly because the response of GPP to e$C_a$ may be quite different to that of leaf net photosynthesis. The leaf-level response of photosynthesis to e$C_a$ is usually measured on sunlit leaves under saturating light (Ainsworth and Rogers, 2007). As a result, these leaf-level e$C_a$ responses largely reflect the responses of the photosynthesis rate when limited by maximum Rubisco activity ($V_{cmax}$). However, depending on the canopy architecture and ambient light condition, the canopy could have many shaded leaves, which would mean that the emergent rate of photosynthesis could actually be limited by RuBP regeneration ($J$). RuBP-regeneration limited photosynthesis has a smaller response to e$C_a$ than Rubisco-limited photosynthesis (Ainsworth and Rogers, 2007), resulting in a smaller response of GPP than leaf photosynthesis under saturating light.

The transition from RuBP-regeneration to Rubisco-limited photosynthesis of the canopy is determined by the ratio of the maximum capacities for RuBP-regeneration and Rubisco activity, $J_{max}$ and $V_{cmax}$ (Friend, 2001; Zaehle et al. 2014; Rogers et al., 2017). Wullschleger (1993) reported a $J_{max}$:$V_{cmax}$ ratio of 2, which has been widely adopted in models (e.g., Wang et al., 1998; Luo et al., 2001; Rogers et al., 2017). However, recent studies have suggested the $J_{max}$:$V_{cmax}$ ratio varies systematically across forest ecosystems and can range from 1 to 3 (Kattge and Knorr, 2007; Ellsworth et al., 2012; Kumarathunge et al., 2018). A lower $J_{max}$:$V_{cmax}$ ratio results in more frequent RuBP-regeneration limitation of photosynthesis, which reduces the response of GPP to e$C_a$.

It is difficult to directly measure the e$C_a$ effect on GPP. In some previous e$C_a$ experiments, GPP has been estimated by scaling up from leaf-level measurements using a canopy model. Wang et al (1998) and Luo et al (2001) both used the tree array model, MAESPA, which can simulate the radiative transfer within and between tree crowns and can be parameterised to describe the spatial locations and sizes of trees in e$C_a$ experiments. In these previous applications of MAESPA, the direct response of GPP to e$C_a$ was consistently half of that observed at the leaf level because of a large contribution of RuBP-regeneration limited photosynthesis to GPP (Wang et al., 1998; Luo et al., 2001). However, the direct effect of e$C_a$ on photosynthesis was modified by two major indirect effects. When LAI increased under e$C_a$, the additional leaf area amplified the GPP response by up to 60%. The other factor is the downregulation of photosynthesis under e$C_a$, or photosynthetic acclimation (Long et al., 2004; Ainsworth and Rogers, 2007; Rogers, et al., 2017). Under long-term exposure to e$C_a$, some plants have been observed to reduce nitrogen allocation to Rubisco, which results in a decrease of photosynthetic capacity (Gunderson and Wullschleger, 1993). The average decrease of $V_{cmax}$ among plants in FACE experiments was found to be 13% for all species and 6% for trees (Ainsworth and Long, 2005). Both Wang et al. (1998) and Luo et al. (2001) tested the impact of photosynthetic acclimation and showed a moderate reduction of canopy GPP (5-6%) due to photosynthetic acclimation (10-20%) at the studied experiments.

Following Wang et al. (1998) and Luo et al. (2001), we used MAESPA (Duursma and Medlyn, 2012) to estimate canopy GPP at EucFACE in ambient and elevated $C_a$ treatments. The model has previously been evaluated with leaf- and whole-tree- scale measurements from EucFACE (Yang et al., in review). Here, we first parameterised the model with physiological~~,~~ and structural ~~and meteorological~~ data measured during the

experiment. Then, we quantified the response of canopy GPP to e$C_a$ and partitioned this response into the direct stimulation of GPP and the indirect effects of photosynthetic acclimation and variation of LAI. The overall goal of this study was to estimate the magnitude of the response of forest canopy GPP to e$C_a$ in order to provide a baseline against which to compare changes in other components of the ecosystem carbon balance.

## 2. Methods

### 2.1 Site

The EucFACE experiment (technical details in Gimeno et al., ~~2016~~2015) is located in western Sydney, Australia (33.617S, 150.741E). It consists of six circular plots, each of which has a diameter of 25 m, enclosing 15-25 mature forest trees (referred to as 'rings' hereafter). The rings are divided into two groups: control (with ambient $C_a$ ; 390-400 µmol mol$^{-1}$ during the study period) and experimental (e$C_a$; +150 µmol mol$^{-1}$). The tree canopy is dominated by *Eucalyptus tereticornis* Sm. which are ~20 m in height and have a basal area of ~24 m$^2$ ha$^{-1}$. The site receives a mean annual precipitation of 800 mm yr$^{-1}$, a mean annual photosynthetically active radiation (PAR) of 2600 MJ m$^{-2}$ yr$^{-1}$, and a mean annual temperature of 17 ºC.

### 2.2 Model

The MAESPA model is a process-based tree-array model (Wang and Jarvis, 1990) that calculates canopy carbon and water exchange (https://bitbucket.org/remkoduursma/maespa/src/Yang_et_al_2019/). At each 30-minute timestep, the model simulates the radiative transfer, photosynthesis, and transpiration of individual trees mechanistically. Soil moisture balance can be calculated dynamically, but here we chose to improve accuracy by using soil moisture as an input to the model (Duursma and Medlyn, 2012).

The model represents the tree canopy as an array of tree crowns. The location and dimensions of each crown are specified based on-site measurements (see 2.3.2 Canopy structure, below). Calculations of carbon and water fluxes are made for each tree crown, which is divided into six layers. Here it was assumed that crowns are represented by an ellipsoidal shape and that leaf area is uniformly distributed across layers within the tree crown. The leaf angles were assumed to follow a spherical distribution to ensure consistency with the method used to estimate leaf area index (LAI) in Duursma et al. (2016). Within each layer, the model evaluates the radiation transfer and leaf gas exchange at 12 grid points such that each crown is represented by a total of 72 grid points. The radiation intercepted at each grid point is calculated for direct and diffuse components by considering shading from the upper crown and surrounding trees and solar angle (zenith and azimuth), and light source (diffuse or direct). Penetration by direct radiation to each grid point is used to estimate the sunlit and shaded leaf area at each grid point. The radiation intercepted by the fraction of sunlit and shade foliage is then used to calculate the leaf gas exchange.

The gas exchange sub-model combines the leaf photosynthesis model of Farquhar et al. (1980) with the stomatal optimisation model, following Medlyn et al. (2011). Stomatal conductance is modelled as:

$$g_s = 1.6 \cdot \left(1 + \frac{g_1}{\sqrt{D}}\right) \cdot \frac{A_{net}}{C_a} \quad (1)$$

where $g_s$ is the stomatal conductance to water vapour (mol m$^{-2}$ s$^{-1}$); $g_1$ is a parameter that represents the $g_s$ sensitivity to photosynthesis (kPa$^{0.5}$; see definition in Medlyn et al., (2011)); $A_{net}$ is the net $CO_2$ assimilation rate

(μmol $m^{-2}$ $s^{-1}$); $C_a$ is the atmospheric $CO_2$ concentration (μmol $mol^{-1}$) and $D$ is the vapour pressure deficit (kPa). The factor 1.6 converts the conductance of $CO_2$ to that of $H_2O$.

The impact of soil moisture on $g_s$ is represented through an empirical function that links soil water availability to $g_1$ following (Drake et al., 2017):

$$g_1 = g_{1.max}\left(\frac{\theta - \theta_{min}}{\theta_{max} - \theta_{min}}\right)^q \quad (2)$$

where the $g_{1.max}$ is the maximum $g_1$ value; $\theta$ is volumetric soil water content (%); $\theta_{max}$ and $\theta_{min}$ are the upper and lower limit within which $\theta$ has impact on $g_1$; $q$ describes the non-linearity of the curve. The equations to calculate $A_{net}$ are in Supplementary (Text S1, Eqns. S1 – S6).

Following Yang et al. (2019), MAESPA considers a non-stomatal limitation to biochemical parameters $J_{max}$ and $V_{cmax}$ at high $D$:

$$V_{max} = V_{max.t}(1 - c_D \cdot D) \quad (3)$$

where $V_{max.t}$ is the $J_{max}$ or $V_{cmax}$ at given leaf temperature (Text S1), and $c_D$ is a fitted parameter (Table 1). This relationship is empirical and fitted to data collected in EucFACE. Incorporating this relationship was shown to improve the predicted photosynthesis by the leaf gas exchange model (Yang et al., 2019).

Combining Eqns. 1- 3 and S1 – S6 yields the $g_s$ and $A_{net}$ of each grid point, which is then multiplied by leaf area at each grid point and summed to give whole-tree photosynthesis. Photosynthesis of individual trees is then summed to give whole-canopy photosynthesis.

### 2.3 Model Parameterisation

#### *2.3.1 Meteorological forcing*

The model is driven by *in situ* PAR, wind speed, air temperature, ~~vapour pressure deficit (*D*)~~*D*, and soil moisture measurements from 2013 to 2016 (Figures 1 and 2). Each ring has a set of PAR (LI-190, Li-cor, Lincoln, NE, U.S.), wind speed (Wincap Ultrasonic WMT700 Vaisala, Vantaa, Finland), humidity, and temperature sensors (HUMICAP ® HMP 155 Vaisala, Vantaa, Finland) at the centre of the ring above the canopy at 23.5 m. The PAR, air temperature, and relative humidity were measured every five minutes in each ring and then were gap-filled by linear interpolation and aggregated to 30 minute-mean time slices across all six rings (Figure 1). ~~Each ring has a set of PAR (LI-190, Li-cor, Lincoln, NE, U.S.), wind speed (Wincap Ultrasonic WMT700 Vaisala, Vantaa, Finland), humidity, and temperature sensors (HUMICAP ® HMP 155 Vaisala, Vantaa, Finland) at the centre of the ring above the canopy at 23.5 m.~~ *D* was calculated from temperature and humidity measurements.

Two levels of $C_a$ were used in the model according to the measured $C_a$ (LI-840, Li-cor, Lincoln, NE, U.S.). The ambient $C_a$ was gap-filled (in total <10 days during four years gaps due to power outage) and aggregated to 30 minute-mean time slices from the five-minute measurements across the three ambient rings (rings 2, 3, and 6). The e$C_a$ was processed in the same way but using data from the experimental rings (rings 1, 4, and 5).

The volumetric soil water content ($\theta$) was used as an estimate of plant water availability and was taken every 20 days using neutron measurements at 25 cm intervals (503DR Hydroprobe, Instroteck, NC, U.S.) and averaged to the top 150 cm (Figure 2). There were two probes in each ring and the average of these probes was used to

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represent the ring average for each measurement date. $\theta$ was updated on the days of measurements and thus not gap-filled.

*2.3.2 Canopy structure*

Trees in MAESPA were represented by their actual location, height, and crown size to mimic the realistic effects of shading. Tree location, crown height, crown base and stem diameter were measured in January 2013 at the start of the experiment. For each ring, a time-series of LAI was obtained based on measurements of above- and below- canopy PAR (Duursma et al. 2016). This LAI represents plant area index, which includes the woody component as well as leaves and does not account for clumping. In order to retrieve the actual LAI, we assumed a constant branch and stem cover (0.8 $m^2$ $m^{-2}$) based on the lowest LAI during November 2013 when the canopy shed almost all leaves. The LAI used in this study was thus the plant area index estimates from Duursma et al. (2016), less 0.8 $m^2$ $m^{-2}$ (Figure 2a). Since LAI is the only parameter beside soil moisture that differed by ring, canopy structure (i.e., the LAI and its distribution) was the major driver of inter-ring variability.

The total leaf area ($m^2$) of each ring was calculated as the product of LAI and ground area of each plot (491 $m^2$). This total leaf area (LA) was then assigned to each tree based on an allometric relationship between the total leaf area ($m^2$) and diameter at breast height (DBH; cm). The allometric relationship was derived from data in the BAAD database (Falster et al., 2015) for *Eucalyptus* trees grown in natural conditions with DBH <1 m to match the characteristics of EucFACE. In total, this database yielded a total of 66 observations with which to estimate the relationship between LA and DBH:

$$L_{allom} = a \cdot DBH^b \quad (4)$$

where $L_{allom}$ is the theoretical leaf area based on allometric relationship to DBH. The values obtained via fitting for $a$ and $b$ were 492.6 and 1.8 respectively, with a root mean square error of 14.4 ($m^2$) and correlation coefficient of 0.83.~~.~~ ~~This~~ Eqn. 4~~relationship~~ was used to assign the total LA of each ring to each tree in the following steps: (i) the $L_{allom}$ for each tree was calculated based on DBH; (ii) the $L_{allom}$ was summed to obtain a total LA for each ring; and (iii) the fractional contribution of each tree to the ring total LA was calculated. The total LA based on LAI was then assigned to each tree based on this fraction.

The crown radius was calculated with a linear function with DBH based on measurements made in August 2016. The data consisted of DBH and crown radius (one on North-South axis and one on East-west axis) of four trees in each ring. The crown radius measurements were averaged by tree and used to fit a linear model with DBH. The estimated slope and intercept of the relationship are 0.095 (m $cm^{-1}$) and 0.765 (m), respectively.

MAESPA also considered the shading from surrounding trees outside the rings. However, no measurements of locations or diameters were available for the trees surrounding the rings. Therefore, a total of 80 surrounding trees were arbitrarily assumed to form two uniform and circular layers around each ring. They were assigned the mean height, mean crown radius, and mean leaf area estimated from all trees in EucFACE. Except for shading, the surrounding trees have no impact on the trees within the rings. Ring 1 is shown in Figure S1 as an example of the representation of canopy structure in MAESPA.

*2.3.3 Physiology*

The physiological parameters were estimated from field gas exchange measurements as described below. The data were collected with portable photosynthesis systems (Li-6400, Li-Cor, Inc., USA). The only parameter found to differ between ambient and elevated $C_a$ rings was $V_{cmax.25}$ ($V_{cmax}$ at 25 ºC; Ellsworth et al., ~~in prep~~2017.). Hence, all other parameters (e.g., the temperature responses of photosynthesis and respiration) were estimated by combining all data across $CO_2$ treatments. Fitted parameter values are given in Table 1.

A set of temperature-controlled photosynthesis-$CO_2$ response ($A$-$C_i$) curves was measured at different leaf temperatures (20-40 ºC) under saturating light in February 2016. The dataset was used to quantify the temperature dependences of $J_{max}$ and $V_{cmax}$ by fitting a peaked Arrhenius function (Eqn. S5) to the measurements. We assumed that these temperature response functions applied throughout the period of the study.

Light- and temperature-controlled $A$-$C_i$ curves were also measured in the morning for ten field campaigns during 2013 to 2016. All $A$-$C_i$ curves were started at the growth $C_a$ of 395 µmol mol$^{-1}$ or 545 µmol mol$^{-1}$ (depending on e$C_a$ treatment) with a saturating light of 1800 µmol m$^{-2}$ s$^{-1}$ and a flow rate of 500 µmol s$^{-1}$ with temperature controlled to a constant based on the seasonal temperature. These data were used to estimate $J_{max}$ and $V_{cmax}$ at 25 ºC using the *fitaci* function in the *plantecophys* R package (Duursma, 2015), using the measured temperature responses of $J_{max}$ and $V_{cmax}$ described in the previous paragraph to correct to 25 ºC.

Repeated gas exchange measurements were made on the same leaves in the morning and afternoon under prevailing field conditions and saturating light (photon flux density = 1800 µmol m$^{-2}$ s$^{-1}$) on four occasions in 2013 ("diurnal"; Gimeno et al., ~~2016~~2015). To expand the diurnal dataset, we obtained the points from $A$-$C_i$ curves at field $C_a$ and combined the two data sets. These data were used to estimate the $g_1$ parameter in the stomatal conductance model (Eqn. 1) using the *fitBB* function in the *plantecophys* R package (Duursma, 2015). One $g_1$ value was fitted to the data from each treatment and date. The $g_1$ values were then regressed against $\theta$ measured in each treatment group to estimate the impact of soil moisture availability on leaf gas exchange, following Eqn. 2. The $g_1$ values were related to the nearest measurements of $\theta$ (within two weeks ~~without rain~~). There has been no rainfall between $g_1$ and $\theta$ measurement dates. Eqn. 2 was fitted to this data set using the non-linear least squares method (Figure 3).

The dark respiration rate of foliage, $R_{dark}$, was measured at least three hours after sunset at a range of leaf temperatures (14-60 °C) in February 2016 also with LiCor 6400. The temperature dependence of $R_{dark}$ was fitted using non-linear least squared method to all of the measured data using Eqn. S6. Light responses of photosynthesis were measured on two trees from each ring in October 2014 (Crous et al., unpublished). This data set was used to constrain the light response parameters ($\alpha_J$ and $\theta_J$) in Eqn. S4. Details of fitting the light response curves are provided in supplementary (Text S1).

**2.4 Model simulations and analysis**

MAESPA was used to simulate radiation interception and gas exchange of all six rings between 1 January 2013 and 31 December 2016 on a half-hourly basis. The model simulated half-hourly gross primary production (GPP) of each tree, which was then summed for all trees in each ring to get the total annual GPP for each ring and year.

Four different sets of simulations were used to estimate carbon uptake under ambient and e$C_a$ and to identify the key limiting factors on canopy GPP response to e$C_a$. Firstly, we carried out a simulation of leaf scale ("leaf

scenario") photosynthesis with measured meteorological data but fixed physiological data ($g_1$ = 3.3 kPa$^{0.5}$, $V_{cmax.25}$ = 91 µmol m$^{-2}$ s$^{-1}$, and $J_{max.25}$ = 159 µmol m$^{-2}$ s$^{-1}$). This simulation aimed to quantify the $CO_2$ response of Rubisco-limited and RuBP-limited photosynthesis at the leaf scale. This calculation was made using the *photosyn* function in *plantecophys* R package (Duursma, 2015). This function implements the leaf gas exchange routine used in MAESPA.

Secondly, MAESPA was run for all six rings with ambient $C_a$ and with $V_{cmax.25}$ from ambient measurements ("ambient scenario"). The results of this simulation were used to calculate the GPP of each ring under ambient conditions. The ambient GPP values were also used to evaluate the inherent variability among the rings.

Thirdly, all six rings were simulated with e$C_a$ and $V_{cmax.25}$ based on measurements from ambient rings ("elevated scenario"). The results of this simulation were compared to those from the ambient scenario to illustrate the instantaneous response of canopy GPP to e$C_a$ in each ring and year. This simulation also quantifies the variation of the GPP response to e$C_a$ across rings and years.

Lastly, we simulated the response of the three rings exposed to e$C_a$ (rings 1, 4, and 5) using the $V_{cmax.25}$ and e$C_a$ measured from these elevated rings ("field scenario"). Results from the field scenario were used for two analyses: (i) to compare GPP from the field scenario to that of the three rings from the elevated scenario (i.e., e$C_a$ and ambient $V_{cmax.25}$), which allows us to quantify the impact of photosynthetic acclimation (i.e., due to a reduction in $V_{cmax}$); (ii) to calculate the difference in GPP between the three ambient rings in ambient scenario and elevated rings in the field scenario to estimate the response of GPP to e$C_a$ in the field.

*Table 1. Summary table of parameter definitions, units, and sources used in this study.*

| Parameters | Definitions | Units | Values | Eqn. |
|---|---|---|---|---|
| $\alpha_J$ | Quantum yield of electron transport rate | µmol electron µmol$^{-1}$ photon | 0.30 | S7 |
| $a$ | Fitted slope of LA and DBH | m$^2$ m$^{-1}$ | 492.6 | 4 |
| $a_{abs}$ | Absorptance of PAR | fraction | 0.825 | S4 |
| $b$ | Fitted index of LA and DBH | - | 1.8 | 4 |
| $c_D$ | Slope of $V_{cmax}$ to $D$ | kPa$^{-1}$ | 0.14 | 3 |
| $\Delta S$ | Entropy factor | J mol$^{-1}$ K$^{-1}$ | 639.60 ($V_{cmax}$); 638.06 ($J_{max}$) | S5 |
| $E_a$ | Activation energy | J mol$^{-1}$ | 66386 ($V_{cmax}$); 32292 ($J_{max}$) | S5 |
| $g_{1.max}$ | Maximum $g_1$ value | kPa$^{0.5}$ | 5.0 | 2 |
| $H_d$ | Deactivation energy | J mol$^{-1}$ | 200000 | S5 |
| $\theta_J$ | Convexity of electron transport rate to $Q_{APAR}$ | - | 0.48 | S8 |
| $\theta_{max}$ | Upper limit ~~which~~ of soil water content above which $g_1$ is maximum ~~$\theta$ has impact on $g_1$~~ | - | 0.240 | 2 |
| ~~$\theta_{min}$~~$\theta_{min}$ | Lower limit of soil water content below which $g_1$ is zero ~~which $\theta$ has impact on $g_1$~~ | - | 0.106 | 2 |
| $J_{max.25}$ | Value of $J_{max}$ at 25°C | µmol electron m$^{-2}$ s$^{-1}$ | 159 | 3 |
| $k_T$ | Sensitivity of $R_{dark}$ to temperature | °C$^{-1}$ | 0.078 | S6 |
| $q$ | The non-linearity of the $g_1$ dependence of $\theta$ | - | 0.425 | 2 |
| $R_{day.25}$ | Light respiration rate | µmol C m$^{-2}$ s$^{-1}$ | 0.9 | S6 |
| $R_{dark.25}$ | Dark respiration rate | µmol C m$^{-2}$ s$^{-1}$ | 1.3 | S6 |
| $R_{gas}$ | Gas constant | J mol$^{-1}$ K$^{-1}$ | 8.314 | S5 |

| | | | | |
|---|---|---|---|---|
| $V_{cmax.25}$ | Value of $V_{cmax}$ at 25ºC | µmol C $m^{-2}$ $s^{-1}$ | 91 (ambient); 83 (elevated) | 3 |

## 3. Results

Figure 4 summarises the results from measurements and the different simulations conducted in this study. It demonstrates that the impact of e$C_a$ diminishes as calculations are scaled from the instantaneous leaf-level response ($A_{inst}$) to the long-term canopy response ($GPP_{field}$) and the various feedback effects are accounted for. Each row of Figure 4 is explained in detail in the following paragraphs.

### 3.1 Instantaneous $C_a$ response of photosynthesis at leaf and canopy scale

The mean instantaneous $C_a$ response of leaf-level photosynthesis ($A_{inst}$) was +33% (Figure 4a). This response ratio was calculated from ~600 light- and temperature-controlled $A$-$C_i$ curves measured in the ambient rings. From the curves, we extracted the photosynthesis at 400 and 550 $C_a$ (µmol $mol^{-1}$) and calculated the instantaneous $C_a$ effect as their ratio. This approach allows an estimation of the direct $CO_2$ response independent of the impact of photosynthetic acclimation.

By contrast, the modelled direct GPP response to e$C_a$ was considerably less, just +11%, as shown in Figure 4d ("$GPP_{inst}$"). This canopy response rate was calculated by comparing the modelled GPP of all six rings under ambient and elevated $C_a$ ("ambient" vs. "elevated" scenario). As a result, this direct canopy GPP response also excludes the impact of photosynthetic acclimation.

Our results show that the major reason for the difference between the direct leaf and canopy photosynthesis responses to e$C_a$ is the relative contributions from Rubisco- and RuBP-regeneration-limited photosynthesis (cf. Figure 4 b and c). Figure 5 shows that the response of photosynthesis to e$C_a$ is considerably higher when Rubisco activity limits photosynthesis ($A_c$) than when RuBP-regeneration limits photosynthesis ($A_J$). When averaged over the range of leaf temperatures experienced during the four years of experiment, the $A_c$ response to e$C_a$ on average (+26%; Figure 4b) is larger than that of $A_J$ (+10%; Figure 4c). Leaf gas exchange measurements were taken in saturating light (1800 µmol $m^{-2}$ $s^{-1}$) and thus, are mostly Rubisco limited. The observed response rate of $A_{inst}$ is thus close to that of $A_c$.

At the canopy scale, a large fraction of the modelled canopy photosynthesis is limited by RuBP-regeneration. In Figure 6, we show the distribution of $A_c$ and $A_J$ during the four years of simulation as calculated by MAESPA. On average, 70% of the canopy photosynthesis is limited by RuBP-regeneration under ambient conditions ("ambient scenario"). The high fraction of $A_J$ is partly a consequence of the relatively low ratio of $J_{max.25}$ to $V_{cmax.25}$ (J:V ratio) which was estimated to be 1.7 (Table 1). In Figure 7, we estimated the PAR level at which Rubisco activity becomes limiting to leaf photosynthesis. The transition point from Rubisco- to RuBP-regeneration-limited photosynthesis was calculated from the leaf gas exchange sub-model by assuming a constant $C_a$ (390 µmol $mol^{-1}$), $D$ (1.5 kPa), $g_1$ (3.3 $kPa^{0.5}$), and $V_{cmax.25}$ (90 µmol $m^{-2}$ $s^{-1}$) but varying leaf temperature. As shown, under these conditions, when temperature = 25 ºC and J:V ratio = 1.7, Rubisco activity limits photosynthesis only when incident PAR > 1800 µmol $m^{-2}$ $s^{-1}$. Using a higher J:V ratio such as the commonly-used value of 2 would decrease the saturating PAR value at which photosynthesis becomes Rubisco

limited. We ran additional simulations assuming a J:V ratio of 2 and found that, with this ratio, MAESPA estimated 48% of photosynthesis to be RuBP-regeneration limited under ambient conditions and a direct GPP response of 15% (data not shown).

The shape of the light response curve also determines the transition point from RuBP- to Rubisco-limited photosynthesis. We explored this effect by investigating the effect of varying the convexity, $\theta_J$, which is assumed to be the same as the convexity of overall photosynthesis~~.~~. At EucFACE, ~~this parameter is~~we estimated ~~to~~ this parameter ~~be~~ as 0.48 ~~based on data~~from light-response curves of photosynthesis collected on site, indicating a shallow curvature and a high light saturation point~~s~~, in contrast to the more commonly assumed 0.85, representing a steeper curvature and a lower light saturation point. Using a value of 0.85 for $\theta_J$ resulted in a much lower PAR required for photosynthesis to became Rubisco limited (dashed curves in Figure 7). With a $\theta_J$ of 0.85 and a J:V ratio of 1.7, MAESPA estimated 40% of photosynthesis to be RuBP-regeneration limited under ambient conditions and a direct GPP response of 16% (data not shown). With a $\theta_J$ of 0.85 and a J:V ratio of 2, MAESPA estimated just 34% of photosynthesis to be RuBP-regeneration limited under ambient conditions and a direct GPP response of 18% (Figure S2). The simulated $CO_2$ response of canopy carbon uptake thus depends heavily on the parameterisation of light response and J:V ratio.

### 3.2 Acclimation of photosynthesis

The above calculations are made considering only the instantaneous response of photosynthesis to e$C_a$. However, photosynthetic acclimation was observed at leaf scale (Ellsworth et al., in prep), and will also reduce the response of GPP to e$C_a$ at the canopy scale. At the leaf-level, photosynthesis measured in the elevated rings after five years of treatment ($A_{long}$) was 19% higher than that measured in ambient rings (Figure 4e; Ellsworth et al. 2017). $A_{long}$ thus accounts for the photosynthetic acclimation in the elevated rings after four years of exposure to e$C_a$. $A_{long}$ is considerably smaller than $A_{inst}$ (19% vs. 33%; Figure 4 a and e), indicating a large effect of photosynthetic acclimation on the e$C_a$ response of light-saturated photosynthesis.

Accounting for the impact of photosynthetic acclimation in MAESPA, by using the $V_{cmax}$ from elevated rings ("field" vs. "ambient" scenarios) reduced the response of GPP to $C_a$ from 11% to 10% ($GPP_{long}$; Figure 4f). As such, the photosynthetic acclimation had a relatively modest impact on the modelled annual GPP in the model. The small impact of photosynthetic acclimation on canopy photosynthesis relative to the effect on leaf photosynthesis can be explained by the fact that the leaf photosynthesis data are measured under saturating light and thus are typically Rubisco-limited, so a reduction in $V_{cmax}$ had a large effect. In contrast, at the canopy scale, much of the photosynthesis was limited by RuBP-regeneration and was largely unaffected by a reduction in $V_{cmax}$.

### 3.3 Influence of LAI

The realised GPP response to e$C_a$ also depends on the canopy structure, specifically the LAI. In this experiment, there was no significant change in LAI with e$C_a$ (-4% ± 5%; Figure 4g; see also Duursma et al. 2016). The effect of e$C_a$ on LAI was calculated as the average effect between elevated and ambient annual mean LAI. However, there was inherent variability in LAI across the rings (Figure 2a), which does not fundamentally

change the effect of e$C_a$ but requires a detailed analysis of the potential effects of natural variability on the response to e$C_a$.

The small pre-treatment difference in LAI across rings gives rise to a range of estimates for the GPP response to e$C_a$ in the field (6% ±8%; Figure 4h). This result is explored further in Figure 8, which combines the results from "ambient", "elevated", and "field" scenarios. The average GPP across all six rings under ambient $C_a$ was 1574 g C $m^{-2}$ $yr^{-1}$ over the four-year simulation ("ambient scenario"; Figure 8). However, there was significant variability in ambient GPP across rings, related in part to the inherent variability in LAI across rings. We characterised the pre-existing differences in LAI by the initial LAI ($LAI_i$), measured on 26 October 2012. These initial values are low, because they are measured immediately before the seasonal leaf flush, but characterise the difference in LAI across rings over the full experimental period. Rings 1 and 4 (both experimental rings) have the lowest $LAI_i$ (<0.3 $m^2$ $m^{-2}$) and thus the lowest average GPP under ambient conditions (1206 g C $m^{-2}$ $yr^{-1}$). Ring 5 (the other experimental ring) has the second highest $LAI_i$ (~0.4 $m^2$ $m^{-2}$) and also the highest GPP under ambient conditions (2359 g C $m^{-2}$ $yr^{-1}$). The variability among rings in ambient GPP (SD = 15%) is thus larger than the modelled direct effect of $C_a$ on GPP, which is similar in all rings (+11%).

Owing to the variability among rings represented by $LAI_i$, the estimated mean GPP response to e$C_a$ across the experimental rings has a sizeable confidence interval (±8%, Figure 4h). The actual e$C_a$ response was estimated as an average effect between the ambient and elevated GPP values considering the impacts of photosynthetic acclimation and inter-ring variability. The average GPP of experimental rings under field conditions (e$C_a$) was estimated to be 1698 g C $m^{-2}$ $yr^{-1}$ while the average GPP of control rings under field conditions (ambient $C_a$) was 1599 g C $m^{-2}$ $yr^{-1}$, an increase of 6% as shown in the Figure 4h. The variation of annual average GPP of the control and experimental groups (blue and red squares in Figure 8) are thus represented by the CI in Figure 4h.

## 4. Discussion

We have showed how a large response of leaf-level photosynthesis to e$C_a$ diminishes when integrated to the canopy-scale, according to the synthesis of four years of leaf measurements at EucFACE with the stand-scale model, MAESPA. We estimated that the canopy GPP of a mature *Eucalyptus* woodland under ambient $C_a$ conditions varied from 1084–2129 g C $m^{-2}$ $yr^{-1}$ by ring and year with a mean of 1574 g C $m^{-2}$ $yr^{-1}$. The model, constrained by site measurements, predicted that once scaled to the canopy, the response of GPP to e$C_a$ only increased by 6% (95% CI of ±8%) compared to the 19% (95% CI of ±5%) observed in leaf-scale measurements. We were able to quantify the response of GPP to e$C_a$ and attribute the reduction in the response to various factors including: (i) Rubisco versus RuBP-regeneration limitations to photosynthesis; (ii) photosynthetic acclimation; (iii) inter-ring variability in LAI. Together these findings provide valuable insights into the relative importance of each factor and help close a key knowledge gap in our understanding of how mature forests respond to e$C_a$.

### 4.1 Performance of MAESPA under ambient conditions

The ambient GPP of EucFACE estimated by MAESPA was comparable to that measured with eddy covariance in similar evergreen Eucalypt forests in Southeast Australia. In a nearby eddy covariance site (<1 km), , Renchon et al. (2018) estimated the ecosystem GPP from eddy convariance to be 1561 g C $m^{-2}$ $yr^{-1}$ during 2013 to 2016 which is within the range estimated for the ambient rings in this study, though this latter site and the EucFACE are not the same in terms of canopy structure and LAI. Furthermore, our version of MAESPA was evaluated against leaf photosynthesis and whole-tree sap flow measurements in EucFACE ($R^2$ of 0.77 and 0.8, respectively; Yang et al., ~~in review~~2019). These comparisons indicate MAESPA is a useful tool to explore the canopy carbon uptake and the predicted GPP could provide a baseline to future studies.

### 4.2 RuBP-regeneration limited photosynthesis

Our results show that the canopy GPP at EucFACE was predominantly limited by RuBP regeneration. The reason for the frequent RuBP-regeneration limitation is that the measured J:V ratio was relatively small in EucFACE (1.7), and stomata tend to close at midday when light levels are higher and Rubisco-limitation is expected (Gimeno et al., ~~2016~~2015). A lower J:V ratio increases the PAR threshold required for the photosynthesis model to switch between the RuBP-regeneration limitation and the Rubisco limitation (from <1000 to <1800 μmol $m^{-2}$ $s^{-1}$; Figure 7). Previous studies have highlighted the need to consider J:V ratio for a correct prediction of $CO_2$ response (Long et al, 2004; Zaehle et al., 2014; Rogers et al., 2017). However, as shown by Zaehle et al. (2014), Medlyn et al. (2015), and Rogers et al. (2017), current models differ in their predictions of the transition from RuBP-regeneration- to Rubisco-limited photosynthesis, suggesting the uncertainty of predicted $CO_2$ response of GPP could be reduced by using a realistic J:V ratio.

Previous modelling studies applying MAESPA to e$C_a$ experiments both assumed higher J:V ratio (2) and estimated higher GPP response to e$C_a$ presumably due to less frequent RuBP-regeneration limitation (Wang et al., 1998; Luo et al., 2001). A J:V ratio of 2 was suggested by Wullschleger (1993) and has been used in many modelling studies (e.g., the seven terrestrial biosphere models assessed by Rogers et al. (2017) all assumed a J:V ratio of 1.9-2). Global terrestrial biosphere models such as JULES and others frequently estimate $J_{max}$ on the basis of this ratio (e.g., Clark et al. 2011). However, the relatively low J:V ratio observed at EucFACE is not unique. ~~In~~ At the Duke Forest FACE site in the US, Ellsworth et al. (2012) reported a J:V ratio of ~1.7 which is the same as that estimated for EucFACE. Kattge and Knorr (2007) analysed $V_{cmax}$ and $J_{max}$ values from 36 species across the world and found a low J:V ratio (<1.8) in herbaceous, coniferous, and broadleaved species. Most recently, Kumarathunge et al. (2018) studied the variation in J:V ratio in datasets obtained from around the globe and found ~~a consistent relationship with~~that it declined with increasing growing season temperature. The ratio varied from 2.5 in tundra environments to < 1.5 in tropical environments. The value of 1.~~7~~ observed at EucFACE falls within this prediction for the prevailing growth temperature at this site. The inclusion of this relationship between ~~this relationship of~~ J:V ratio and temperature will thus be important for capturing the GPP response to e$C_a$ globally.

We also found that the ~~curvature~~ convexity of the light response of photosynthesis affected the predicted GPP response to e$C_a$ (Figure 7). The parameter value we fitted to data measured *in situ* ($\theta_J$ = 0.48) is lower than the value commonly assumed in the models (e.g., 0.7 in Bonan et al., 2011~~typically around 0.85, e.g., 0.9 in Medlyn et al., 2002; 0.7 in Bonan et al., 2011; 0.85 in Harverd et al., 2018~~). Note that some model studies

assume that $\theta_J$ to be lower than the convexity of overall photosynthesis (typically over 0.8; e.g., 0.9 in Medlyn et al., 2002; 0.85 in Haverd et al., 2018). Here we assumed that the convexity of electron transport rate and overall photosynthesis are the same (see Supplementary Text S1 for details). Nonetheless, our relatively low $\theta_J$ value (<0.7) is not unique, as it is also supported by a number of studies on different species around the world (Ögren, 1993; Valladares et al., 1997; Lewis et al., 2000; Hjelm and Ögren, 2004). The inclusion of higher $\theta_J$ value would predict a much higher direct GPP response to e$C_a$ (e.g., 16% versus 11% in this study), because higher $\theta_J$ results in a large proportion of GPP being Rubisco-limited. This finding calls for careful examination of the light-response of photosynthesis, which has a large effect on the predicted e$C_a$ response

**4.2 Photosynthetic acclimation**

Some degree of photosynthetic acclimation (i.e., a long-term reduction of $V_{cmax}$ under e$C_a$) has been widely reported in FACE studies and has been attributed to a reduction of leaf nitrogen concentration (Saxe et al., 1998; Ainsworth and Long, 2005). The response of GPP to $eC_a$ would be linearly related to $V_{cmax}$ if photosynthesis were mostly limited by Rubisco activity. Photosynthetic acclimation was responsible for the reduced response of leaf-scale light-saturated photosynthesis from 33% ($A_{inst}$) to 19% ($A_{long}$). However, this reduction in $V_{cmax}$ translated into only a ~2% reduction in GPP modelled by MAESPA. Wang et al. (1998) also showed that photosynthetic acclimation (-21% in $V_{cmax}$) reduced modelled canopy GPP by only 6% due to RuBP-regeneration being the primary limitation of canopy photosynthesis. These findings thus suggest that photosynthetic acclimation may only have a small effect in the GPP response to e$C_a$ when canopy photosynthesis is mostly RuBP-regeneration limited. This response is thus consistent with the hypothesis that the reduction in $V_{cmax}$ represents a re-allocation of nitrogen to optimise nitrogen use efficiency under e$C_a$ (Chen et al., 1993; Medlyn et al., 1996).

**4.3 Constraining the carbon balance response to e$C_a$**

At EucFACE, after four years of e$C_a$ treatment, there was no evidence of increased above-ground tree growth (Ellsworth et al., 2017). Nor have the trees at EucFACE shown any significant change in LAI (Duursma et al., 2016). The relatively small response of GPP and the effect of ring-to-ring variation provides important context for these statistically non-significant responses of tree growth at the stand scale at EucFACE. Firstly, the effect size calculated for GPP of +11% (+ 169 g C $m^{-2}$ $yr^{-1}$) constrains the likely effect size for plant growth and other components of the ecosystem carbon balance and is a more useful baseline for comparison than the response of light-saturated leaf photosynthesis (+19% = 299 g C).

Secondly, the inherent ring-to-ring variation in this natural forest stand is ~~even higher~~larger than the GPP response, which highlights the importance of considering both the effect size and ~~uncertainty~~ variability in the observations than to focus on statistical significance. It is important to note that the EucFACE site could be considered relatively homogeneous for a mature woodland. The site is flat, trees appear similar-aged, and almost all the overstory belongs to a single species. In addition, plots were carefully sited to minimise variation in basal area. However, there are small-scale variations in soil type, depth, and nutrient availability that cause variation in LAI. This scale of variation is likely to present in other natural forests, and indeed, other studies on mature trees also note that background variability can contribute to the lack of statistically significant findings (Fatichi and Leuzinger, 2013; Sigurdsson et al. 2013). We highlight the need to focus on effect size and its uncertainty,

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rather than the dichotomous significant/non-significant approach when evaluating experimental results from native forests.

### 4.4 Implications for terrestrial biosphere models

Seven Terrestrial Biosphere Models (TBMs) were used to predict GPP and LAI responses to e$C_a$ in advance of the EucFACE experiment (Medlyn et al. 2016). The predicted e$C_a$ responses of GPP ranged from +2 to +24% across the seven models, while the predicted responses of LAI ranged from +1 to +20%. With our results, it is possible to falsify some of the assumptions made in these model simulations and identify directions for model improvement. The model with the lowest GPP response (CLM4-P) assumed very strong down-regulation of photosynthesis owing to phosphorus limitation. However, this down-regulation was not observed here. The models with the highest GPP responses (GDAY, O-CN, SDGVM) had a J:V ratio of 2 which is higher than that observed at EucFACE, and also had a positive feedback to GPP via increased LAI (+5-15%), which did not occur (Duursma et al., 2016). The model rendering most similar prediction for the GPP response to e$C_a$ to the output of MAESPA incorporating empirical observations was the CABLE model. This latter model predicted an e$C_a$ response of GPP of ~12% with a large proportion of RuBP-regeneration limited photosynthesis, both of which are similar to the findings in this study. Future TBMs may benefit from incorporating a more realistic representation of the relative contribution of RuBP-regeneration- to Rubisco- limited photosynthesis to GPP. For instance, adding the temperature dependency of J:V ratio could help capture the variation of J:V ratio globally (e.g., Kumarathunge et al., 2018).

Our study provides a number of process-based insights that can be used to improve model performance both qualitatively and quantitatively. Our modelling exercise is also a major contribution to the understanding of the EucFACE experiment by quantifying the amount of extra carbon input into the system by canopy-level photosynthesis and thus providing a reference for assessing the impacts of e$C_a$ on growth and soil respiration. Finally, our study highlights that the e$C_a$ effect on canopy-scale GPP may be considerably lower than the effect on photosynthesis of the light-saturated leaves, due to contrasting relative limitations to photosynthesis operating and different scales. In future work, our GPP estimates will be used as an input to calculate the overall effect of e$C_a$ on the carbon balance at the whole EucFACE site.


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### Author contribution statement

JY, BM, MDK, and RD conceived and designed the analysis. KC, DE, and TG designed sampling of leaf physiological data, while DE and RD designed sampling of canopy structure data. KC, DE, TG, AWK, RD and JY collected data. RD and DK provided analysis tools. JY and BM performed the analysis. JY, BM, MDK, and MJ wrote the paper. All authors edited and approved the manuscript.

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**Figures and Captions**

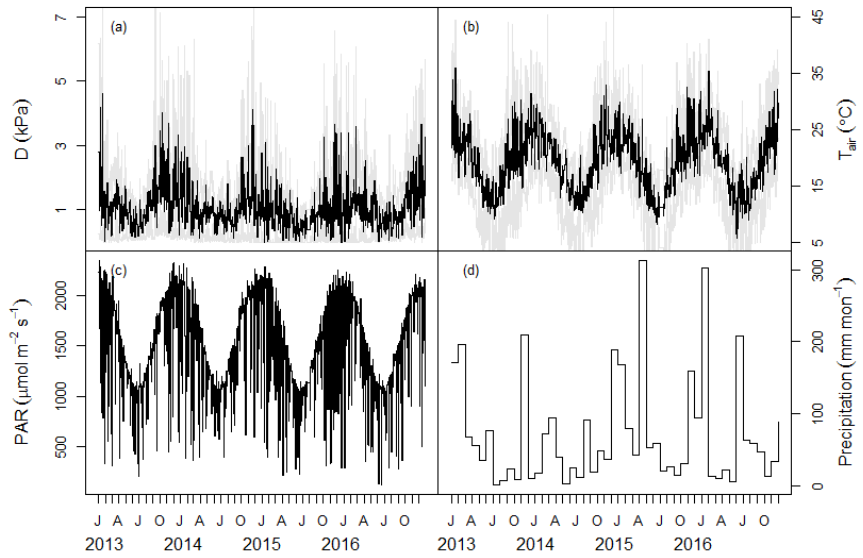
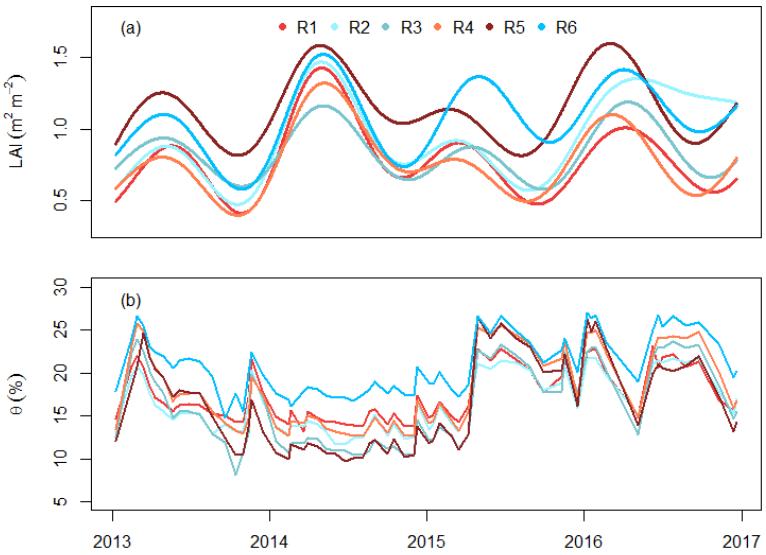



*Figure 1. Meteorological data measured at the site during the period 2013-2016. Panels show (a) daily mean vapour pressure deficit (D) with shaded area marking the maximum and minimum of the day, (b) daily mean air temperature ($T_{air}$) with shaded area marking the maximum and minimum of the day, (c) daily maximum photosynthetically active radiation (PAR), and (d) monthly total precipitation. Note that precipitation has no direct impact in the model but modifies stomatal conductance via the change in soil moisture.*


(a)
R1
R2
R3
R4
R5
R6
LAI (m² m⁻²)
0.5
1.0
1.5
(b)
θ (%)
5
10
15
20
25
30
2013
2014
2015
2016
2017

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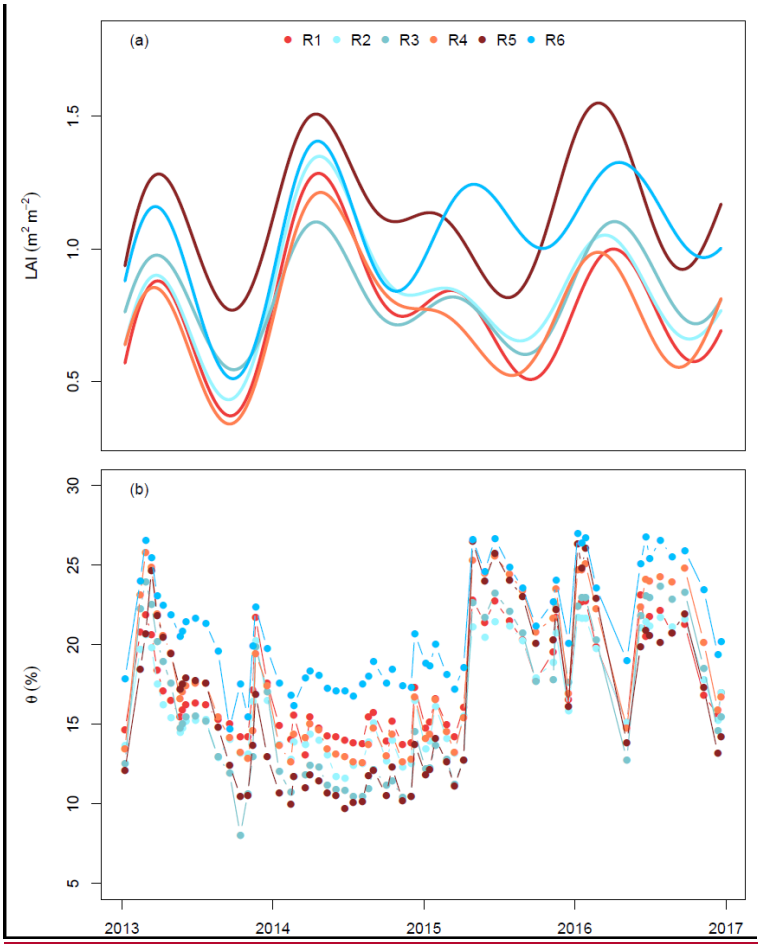



*Figure 2. (a) Leaf area index (LAI) and (b) soil volumetric water content (θ) used to drive the model. LAI was ~~measured~~ estimated in each ring ~~using the measured absorbed~~from measurements of understorey PAR and smoothed using a generalized additive model following Duursma et al. (2016). θ was measured using neutron probes ~~at~~ in the top 150 cm biweekly ~~and gap-filled using a linear interpolation between two nearest available data~~ (Gimeno et al. 2018). Each line colour indicates a different plot. Red colours show elevated $CO_2$ plots (treatment), while blue colours show ambient $CO_2$ plots (control). The x-axis ticks mark the start of each year.*

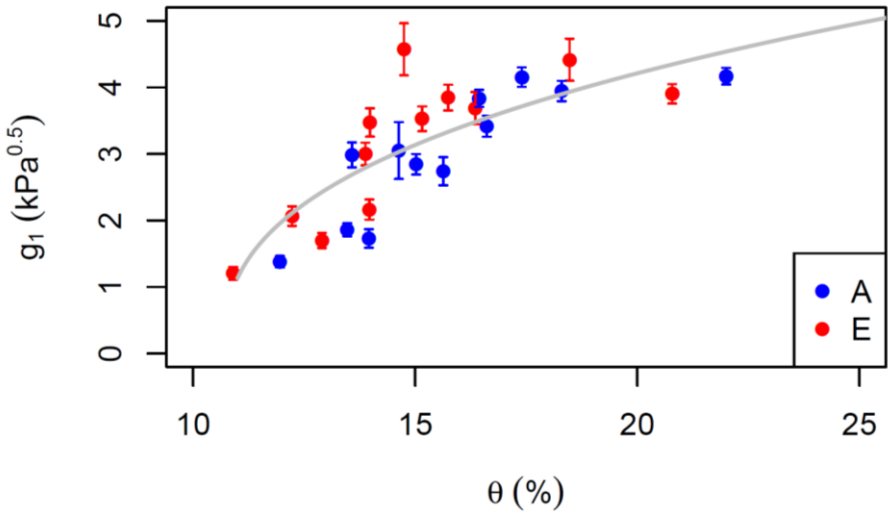
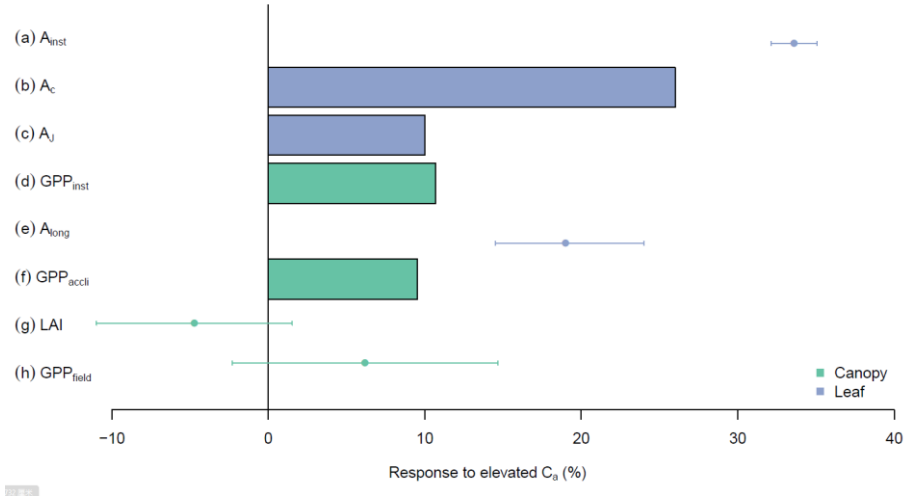



*Figure 3. The impact of soil moisture content (θ) ~~at~~ in the top 150 cm on stomatal regulation. $g_1$ parameter values are fitted to measurements of leaf gas exchange grouped by month and treatment. Red dots are fitted to data from elevated rings while blue are ambient rings. ~~The~~ Error bars ~~mark~~ indicate the standard error~~s~~ of the fitted values. The grey line shows the fit of Eqn. 2 to the data.*



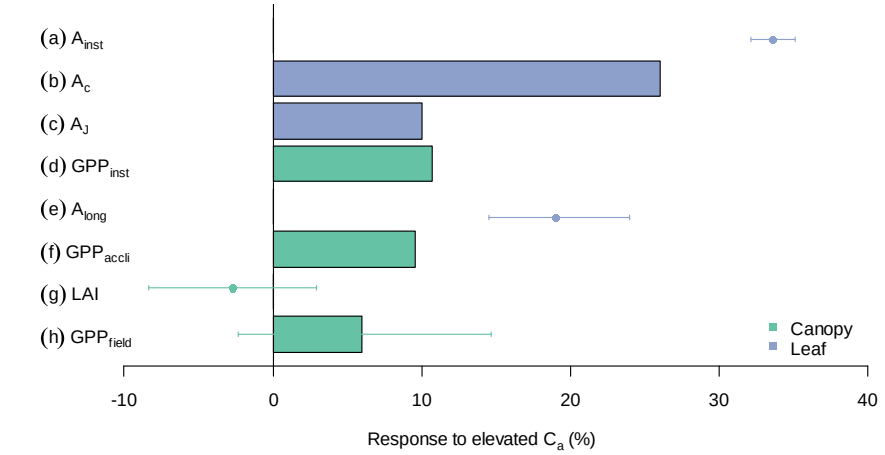




*Figure 4. The response of photosynthesis to $eC_a$ on different scales and limited by different factors. In summary, from top to bottom, the figure demonstrates how a large increase in leaf photosynthesis can diminish into a non-statistically significant change in canopy GPP under $eC_a$. Entries from top to bottom are as follows. (a) $A_{inst}$, the instantaneous response of leaf photosynthesis to $eC_a$ obtained from A-$C_i$ measurements in ambient rings (error bars indicate 95% CI). (b) $A_c$, the modelled response of Rubisco-limited leaf photosynthesis, assuming no down-regulation, averaged over the range of diurnal air temperatures experienced during the experimental period. (c) $A_J$, the modelled response of RuBP-regeneration limited leaf photosynthesis. (d) $GPP_{inst}$, the direct effect of $eC_a$ on canopy GPP, modelled with MAESPA, assuming no downregulation of photosynthesis and averaged across all six rings. (e) $A_{long}$, the long-term response of leaf photosynthesis to $eC_a$ obtained from leaf photosynthesis measured at treatment $CO_2$ concentrations (see Ellsworth et al. 2017). This value is different from $A_{inst}$ because*

*it incorporates photosynthetic acclimation. (f) $GPP_{long}$, the effect of $eC_a$ on canopy GPP once the measured down-regulation of $V_{cmax}$ is taken into account. (g) LAI, the measured difference in average LAI between $eC_a$ and ambient $C_a$ rings over the experiment period (data from Duursma et al. 2016). (h) $GPP_{field}$, the GPP response modelled with MAESPA comparing the three elevated rings with the three ambient rings. The bars represent model outputs while points represent observations. See text for further explanation.*

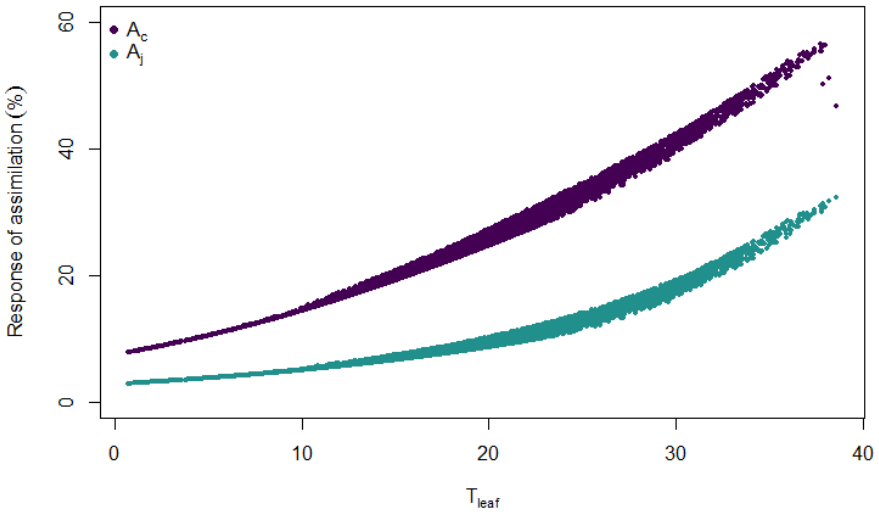



*Figure 5. The modelled $C_a$ response of Rubisco-limited leaf photosynthesis ($A_c$) and RuBP-regeneration-limited leaf photosynthesis ($A_J$) ~~against~~ to leaf temperature ($T_{leaf}$). The responses are calculated for temperatures during the period 2013-2016. Parameters are as given in Table 1, except that $V_{cmax.25}$ and $g_1$ were assumed to be constant for clarity ($g_1$ = 3.3 $kPa^{0.5}$ and $V_{cmax.25}$ = 90 $\mu mol\ m^{-2}\ s^{-1}$).*

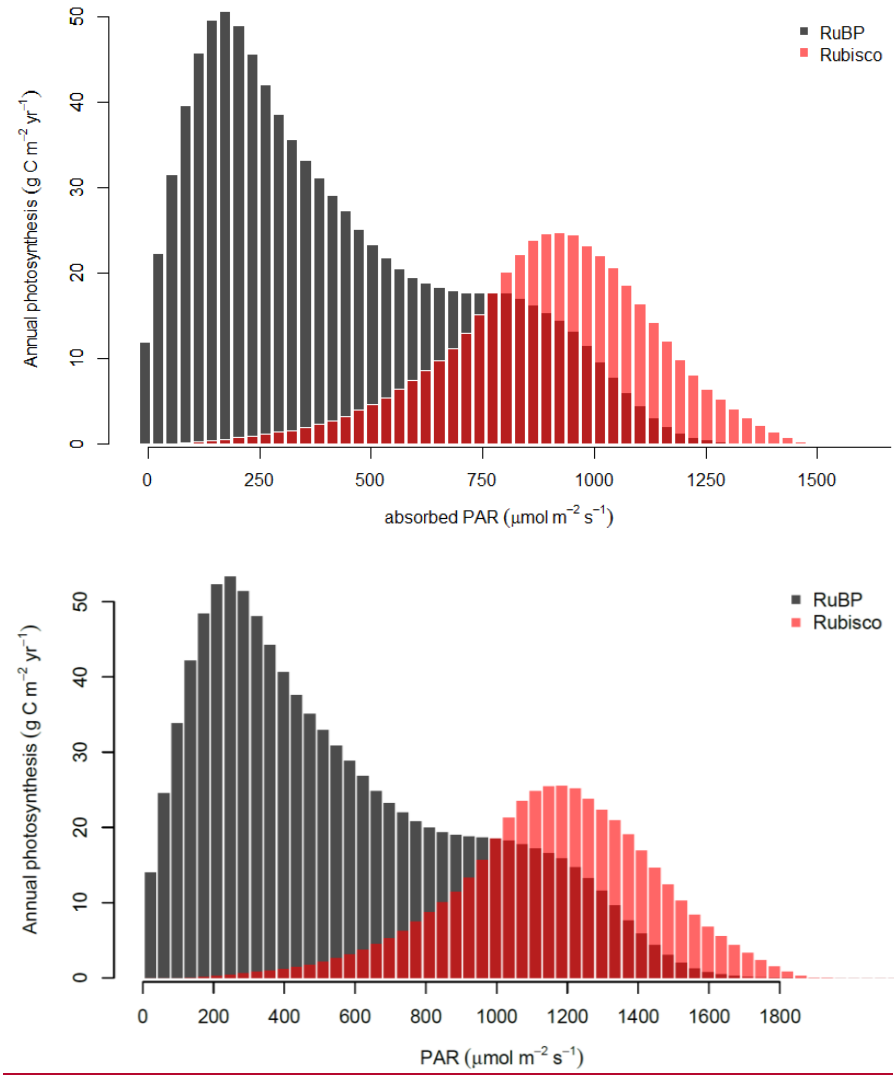
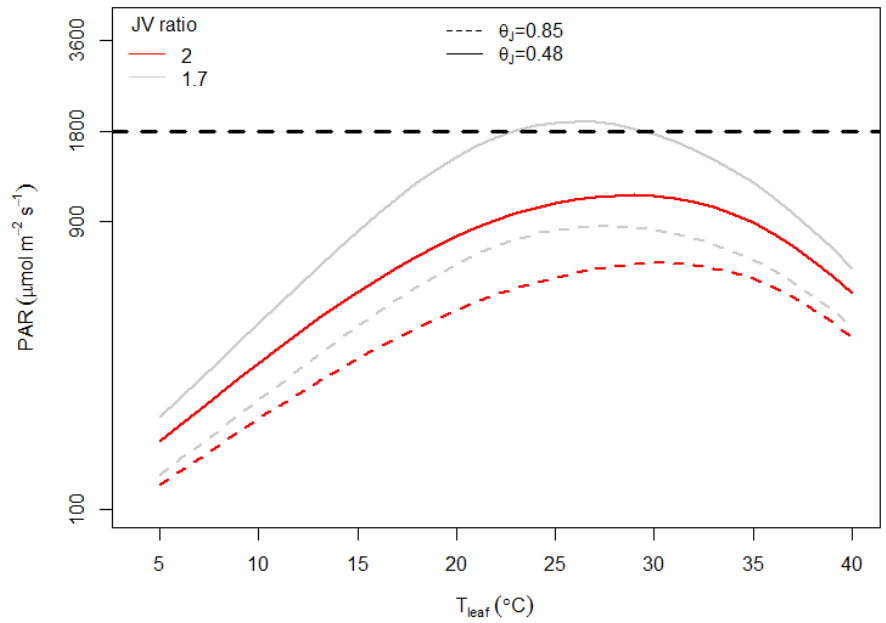



*Figure 6. Distribution of average annual photosynthesis limited by Rubisco activity and RuBP-regeneration in bins of ~~absorbed~~ PAR (~~25~~ 30 µmol m$^{-2}$ s$^{-1}$)., as calculated by MAESPA across all rings during 2013-2016. The histogram was constructed by calculating the photosynthesis (either limited by Rubisco or RuBP) falling into each bin for every half-hour in the "ambient scenario". These values were then summed to each year and ring and averaged over six rings and four years.*



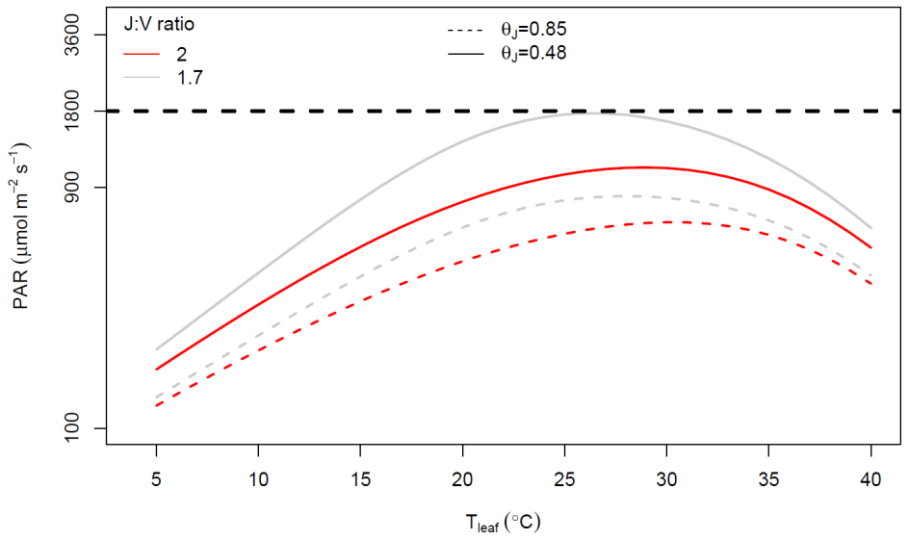




*Figure 7. Estimated PAR value at which limitation to photosynthesis shifts from RuBP regeneration to Rubisco at different leaf temperatures and J:V ratios. Rubisco limitation occurs at PAR values above the curves; RuBP regeneration limitation occurs below the curves. The curves were calculated using the* Photosyn *function in the* plantecophys *R package (Duursma, 2015). The parameters other than PAR and* $T_{leaf}$ *were assumed to be constant:* $C_a$ *= 390 µmol mol*$^{-1}$*; D =1.5 kPa;* $g_1$ *= 3.3 kPa*$^{0.5}$*;* $V_{cmax.25}$ *= 90 µmol m*$^{-2}$ *s*$^{-1}$*. The temperature and*

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*light dependences of photosynthesis were assumed to be the same as in MAESPA. The grey line was predicted by assuming $J_{max.25}$ = 153 µmol $m^{-2}$ $s^{-1}$ (i.e., J:V ratio= 1.7). This J:V ratio was observed consistently in EucFACE across campaigns and rings. The red line was predicted by assuming $J_{max.25}$ = 180 µmol $m^{-2}$ $s^{-1}$ (i.e., J:V ratio= 2). This J:V ratio was commonly reported and used in other studies. The horizontal dashed line shows the PAR = 1800 µmol $m^{-2}$ $s^{-1}$ at which leaf-level measurements of EucFACE were made. Note the log scale of the y axis. The dashed curves~~d~~ are based on quantum yield of electron transport ($\alpha_J$; mol $mol^{-1}$) and c(~~C~~onvexity of light response of RuBP; $\theta_J$ ; unitless)values from CABLE model (Haverd et al., 2018). ~~The PAR value could be converted to absorbed PAR in Figure 6 with a fraction of 0.8 at our site.~~*

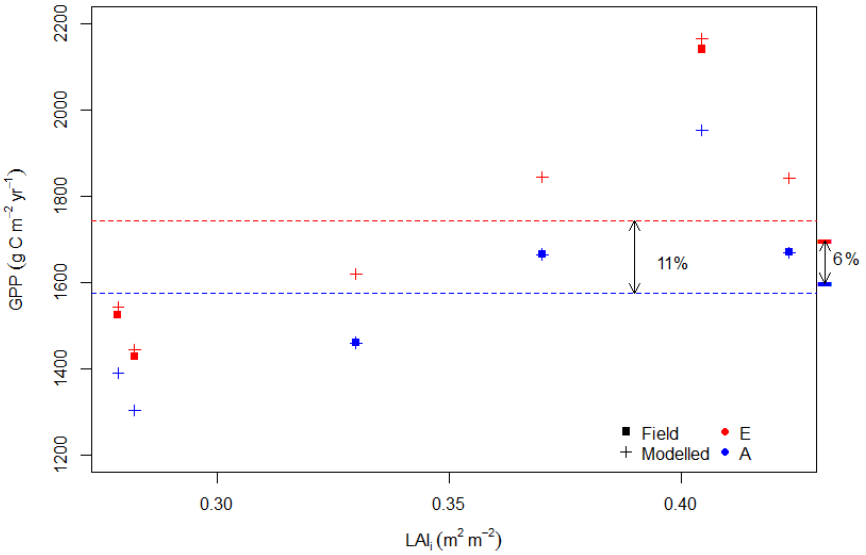


*Figure 8. The four-year average GPP of all six rings under ambient and $eC_a$ plotted against initial leaf area index ($LAI_i$). $LAI_i$ is the LAI measurement taken on the 26 October 2012 and is a proxy ~~of~~ for the inherent variation among the rings. For all six rings, estimated GPP is shown for ambient $C_a$ (blue) and $eC_a$ (red). Crosses indicate GPP from simulations by varying $C_a$ and squares indicate GPP as under field conditions. The flat bars on the right hand-side of the plot indicate the average ambient $C_a$ GPP for ambient rings only (the average of blue squares) and average $eC_a$ GPP for elevated rings only (the average of red squares). Dashed lines indicate average ambient $C_a$ (the average of blue crosses) and $eC_a$ GPP across all six rings (the average of red crosses). The flat bars thus mark the modelled response without inter-ring variability while the dashed lines mark the modelled realized response, including inter-ring variability.*

**Supplementary**

**TEXT S1. Additional equations of photosynthesis and respiration**

$A_{net}$ was modelled as:

$$A_{net} = min(A_c, A_J) - R_{day} \quad \text{(S1)}$$

where $A_c$ is the gross photosynthetic rate limited by carboxylation rate, while $A_J$ is the photosynthetic rate limited by electron transport rate; $R_{day}$ is the light respiration rate in absence of photorespiration (μmol $m^{-2}$ $s^{-1}$).

$A_c$ is calculated as a function of maximum carboxylation capacity ($V_{cmax}$; μmol $m^{-2}$ $s^{-1}$) and intercellular $CO_2$ concentration ($C_i$):

$$A_c = V_{cmax} \frac{C_i - \Gamma^*}{K_c(1+\frac{O_i}{K_0})+C_i} \quad \text{(S2)}$$

where $K_c$ and $K_o$ are the Michaelis–Menten coefficients of Rubisco activity for $CO_2$ and $O_2$, respectively (μmol $mol^{-1}$ and mmol $mol^{-1}$, respectively), and $\Gamma^*$ is the $CO_2$ compensation point in the absence of mitochondrial respiration (μmol $mol^{-1}$); $O_i$ is intercellular $O_2$ concentration (mmol $mol^{-1}$). The $K_c$, $K_o$, and $\Gamma^*$ are temperature dependent following Bernacchi et al. (2001).

$A_J$ is calculated according to:

$$A_J = \frac{J}{4}\frac{C_i - \Gamma^*}{C_i + 2\Gamma^*} \quad \text{(S3)}$$

where $J$ is the electron transport rate calculated by solving:

$$\theta_J \cdot J^2 - \left(a_{abs} \cdot \alpha_J \cdot Q_L + J_{max}\right) \cdot J + a_{abs} \cdot \alpha_J \cdot Q_L \cdot J_{max} = 0 \quad \text{(S4)}$$

where $\theta_J$ describes the curvature electron transport rate (unitless); $\alpha_J$ is the quantum yield (μmol $μmol^{-1}$); $Q_L$ is the PAR incident on the leaf; $a_{abs}$ is the absorptance of PAR (1 minus leaf reflectance and transmittance; fraction); $J_{max}$ is the maximum electron transport rate at the given temperature (μmol $m^{-2}$ $s^{-1}$). Both $J_{max}$ and $V_{cmax}$ depend on leaf temperature and are modelled using a peaked Arrhenius function:

$$k_T = k_{25} \cdot \exp\left(E_a \frac{T_k - 298.15}{298.15 \cdot R_{gas} \cdot T_k}\right) \cdot \left(1 + \frac{\exp(298.15 \cdot \Delta S - H_d)}{298.15 \cdot R_{gas}}\right) / \left(1 + \frac{\exp(T_k \cdot \Delta S - H_d)}{T_k \cdot R_{gas}}\right) \quad \text{(S5)}$$

where $k_t$ is the value of $J_{max}$ or $V_{cmax}$ at a given temperature (μmol $m^{-2}$ $s^{-1}$); $k_{25}$ is the value of $J_{max}$ or $V_{cmax}$ at 25 ºC; μmol $m^{-2}$ $s^{-1}$); $T_k$ is the leaf temperature in Kelvin; $E_a$ is the activation energy which describes the rate of increase of $k_t$ to temperature (J $mol^{-1}$); $H_d$ is the deactivation energy which describe the rate of decrease of $k_t$ to temperature (J $mol^{-1}$); $\Delta S$ is known as the entropy factor (J $mol^{-1}$ $K^{-1}$); $R_{gas}$ is the gas constant (J $mol^{-1}$ $K^{-1}$).

The model also assumes $R_{day}$ to be a fixed fraction (0.7) of $R_{dark}$ (dark respiration rate; μmol $m^{-2}$ $s^{-1}$), and uses an Arrhenius temperature response function:

$$R_{dark} = R_{dark.25} \cdot \exp\left(kT \cdot \left(T_{leaf} - 25\right)\right) \quad \text{(S6)}$$

where $k_T$ is the sensitivity of $R_{dark}$ to temperature ($ºC^{-1}$); and $T_{leaf}$ is the leaf temperature (ºC). MAESPA calculates the leaf temperature that closes the energy balance iteratively (Medlyn et al., 2007).

The light response parameters $\alpha_J$ and $\theta_J$ of $J$ were fitted to light response curves measured *in situ*. We assumed that $\alpha_J$ is related to quantum yield of photosynthesis ($\alpha_A$):

$$\alpha_J = 4 \cdot \alpha \cdot \frac{C_i + 2 \cdot \Gamma^*}{C_i - \Gamma^*} \quad \text{(S7)}$$

A linear model was fitted to the measured photosynthesis fluxes and absorbed PAR from the initial part of the light response curves (< 100 µmol $m^{-2}$ $s^{-1}$) and the fitted slope was assumed to be $\alpha_A \alpha$. This slope was converted to $\alpha_J$ using Eqn. S7. The curvature of $J$ ($\theta_J$) was here assumed to be the same as that for photosynthesis and thus ~~could be~~was estimated by fitting the following quadratic relationship:

$$A_{net} = \frac{a_{abs} \cdot \alpha_A \alpha \cdot Q_L + A_{max} - \sqrt{(a_{abs} \cdot \alpha_A \alpha \cdot Q_L + A_{max})^2 - 4 \cdot a_{abs} \cdot \alpha_A \alpha \cdot Q_L \cdot A_{max} \cdot \theta_J}}{2 \cdot \theta_J} + R_{day} \quad \text{(S8)}$$

where $A_{max}$ is the maximum of $A$, $Q_L$ is the incident PAR and $a_{abs}$ is the absorptance, which was calculated to be 0.825, by subtracting the fractions of reflectance (0.082) and transmittance (0.093). Eqn. S8 was fitted to the full light response curves using non-linear least squared method to obtain the values of $A_{max}$ and $\theta_J$, assuming $\alpha_A \alpha$ from above. Since the fitting ~~is~~ was not significantly different in the ambient and elevated data, this study used one $\theta_J$ value fitted to all the data. The assumptions of the quantum yield and convexity being the same between J and overall photosynthesis are further explored by comparing the photosynthesis predicted by the fitted $\alpha_A$, $A_{max}$, and $\theta_J$ to the measured light response curve. There's good agreement with a root mean square error of 2.97 µmol $m^{-2}$ $s^{-1}$ and a coefficient of correlation of 0.9, suggesting the assumptions are appropriate in our site.

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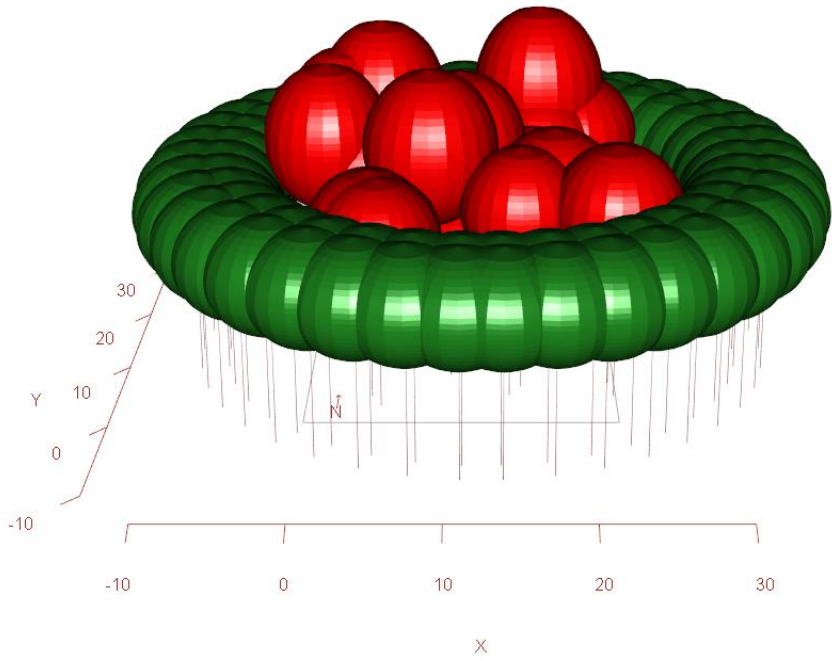


*Figure S1. Example of tree stand as represented in MAESPA. The figure shows the trees in ring 1 (red) and the surrounding trees outside the ring (green). Other rings look similar with realistic tree locations and sizes.*

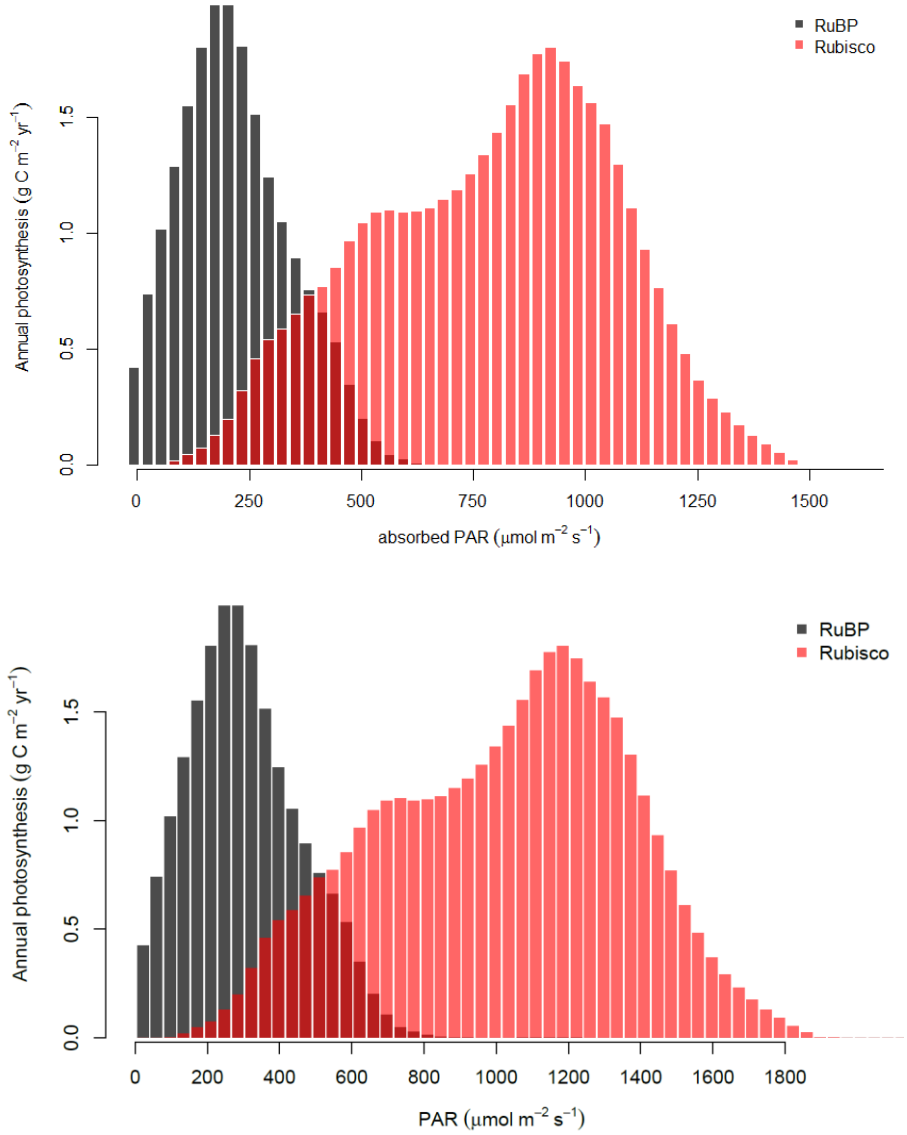


*Figure S2. Distribution of average annual photosynthesis limited by Rubisco activity and RuBP-regeneration in bins of ~~absorbed~~ PAR (~~25~~ 30 µmol m$^{-2}$ s$^{-1}$), as calculated by MAESPA for all rings during 2013. This figure is produced with a $\theta_J$ of 0.85 and a J:V ratio of 2, which represents common model assumptions for these values~~.*