

Authors' response to reviewer comments for manuscript bg-2016-187 "*Moore et al., Tree-grass phenology information improves light use efficiency modelling of gross primary productivity for an Australian tropical savanna*"

We wish to thank all three reviewers, and Dr. Migliavacca, for their helpful and constructive comments regarding our manuscript. Their comments are relevant and we feel have improved our manuscript. Below we outline our response and the way in which we have addressed each of their comments. Some additional pieces of analysis have been provided in a supplementary materials file in order to balance manuscript length with our response to their suggestions.

Dear authors,

The reviewers of the manuscript "Tree-grass phenology information improves light use efficiency modelling of gross primary productivity for an Australian tropical savanna" recognized the work as relevant for the audience of Biogeosciences, so do I. The Reviewers' suggested a series of additional analysis and editorial modifications to improve both the readability and the robustness of the analysis. In the Interactive Comment the authors nicely discuss how the reviewers' comments can be incorporated in the revised manuscript. Therefore, the manuscript should be reconsidered after the major revisions suggested by the Reviewers' will be included.

One contrasting comment from the reviewers was about the trade off between length of the paper and methodology details provided. I agree with the authors' consideration that, although the paper is lengthy, it needs to include a range of measurements that need to be properly described for sake of repeatability. The use of supplementary materials can be an option.

During the review I suggest the authors to address the issue raised by Reviewer 1 about the calculation of APAR, which can also help to address the comments of Reviewer 2 and 3 about the time lag between GCC, APAR, and GPP, as well as the differences between GCC and APAR.

Also, the authors to discuss more deeply the issue raised by Reviewer 1 about the estimation of the peak LUE. I consider valuable the idea of the Reviewer to use running means instead of the average by months. Another option for the authors is to optimize the peak LUE value.

The reviewers suggested also a valuable analysis to assess the robustness of the indices extracted from the digital camera data.

Last but not least the Reviewers pointed out a series of modifications to Tables and Figures that need to be included.

Looking forward for reading the revised version.

Best Regards,

Mirco Migliavacca

Reviewer #1

Firstly, I would like to congratulate the authors to a very interesting and well written manuscript. I truly enjoyed reading it and I learned a lot. However I have some questions that I would like to get answered before I can recommend this manuscript for publication:

This manuscript is not focusing on the EC based understory estimates of CO₂ fluxes, but I am still confused. The eddy covariance method is based on the assumption that measurements are done in the inertial surface layer, i.e. in the layer within the atmosphere where there are no vertical changes in fluxes depending on height of the sensors (Foken, 2008). This is not the case inside a canopy. Inside a canopy turbulence is very chaotic, and turbulent transport is much more efficient than above a canopy (Denmead and Bradley, 1987; Foken, 2008; Kaimal and Finnigan, 1994; Raupach, 1989). Additionally, there are sinks and sources in all directions in space. Fluxes can thereby basically come from any direction; the NEE estimated by the EC system is thereby not only a result of fluxes from the understory, it can equally as well be a result of respiration or CO₂ uptake by the canopy cover above the EC system.

The understory EC data used in this study is that which is already published in the same special issue of Biogeosciences (Moore et al., 2016). This paper discusses and validates the use of an understory flux tower for savanna research in more detail. In particular, it presents results from a cospectral analysis, based on the work of Kaimal and Finnigan (1994) (as referenced by the reviewer), to show that the flux tower does primarily record vertical transport during daytime turbulent conditions. We referred to Moore et al. (2016) within section 2.2 to direct readers to this more detailed discussion. Given all three reviewers commented on the length of the manuscript, we feel it would be ineffective to elaborate on this further. However, we have expanded the sentence on page 5 that discusses the validation of the understory to now read: “*The understory tower primarily recorded vertical transfer during turbulent conditions, which was validated via power spectra analysis (Moore et al., 2016a) that followed idealised curves for vegetated canopies (Kaimal and Finnigan, 1994).*”

(P8 L20) In case you do not include the reflected PAR in the estimates of fraction of absorbed PAR (FAPAR), it is not FAPAR, it is the fraction of intercepted PAR (FIPAR). This is not the same thing. Generally, FIPAR is much more stable over the seasons than FAPAR, and this can make a difference in the estimate of the seasonal variation in GPP. Why did the reflected PAR data result in negative values during the dry season? It indicates some issues with the calibration of the sensors. Is there no way to inter-calibrate the sensors and recalculate the data? FAPAR is generally estimated as:

$$FAPAR = \frac{PAR_{in} - PAR_{ref} - (1 - \alpha) \times PAR_{tr}}{PAR_{in}}$$

Where PAR_{in} is incoming photosynthetic active radiation (PAR), PAR_{ref} is reflected PAR, α is PAR albedo of the soil, and PAR_{tr} is PAR transmitted through the vegetation.

The reviewer is correct here and given reviewer 2 and 3 also highlighted this point, it prompted us to re-check our analysis of fPAR and APAR.

Initially the reason for omitting reflected PAR was due to fPAR values often being negative in the understory in the late dry season. This was most likely due to the lack of vegetation in the understory in the late dry season around some of the towers, which caused incoming PAR below the understory to be almost equal to that of PAR above the understory. For one tower, PAR below the understory was higher than PAR above the understory, which is a result of

the heterogeneous nature of the savanna ecosystem at these point scales. By omitting this tower from the analysis during the late dry season, negative fPAR values no longer occurred in the understory. This data was then used to calculate APAR, not IPAR.

Basically, there was a bug in the code that was missed on previous checks before submission. This bug was due to an incorrect labelling of the APAR variable to an alternative version, which omitted the reflected/upwelling PAR to test the above theory about the negative fPAR values. Therefore, we incorrectly concluded that by omitting the reflected PAR, the model performed better, when in fact it was actually using the correct, reflected PAR-included APAR values.

To sum up, we are grateful for the keen eyes of all three reviewers here for picking up on this mistake before the manuscript made it further in the review process. Thankfully, the data presented are correct, they were just interpreted incorrectly on our behalf. We have made the necessary changes to equations 3-5 in the manuscript, which now include the relevant reflected PAR information, and have removed the sentence stating the reason for leaving it out in the first place.

I do not understand how the model can overestimate the GPP? You estimate a maximum LUE based on an average LUE for Dec-Mar. Then you use scalars with a value of between 0 and 1 to downscale the maximum LUE to a lower value. But since maximum LUE is based on the same time series of GPP as you use for the evaluation, it should not be possible for modelled GPP to be overestimated. Or did I misunderstand something? Please clarify.

We are a little unsure as to what the reviewer is referring to with this statement, if it is one aspect of the text/figure or if it is our general approach to our research question. However, to answer this query at a general level, the model can most definitely overestimate GPP (or underestimate it) as LUE is not the only input to the GPP model. APAR is also an input, which in the case of the savannas is often overestimated during the transition periods between wet and dry seasons (i.e., Kanniah et al., 2009, Whitley et al., 2011). Meteorology also drives the down-regulation of maximum LUE to daily LUE variability, so although we obtained maximum (peak) LUE from our GPP estimates, the application of this down-regulation process means the two parameters are no longer directly related. Therefore, by using APAR and LUE in the model, GPP can be over- or underestimated. This is why we chose to test whether including phenology information would improve the model's ability to capture flux tower GPP, given this savanna ecosystem displays such a distinct boom-bust seasonal phenology.

Specific comments:

L11, it sounds like all grass in savannas is C4 species, which is absolutely not the case. Please just rephrase a bit.

The sentence has been changed to read "..., whereas the grasses more commonly use the C4 pathway, ..."

P6 L1 Please describe very shortly the partitioning method used. Was it based on a light response curve or night time NEE-temperature curves?

We used a u^* filter and artificial neural network approach, with soil water, soil temperature, air temperature and EVI as the main model drivers, to determine respiration (R), assuming all night time NEE was R. This was extrapolated to the daytime and GPP was calculated as the difference between R and NEE. Further information about this process can be found in Beringer et al. (2016), also an article in the special issue our manuscript is a part of. Hence, we have added this short description to P6, L1 and direct the reader to Beringer et al. (2016) for further information.

Generally in the method section there are very many technical details. These are nice to have, but I think they could be moved to supplementary material to ease the reading of the manuscript. But, it is ok the way it is now as well, it is just a suggestion.

We have revised the manuscript and reduced the wordiness of the methods section from 3300 words to 2885 words. In particular, we divided section 2.4 into three new sections, to more explicitly identify the phenocam image processing, the radiation data processing and the LAI and biomass measurements. While the use of supplementary material was suggested for this section to reduce its wordiness, we felt the processes discussed in each section were important enough to remain in the main body of the paper, so we chose to reduce wordiness where possible instead. For some of the additional analyses suggested by the reviewers, we have included them as supplementary material to ensure we did not add to our shortened methods section.

P9L18 APAR is in MJ d-1.

We have fixed this in the text.

P5 please indicate the study period of the EC measurements, and other measurements by the way.

The study period was from 12th December 2012 to 14th October 2014, for all measurements. We will add this to the text.

P9 L24 Why is $n=8$? In the figures it looks like the measurements started in January 2013, which would mean $n=7$?

$N=8$ because it includes the months of Dec through to Mar (inclusive), which each occur twice during the study period. We stated this in the text on P9, L22, but have made it clearer by also stating the timeframe of the study ($n=8$, across two years)

P9 L22 Why did you bin the LUE to months, this does not necessarily give the best indicator of maximum LUE. I would say that better would be to use a running mean for the estimates of

seasonal dynamics in LUE, and then use the maximum value. Why should the average of 3 months give the best estimate for a maximum?

We binned LUE by month and termed it peak LUE, rather than maximum LUE, because true maximum LUE is not easy to obtain from EC measurements. What we wanted to get at was a representative maximum LUE that was obtained during conditions that were not limiting to growth. A similar approach was used by Kanniah et al. (2009), so we intended to mirror their approach in terms of calculating a maximal LUE estimate from EC measurements. To reduce this confusion caused by our use of the term ‘peak’, we have changed back to ‘maximum’, but have clarified that for our study, LUE_{max} is the general maximum light use efficiency during the wet season.

To address the reviewer’s suggestion about calculation of LUE_{max} using a running mean approach, we revisited our calculation process of LUE and found that FIPAR was used instead of FAPAR in the calculation of LUE. As such, Figure 3 should look like Figure 3.2 instead (below), which changes the LUE_{max} values slightly, based on the Dec-Mar averaging approach. This is likely the result of the confusion identified by the reviewers about our use of FIPAR instead of FAPAR throughout the manuscript. Using the now correct LUE timeseries, we applied a 30-day running mean approach, as suggested by reviewer 1, to calculate an alternative LUE_{max} . This approach produced Figure 3.3. While it was a good idea to calculate LUE_{max} using a running mean approach, we feel it produced unrealistically high values, particularly for the understory ($4.59 \text{ g C MJ}^{-1} \text{ APAR}^{-1}$), when compared against other LUE_{max} values reported for savanna ecosystems (i.e. 0.33 to $3.5 \text{ g C MJ}^{-1} \text{ APAR}^{-1}$). In addition, the running mean approach also gave a higher LUE_{max} value for the overstory than that for the savanna ecosystem. The ecosystem LUE_{max} should reflect a combination of overstory and understory LUE, and as such, should be at least slightly higher than the overstory. Given this, we feel our Dec-Mar averaging approach gave the most realistic LUE_{max} values.

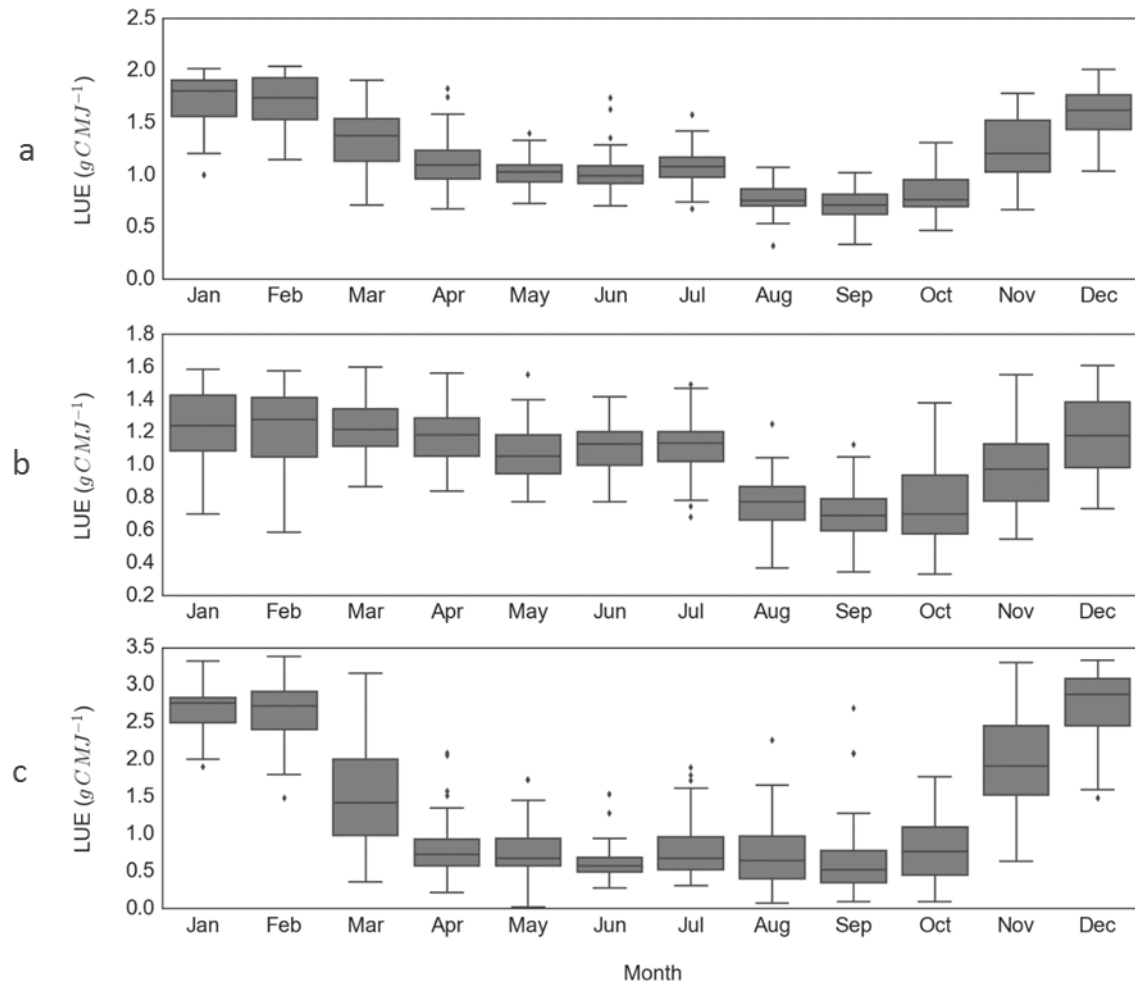


Figure 3: Original LUE figure displayed in manuscript, where a) Ecosystem, b) Overstory, and c) Understory.

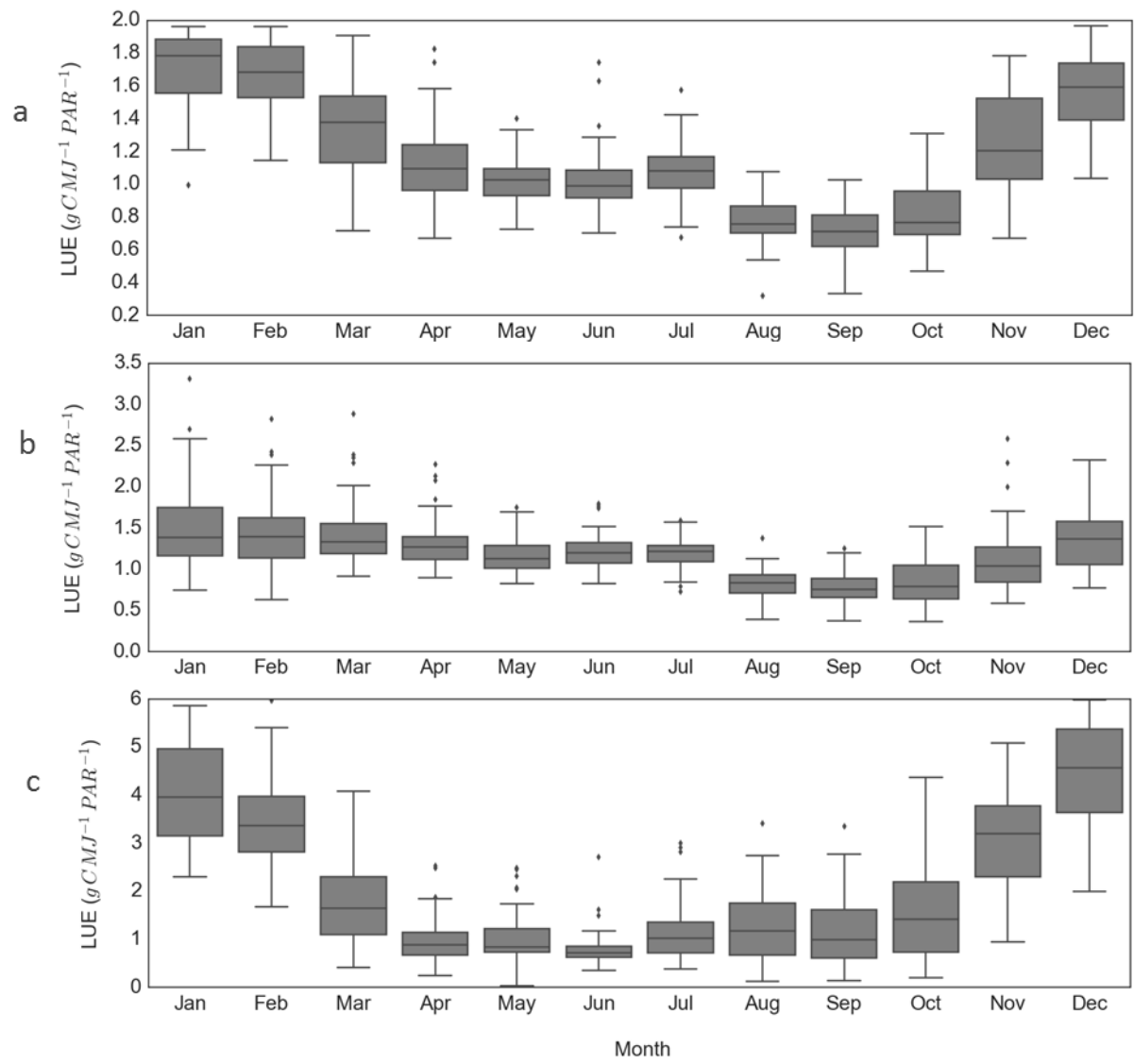


Figure 3.2: Updated figure to be included in resubmission. LUE is calculated using APAR, not FIPAR.

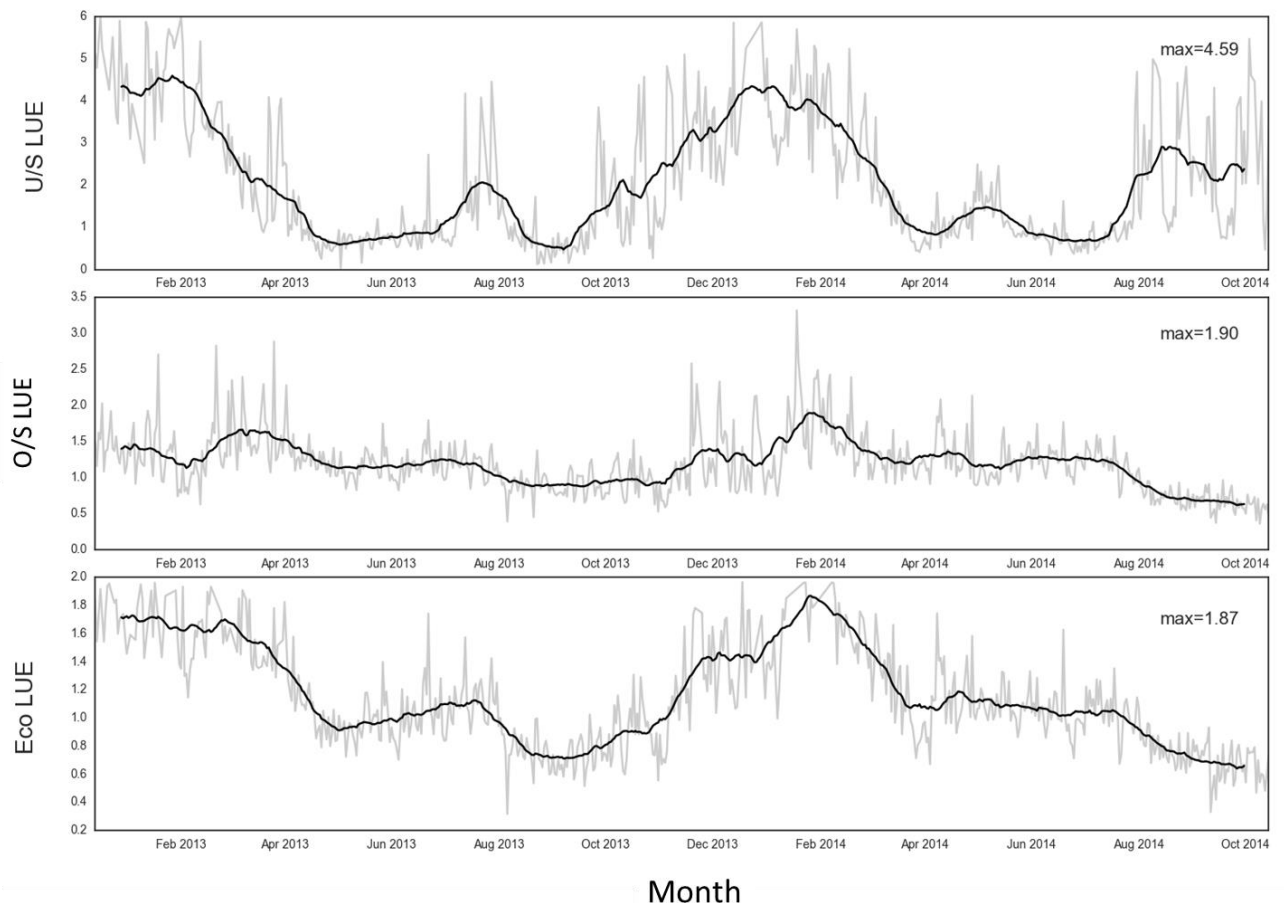


Figure 3.3: LUEmax calculated from a 30-day running mean approach. Shading indicates daily LUE values.

P16 L 17 Why did you use GCC as a proxy for FAPAR, and not as a scalar for LUE? There is strong seasonal variability in LUE depending on phenology of the vegetation, so I would think that it is more realistic to use the phenology as a direct scalar on LUE.

We used GCC as a proxy for fPAR because the high values of fPAR in the transition periods were what we believed to be the source of the error in the model. LUE reduces rapidly from Feb to May, which is more characteristic of the phenology response seen in the field (i.e. Figure 3). Given this, the LUE was more indicative of phenology driven GPP than APAR, so was less likely to be the source of the error in the model than APAR. In addition, we calculated maximum LUE from the GPP data, which was then downregulated with VPD (or EF) and Ta to give a LUE time series. Therefore, we did not feel it appropriate to use GCC in place of LUE.

P10 L29 I assume that the regression was not used to replace APAR, but to replace FAPAR?

The phrasing of this sentence is misleading. It now reads “Daily EVI were regressed against site-based daily ecosystem fPAR, and the regression was used along with incoming PAR information to replace APAR in Eq. (6).”

P12 L34 What limitations?

The limitations refer to those mentioned in line 29 of the same paragraph. We have removed this part of the sentence, given it is largely a repeat of the information in line 29.

P13 L4 I would not consider a R^2 value of 0.09 and 0.23 a well correlated relationship. These relationships are not well correlated just because the p -value is significant. The assumptions for testing of significance is not fulfilled; there is high auto-correlation present in eddy covariance time series, so the true N is nowhere near the observed N . For example, Desai (2014) addresses this issue using a reduced degree of freedom calculation to show that the vast majority of flux tower regression is actually over-confident.

We agree with the reviewer here, better would be to say more broadly that the relationship was stronger for the understory than for the overstory. We will change this in the text accordingly.

Fig 8-10. I suggest to incorporate subplots just like you did in Fig 7. Where you include a subplot with modelled GPP on the y-axis and the measured GPP on the x-axis. This really helps to see how well the models perform.

This is a good idea. The reason we did not do it from the beginning was because we felt it made the figures too busy, so we included this information in Table 2 instead. However, we do agree that it would add to the figures, so we have included them in our resubmission.

P15 L25-L27 Are you certain that RMSE is higher for the GCC included model (RMSE =1.43) than for the GCC and EF combined model (RMSE=1.36)? When looking at Fig 8 it does not look like RMSE can be higher. In Figure 8, it looks like the errors are much smaller; this should also be seen in the RMSE values.

Using slightly adjusted maximum LUE values in this analysis (as per reviewer # 1's previous comment) has resulted in slight adjustments to most values in Table 2. Now, the RMSE for the LUE_GCC included model for the overstory is slightly lower (= 1.56) than for the LUE_EF_GCC model (=1.59), which is more in line with what is shown in Figure 8. In saying this, these metrics are by themselves only one indication of error in the model, which is why a combination of all three have been used as a test for model function. The RMSE approach is particularly susceptible to the cancellation effects of over- and under-estimation throughout the year, which is evident in the overstory dataset. In contrast, there is substantial variability between the RPE or the two models, with the LUE_GCC model showing far less over-prediction than the LUE_EF_GCC model (6.47 vs 16.45, respectively). This highlights the importance of considering all three metrics when assessing the effectiveness of these model runs.

Table 2 has been updated, as have the values referred to within the text from it.

Reviewer #2

The use of GCC in the LUE model is thought to improve the GPP estimation because of the strong phenological cycle of the target. In my opinion the phenological cycle is very well represented when fAPAR is used. So the reason for using GCC must be different: replacing fAPAR measurements or testing if a “green” index (likely a proxy of a “green” fAPAR) provides a better description of photosynthesis than that of total fAPAR.

The reviewer raises a valid point here, in that fAPAR does capture the phenological cycle reasonably well. However, it does not capture it perfectly and is particularly poor during the transition from the wet to dry season (or dry to wet). We believe this is due to the senescence of the understory grasses that changes the greenness and GPP of the savanna despite fPAR remaining high. Currently, savanna productivity models poorly capture this change (i.e., Kanniah et al., 2009, Whitley et al., 2011, Whitley et al., 2016), and we would argue it is because they do not capture the understory phenology dynamics as well as they could. Moore et al. (2016) found that the understory accounts for 1/3 of savanna GPP, which is heavily dominated by the annual grasses that show this strong phenology. When models only use the fPAR(or APAR) information, they fail to capture the transition from wet to dry (and dry to wet) and over-estimate GPP. By using the GCC information, which provides a more accurate representation of phenology when compared with APAR for this savanna, the LUE model performs better. Ma et al. (2014) also reached a similar conclusion when they used EVI to incorporate better phenology information into their GPP model.

Cameras pointing to trees: as large part of the ROI is occupied by the background (the sky), I wonder if the observed (and reduced) variability in GCC is not related to variations in sky optical properties during the year. The relation with LAI (Fig 6b) is not helping to figure it out, as the observed relation between GCC and LAI may be spurious (i.e., LAI increase and decrease in parallel to changes in sky optical properties). To disentangle the two effects it would be useful to define some additional ROIs with sky only and analyse the difference with the tree-ROIs selected.

This was a great idea suggested by the reviewer, so we thank them for it. We proceeded to analyse a sky-only ROI for the three overstory cameras used to generate the chromatic coordinate and excess indices. The outcome of this analysis is shown in the following figure (a), where the original Gcc timeseries for one of the towers is depicted alongside its corresponding sky-ROI timeseries. At any given time, the sky GCC timeseries is always less than that of the large ROI. Given this, we incorporated into our GCC image processing procedure a step where the GCC value for each pixel is excluded from the analysis if it is equal or less than the sky-ROI GCC value for that same image. This resulted in a new GCC timeseries which omitted the pixels that were sky. Thus, the new GCC timeseries (Figure a) is more representative of how the green foliage in the overstory changes over time. Given the sky threshold applied was calculated specifically for each day, the effects of changing sky conditions on each of the images has also been reduced. We applied the same technique to calculate the red (RCC) and blue (BCC) chromatic coordinates, as well as the excess coordinates. Therefore, the overstory analysis within the text has been updated, as have the relevant figures and tables. We have also included a supplementary material file outlining the

steps used in this process, in an effort to keep the length of the methods section at a minimum. We make reference to this material in section 2.4 and 3.1.

Performances of the different GPP models (4, all LUE based) are assessed in terms of r , RMSE and RPE. However, model 1 and 2 (eq 6 and use of EF) are used in prediction while (if I got it well) model 3 (using phenocam index) is in fitting (as two parameters, m and c coefficients) are adjusted. Model 4 (using MODIS) is in between, because a relationship is tuned between EVI and fAPAR. Therefore, results are not comparable in my opinion (see the discussion at page 15).

Each model combination is compared against flux tower-derived GPP estimates and the r , RMSE and RPE provide an indication of which model is best at capturing tower GPP. Our discussion on pg 15 discusses which of the model combinations was best at capturing tower GPP, finding that the inclusion of phenology information did the best job.

An interesting point is that the use of the phenocam index appears to eliminate the lag between measured and modelled GPP. The reason for this could be that the total fAPAR used by the other model is the source of this lag. On the contrary GCC may represent a kind of “green” fAPAR that is more in line with photosynthesis. A dedicated section comparing phenocam indexes and fAPAR would be very useful.

We have created plots of APAR and fPAR vs. GCC and included them in a supplementary materials file. We discuss these plots in section 3.3 and suggest that the GCC likely represents a ‘green APAR’ that is able to more closely track vegetation productivity over time.

Specific comments:

1 L 32 r_2 ranging from 0.1 to 0.2 (overstory) is much lower than that of understory but they are both indicated as “well correlated”.

Agreed, we have amended our statement in the text, as per our response to reviewer 1 above.

3 L 23 I don’t understand what is meant by “Core issues surrounding the remoteness of satellite sensors”

Here we meant to identify that one of the limitations of satellite remote sensors is their remoteness from the ecosystems they measure. We have re-phrased the sentence to state this more clearly.

3 L23-25 this sentence is rather obscure (“the diffuse nature of light”?). I would suggest to omit it and only mention that the highest temporal frequency available is one composite every 8-16 days.

We have omitted the “diffuse nature of light” segment identified by the reviewer so the sentence reads more concisely.

3 L 34 I don't understand “via leaf emergence and senescence”. Please rephrase.

This sentence is talking about the value of phenocams for identifying leaf-level changes, such as leaf emergence and senescence, so we have rephrased the sentence to more clearly show this. In particular, we have removed the word “via” as this seemed to be the most misleading part of the sentence.

4 L1-3 Here you are saying that LUE models describes GPP through the relation between APAR and LUE. There is no relation, they are both used to estimate GPP.

Here we used the word ‘relation’ to indicate that the two parameters were multiplied to obtain GPP. We have simplified this sentence to now reads “Phenocam data have also been used for parameterising light use efficiency (LUE) models... that describe ecosystem GPP using absorbed... APAR and plant LUE”

Section 2.3 The final field of view of the camera could be provided.

This has been calculated for the understory as 4 m x 2 m (horizontal x vertical) based on an object distance of 5 m, and for the overstory as 8 m x 5 m based on an object distance of 10 m. This information has been provided in section 2.3.

Section 2.3 Can you comment on possible effects of the automatic (and variable) white balance? This can variable from measure to measure. What is the effect on calculated indexes? Few numerical simulations may help in this assessment.

We do discuss, albeit briefly, the effects of white balance on image collection in the limitations section of our manuscript. The reviewer is correct in their assessment that white balance can vary from image to image, which is particularly more prevalent during lower sun angles i.e. dawn/dusk. By using middle of day values, the effects of white balance can be reduced. However, white balance was set to zero in our analysis, which is a limitation in that it increases the scene illumination noise in our images. However, given that we only analysed middle of day images in an environment that is highly dynamic, the phenology signal was still identifiable. This may not be the case for a less dynamic ecosystem. Migliavacca et al. (2011) discuss the uncertainty and limitations of using digital camera imagery, which we make reference to in section 3.4. We have included some additional thought on this issue in section 3.4, indicating that we believe the strong phenology of the savanna studied allowed the signals to be identified despite the potential for variable white balance.

8 eq 16-18 Why is the reflected PAR is not used? This is fIPAR. And the resulting flux is IPAR not APAR

Our answer to reviewer 1 about this should help to clarify this point.

10 L 34 In which sense “predictive” is used here? Is there any validation / prediction on independent data (i.e. not used in fitting)?

The relative ‘predictive’ error indicator we used in our analysis is simply a calculation of the % mean difference between two datasets. It provides an indication of the direction of change in the predicted values relative to the measured values in a relative sense. See Kanniah et al. (2009) Appendix 1 for further explanation and formulas for calculation. We have altered the sentence slightly so that it reads “...relative predictive error (RPE) to represent the percentage difference and degree of over- (+) or under- (-) estimation of the model.”

Section 3.1 It would be interesting to see the FAPAR curves along with that of the various camera-indexes

This was a nice idea, but in the interest of balancing the additional information requests and the length of the manuscript in its current form, we think that creating and discussing an additional plot within the manuscript would make the manuscript unwieldy (there are already 10 figures and 2 tables in it). However, we have created plots of APAR and fPAR along with Gcc and included them in supplementary material, making reference to them in section 3.3.

Figure 7. Sorry, I am not getting what the 1:1 line refers to. The two variables on the scatterplot have different units and ranges

We can see why this would be confusing, it was meant to simply provide a guide of the deviation of the data, so we have removed the line from the resubmitted version.

Technical corrections:

3 L 4 Why “cover”?

We have removed the word ‘cover’ in the sentence to simply read “phenological change”

7 L 5-7 This sentence says that it is homogeneous and it is not. It’s a matter of scale. It can be rephrased.

This is absolutely true, but the sentence in question does state this: “While the understory is largely homogenous in species distribution at the flux tower scale (i.e. >50 m), variation from one point to another does exist in the understory due to its vegetation composition.” The sentence has been amended to read “...variation does exist at the smaller scale (i.e. < 5 m) in the understory due to...” to be a bit clearer on the subject.

8 L 13 “Absorbed” instead of “used”.

We have fixed this in the revised version.

11 L9 RCC/ExR looks like a ratio. I would suggest to use “and”.

We have fixed this in the revised version.

13 L1 I miss the integration in this section. The title of this section could be “Relation between GPP and time series of phenocam and MODIS indexes”

This section is about using the phenology information to improve estimates of GPP. Given this, we agree with the reviewer that the heading is misleading, therefore we have changed it to “Phenocam and MODIS phenology in relation to GPP”.

P14 L5-7 Probably not needed, already described.

We have removed this sentence from the text.

Reviewer #3

The utility of phenology information for improving GPP modeling results is an important research objective and I find the present work interesting and relevant. The paper is well written, methods are sound and results are carefully discussed. However, descriptions are generally very (too) detailed and several sections would benefit from a slightly more concise format. The structure of parts of the methods section should also be improved for improved overview, flow and clarity.

We are pleased the reviewer enjoyed our manuscript and do agree that it is quite lengthy in parts. Given we used a rather home-made camera for our phenocams, we felt we should provide more detail about our methods. However, we have revised the manuscript and made the methods, in particular, more concise. For example, the method section was originally 3300 words in length, now it is only 2885 words.

Some detailed and relatively minor comments:

1. Page 1 L32: An R^2 of 0.09 – 0.23 does not constitute a well correlated relationship as I see it.

This was also identified by reviewers 1 & 2, so we have fixed this in the text as per our response to reviewer 1.

2. Page 2 L16: I believe fire should be capitalized as in “..2015). Fire: : :”

Yes it should, we have fixed this in the revised manuscript.

3. Page 3 L19: What does the A2/A3 refer to? Is this information needed here?

The A2/A3 information refers to the sub-product of MOD17 used, as it is a combination of both GPP (A2) and NPP (A3) obtained from the Terra satellite. Given we only used the MOD17 A2 (i.e. GPP) product, we have omitted the A3 reference, but feel the A2 reference should be kept for clarity.

4. Page 3 L20: MOD17 is mentioned to provide the most reliable means of estimating large-scale productivity. In comparison to what other products/estimates? MOD17 is known to be associated with significant uncertainty (related predominantly to the specification of the effective LUE), and I'm not convinced it will outperform other products given a full suite intercomparison.

We agree with the reviewer here in that there are a suite of GPP model products available. However, it is out of the scope of our study to compare all products. This sentence has therefore been amended to remove the “most reliable” portion to now read “...the MODIS GPP product is widely-used means of estimating...” instead.

5. Page 3 L23: “Core issues surrounding: : :”; Odd sentence. Suggest rewording. The full sentence structure (L23 to L28) should be rewritten for better language and clarity.

This statement was also identified by reviewer 2, so we have fixed the sentence based on our response provided previously.

6. Section 2 introduction (Page 4): This intro piece doesn't outline the overall methodology well and/or the sub-division of the methods sections. I would probably leave it out completely or provide a more elaborate and cohesive piece.

The intention of this short section was to provide a brief overview/blurb of the methods before describing what was done. Given the reviewers all commented on the length of our manuscript, we have omitted it in the resubmission.

7. Page 6 L2: I don't think that it is necessary to know the type of coding language (Python) used..

We have removed this from the section identified.

8. Page 6 L31: “f/stop”?

This is a photography term that refers to the ratio of a lens' focal length to the diameter of the point where light enters the camera. It can be referred to as a focal point. We have added “(focal point)” after it in the text.

9. Sections 2.3 and 2.4: The methods are described in great detail. I would suggest reducing the wordiness as much as possible only including the most essential elements.

We have taken these comments on board and have reduced the length of the methods section from 3300 words to 2885 words.

10. Section 2.4: I would include separate sub-sections for the phenocam and radiation data processing for improved flow and readability. Line 13 on page 8 could be the start of the LUE sub-section.

This is a great suggestion and we have split the section where indicated by the reviewer.

11. Page 7 L24-26: I feel that this information is redundant.

We have removed this information in the re-submitted manuscript.

12. Page 8 L22: Shouldn't leaf absorptance be considered in the APAR calculation? You are using fPAR and not fAPAR, right?

Our response to reviewer 1 regarding this should help clarify this point.

13. Page 8 L24-: The information on LAI collection, clumping etc is out of place. You will need a separate section on this.

We have also separated this section into a new subsection in the methods.

14. Page 10 L1-4: Is it valid to adopt the default MOD17 savanna values for your study site? Did you verify these against the tower observations?

The Tmin and VPD values were previously validated for the Howard Springs site by Kanniah et al. (2009). However, we found slightly higher maximum VPD for our study period than that of Kanniah et al. (2009). Therefore, we cited the original values of Running & Zhao (2015) for our study. Given Kanniah et al. (2009) did perform a validation of earlier values of Running et al. (2006) for savannas, we have included Kanniah et al. (2009) in our citation of the section identified.

15. Section 3.1 is very detailed and would benefit from a more concise format, if possible.

We have shortened this section from 980 words to 772 words.

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Tree-grass phenology information improves light use efficiency modelling of gross primary productivity for an Australian tropical savanna

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Abstract

The coexistence of trees and grasses in savanna ecosystems results in marked phenological dynamics that vary spatially and temporally with climate. Australian savannas comprise a complex variety of life forms and phenologies, from evergreen trees to annual/perennial grasses, producing a boom-bust seasonal pattern of productivity that follows the wet-dry seasonal rainfall cycle. As the climate changes into the 21st Century, modification to rainfall and temperature regimes in savannas is highly likely. There is a need to link phenology cycles of different species with productivity to understand how the tree-grass relationship may shift in response to climate change. This study investigated the relationship between productivity and phenology for trees and grasses in an Australian tropical savanna. Productivity, estimated from overstory (tree) and understory (grass) eddy covariance flux tower estimates of gross primary productivity (GPP), was compared against two years of repeat time-lapse digital photography (phenocams). We explored the phenology-productivity relationship at the ecosystem scale using moderate resolution imaging spectroradiometer (MODIS) vegetation indices and flux tower GPP. These data were obtained from the Howard Springs OzFlux/Fluxnet site (AU-How) in northern Australia. Two greenness indices were calculated from the phenocam images; the green chromatic coordinate (GCC) and excess green index (ExG). These indices captured the temporal dynamics of the understory (grass) and overstory (trees) phenology, and were ~~mostly~~ well correlated with tower GPP for understory ($r^2 = 0.65$ to 0.72) and ~~but less so for the~~ overstory ($r^2 = 0.09$ to 0.23). The MODIS enhanced vegetation index (EVI) correlated well with GPP at the

ecosystem scale ($r^2 = 0.70$). Lastly, we used GCC and EVI to parameterise a light use efficiency (LUE) model and found it to improve the estimates of GPP for the overstory, understory and ecosystem. We conclude that phenology is an important parameter to consider in estimating GPP from LUE models in savannas and that phenocams can provide important insights into the phenological variability of trees and grasses.

Key Words

Eddy covariance, phenocam, leaf area index, photosynthetically active radiation, light use efficiency, MODIS, OzFlux

1 Introduction

Savanna ecosystems are defined by the coexistence of trees and grasses, and have evolved to dominate one fifth of the terrestrial land surface (Scholes and Archer, 1997; Grace et al., 2006). In tropical savanna, trees utilise the C_3 photosynthetic pathway, whereas the grasses more commonly use the ~~more-recently-evolved~~ C_4 pathway, being more efficient at taking up carbon in hot environments with limited water and nutrient availability (Sage, 2004; Osborne and Beerling, 2006). Savannas are typically found in wet/dry climates that over time have shaped the tree-grass structure and phenology seen today. Fire also plays a role in shaping savanna phenology and structure, with recurrences often every 1-5 years (Hoffmann et al., 2012; Beringer et al., 2015). Fire consumes cured grass biomass in the dry season and suppresses growth of juvenile overstory species, resulting in a range of plant phenology responses to deal with it (Bond, 2008; Murphy et al., 2010; Werner and Franklin, 2010). Herbivory, drought and land-use change are additional disturbances that commonly occur in savannas (Hutley and Beringer, 2011). These complex interactions are believed to be the primary reason for the co-dominance of trees and grasses in savanna ecosystems, as well as for the phenological variability displayed (Bond et al., 2003; Van Langevelde et al., 2003; Bond, 2008; Hanan and Lehmann, 2010; Lehmann et al., 2014).

The climate and disturbance regime in savannas plays an important role in shaping plant phenology. C_4 savanna grasses typically follow a boom-bust phenological cycle, where they rapidly produce biomass in the wet season and display an annual or perennial die-back phenology in the dry season (Bond, 2008; Ratnam et al., 2011). C_3 savanna trees, in contrast, can range from having a fully deciduous phenology to remaining evergreen throughout the dry season. In Australian savannas, the understory is dominated by C_4 annual grasses with a small portion represented by juvenile overstory species (Werner and Franklin, 2010; Werner and Prior, 2013) and perennial grasses. Evergreen eucalypt species make up the bulk (~ 80 %) of the overstory in Australian savannas (Hutley et al., 2011), however, semi-, brevi- and fully deciduous species are found to a lesser degree throughout (Williams et al., 1997) and contribute to the seasonal fluctuation of canopy leaf area (O'Grady et al.,

2000;Whitley et al., 2011). Tree-grass ratios are driven by annual rainfall, and in Australia there is a strong rainfall gradient from the coast inland (Rogers and Beringer, 2016), resulting in northern high rainfall (mesic) regions supporting higher tree-grass ratios and drier southern (xeric) regions supporting higher grass-tree ratios (Hutley et al., 2011;Ma et al., 2013).

The monitoring of savanna phenology can inform how savannas might respond to climate change. At the regional scale, the timing of phenological events varies widely for savannas due to variability in the occurrence and duration of rainfall events (Ma et al., 2013). Phenology, in turn, influences the productivity and growth (carbon cycle) of an ecosystem, as well as its water and nutrient cycles (Noormets, 2009;Richardson et al., 2013). The savanna region of Australia is projected to experience warming and increased rainfall (variability and amount) under climate change (Reisinger et al., 2014), which is likely to impact savanna phenology and its interactions with the carbon, nutrient and water cycles (Kanniah et al., 2010;Scheiter et al., 2015). There is a need for better understanding of what governs savanna phenology in order to predict how it may be affected by climate change (Beringer et al., 2016a).

Due to the large extent and spatial variation of savannas, satellite remote sensing provides a useful tool (Broich et al., 2015) for examining the interactions of savanna phenology with productivity. Vegetation indices such as the normalised difference vegetation index (NDVI) (Tucker, 1979) and enhanced vegetation index (EVI) (Huete et al., 2002) provide valuable measures of savanna phenological variability from the landscape to global scale (Ma et al., 2013;Ma et al., 2014). Likewise, the MODIS gross primary productivity (GPP) product (MOD17 A2/A3, Running and Zhao, 2015) is a widely-used offers the most reliable means of estimating large scale savanna productivity (Grace et al., 2006;Ryu et al., 2011), but has been shown to underestimate savanna GPP, particularly during the transition between the wet and dry seasons (Kanniah et al., 2009;Whitley et al., 2011;Ma et al., 2014). The remoteness of satellite sensors from the ecosystems they measure, along with Core issues surrounding the remoteness of satellite sensors, the effects of cloud contamination on daily data collection, the diffuse nature of light and the need to aggregate imagery spatially and temporally for contiguous scenes, results in coarse temporal resolution (i.e. 8 or 16 day) satellite data products that can be problematic for identifying change in seasonally cloudy tropical environments (Eberhardt et al., 2016) where rapid (i.e. 1-2 weeks) phenological change is common (Williams et al., 1997;Moore et al., 2016c).

A novel approach to alleviate some of the limitations of satellite remote sensing is to use *in situ* automated time-lapse cameras (phenocams) that can collect high temporal resolution (hourly to daily) images of vegetation within and above an ecosystem (Richardson et al., 2007;Hufkens et al., 2012;Sonntag et al., 2012;Moore et al., 2016c). The proximity of these cameras to ecosystem vegetation allows them to capture important information about vegetation cover change, particularly

~~that of -via~~ leaf emergence and senescence (Richardson et al., 2007; Richardson et al., 2009a; Wingate et al., 2015) that can be linked with measures of ecosystem GPP (Toomey et al., 2015; Richardson et al., 2010; Filippa et al., 2016). Phenocam data have also been used for parameterising light use efficiency (LUE) models (in a similar way to MODIS GPP) that describe ecosystem GPP ~~through the relationship of using~~ absorbed photosynthetically active radiation (APAR) ~~with that of and~~ plant LUE (Migliavacca et al., 2011).

In this study, we aim to contribute a detailed assessment of phenological ~~cover~~ change, and its relationship with productivity, for a mesic tropical savanna in northern Australia over 2 years. Our objectives are to (i) determine the utility of phenocams for identifying change in overstory and understory vegetation greenness; (ii) quantify the relationship between savanna overstory and understory phenology and productivity on seasonal and annual timescales; (iii) test if phenocam indices can be used as a proxy for improvement of a LUE model that is widely used to estimate GPP; and (iv) test the applicability of MODIS EVI for improving estimates of ecosystem scale GPP. To do this we utilise one of the first phenocam datasets obtained in Australian ecosystems, along with MODIS EVI, and couple them with previously collected ecosystem, overstory and understory eddy covariance data (Moore et al., 2016a) to tease apart the tree and grass phenology-productivity relationship in Australian savanna.

2 Methods

~~To address each of our objectives, we used a combination of eddy covariance and phenocam imagery along with information about overstory leaf area index (LAI), understory biomass and the radiation use of the overstory, understory and ecosystem over time. These data were used to tease apart the relationship between productivity and phenology for the trees (overstory) and grass (understory) so we could identify how they varied throughout the 2 year study period. Phenocam greenness phenology information and MODIS EVI were also used to parameterise a LUE model that we then used to estimate overstory, understory and ecosystem GPP.~~

2.1 Site Description

This study was conducted at the Howard Springs OzFlux (www.ozflux.org.au/) and Fluxnet (AU-How) site (Beringer et al., 2016a) near Darwin in the Northern Territory, Australia. A record of carbon, water and energy flux, as well as meteorological and soil measurements, was first established at Howard Springs in 1997 (Eamus et al., 2001). As such, many detailed site descriptions exist (Beringer et al., 2007; Hutley et al., 2013; Beringer et al., 2015; Moore et al., 2016a). ~~so only a brief description is provided here. In brief, a~~ Annual rainfall for the Howard Springs area is 1732 mm (\pm 44 SE) mm, (Australian Bureau of Meteorology (BoM), station ID: 014015, www.bom.gov.au) of which 90-95 % falls within the ~~rainy (wet)~~ season months of October to April. ~~For this study~~ As such, we

defined the wet season as a 6 month period from October 15th ~~through~~ to April 15th and the dry season as April 16th to October 14th based on the work of Cook and Heerdegen (2001). Mean daily maximum air temperature varies annually between 30.6 to 33.3 °C and mean daily minimum air temperature ranges from 19.3 to 25.3 °C (Australian Bureau of Meteorology, www.bom.gov.au/). Howard Springs is ~~defined as~~ a mesic savanna because it receives >1200 mm rainfall annually (Hutley et al., 2011) and is classified as ‘open forest savanna’ based on its canopy cover fraction (50-60 %) after Specht (1972). Soils are mostly red Kandosols (Isbell, 1996) that are sandy-loamy, well weathered and nutrient poor.

Vegetation consists of a C₃ woody overstory ~~that is~~ dominated by evergreen *Eucalyptus miniata* (Darwin woollybutt) and *E. tetrodonta* (Darwin stringybark). A smaller portion of the ~~tree canopy and mid-canopy layer~~ woody overstory is made up of semi-, brevi- and fully deciduous species such as *Erythrophleum chlorostachys* (Ironwood) and *Terminalia ferdinandiana* (Kakadu plum) (Williams et al., 1997; Hutley et al., 2011). Mean canopy height is 18 m (Hutley et al., 2011). The understory is dominated by the annual C₄ grass *Sorghum intrans* (spear grass) and perennial C₄ grasses *Heteropogon triticeus* and *S. plumosum*. ~~Also~~ Sharing the understory with the grasses are saplings (juveniles) of overstory species, the shrub *Buchanania obovata* and the cycad *Cycas armstrongii*. Due to the frequent occurrence of fire in Australian savanna (Beringer et al., 2015), control burning was performed at the beginning of each dry season to protect the monitoring equipment at the ~~Howard Springs flux~~ site.

2.2 Productivity measurements

To estimate productivity from the savanna ecosystem and partition it into tree (overstory) and grass (understory) GPP, we used the eddy covariance technique (Baldocchi et al., 2001) as detailed for Howard Springs by Moore et al. (2016a). Two eddy covariance towers were in operation at Howard Springs to measure the fluxes of carbon, water and energy from both the understory (within tree canopy tower at 5 m) and the ecosystem (above tree canopy tower at 23 m) from the 12th December 2012 through to 14th October 2014. ~~The Overstory fluxes component is~~ simply the difference between ecosystem and understory fluxes, which ~~and~~ represents the above ground tree fluxes. Instrumentation, validation of the understory tower, data quality assurance and quality control (QA/QC) and flux partitioning information is also provided in Moore et al. (2016a), so a summary is provided here. ~~Therefore, we provide only a brief description of the site instrumentation and flux data processing.~~

Core eddy covariance instruments on each tower consisted of a 3D sonic anemometer (CSAT3, Campbell Scientific, Logan UT) and an infra-red gas analyser (LI-7500, Li-COR Biosciences, Lincoln, NE). These instruments sampled at a rate of 10 Hz and provided 30-min flux averages. Soil heat flux (HFT3, Campbell Scientific, Logan, UT) and net/short/long wave radiation components were also recorded on the ecosystem tower (CNR4, Kipp and Zonen, Delft, NL). The raw 30-minute data were

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QA/QC'd to level 3 standard using the OzFluxQC (v2.9.4) python scripts. Energy balance closure analysis of the ecosystem tower, based on daily data (Silva et al., 2011), gave a slope of 0.89 and an r^2 of 0.92. The understory tower primarily recorded vertical transfer during turbulent conditions, which was validated via co-spectral power spectra analysis (Moore et al., 2016a) that followed idealised curves for vegetated canopies (Kaimal and Finnigan, 1994). Level 3 data were then gap filled and used to partition net ecosystem exchange (NEE) into respiration and GPP using the Dynamic INtegrated Gap filling and partitioning for OzFlux (DINGO, (Beringer et al., 2016b)) package. This package applied a u^* filter and artificial neural network approach, with soil temperature, air temperature and EVI as the main model drivers, to determine respiration, assuming all night-time NEE was respiration. This was extrapolated to the daytime and GPP was calculated as the difference between NEE and respiration (Beringer et al. 2016). Both OzFlux and DINGO packages were written using python scripts.

2.3 Phenology and light use efficiency (LUE) measurements

Alongside ~~the flux~~ tower estimates of tree and grass productivity (12th December 2012 to 14th October 2014), we recorded ~~time series of~~ incident, reflected and absorbed PAR, ~~as well as~~ and vegetation cover change. While the understory is largely homogenous in species distribution at the flux tower footprint scale (i.e. >50 m), variation ~~from one point to the next~~ does exist at the smaller scale (i.e. < 5 m) in the understory due to its vegetation composition. To obtain a rigorous time series, spatial replicate measurements of vegetation cover change and PAR variability were recorded at five locations (on 5 tall mini towers) within a 50 m pentagon shape of the main ecosystem flux tower (Fig. 1). ~~We used five towers (mini towers), each of which were 5 m tall and made from steel square hollow section with a cross arm to attach the instruments and a logger solar panel array. The towers were stabilised using guy wires and a base plate. A winch system was used to manoeuvre the instruments up and down the tower for data download and maintenance. The towers were set up at a distance of 50 m in a pentagon shape around the main ecosystem flux tower and faced an east west direction (Fig. 1).~~

~~To measure PAR~~ the components ~~of PAR in the savanna, we installed~~ were measured from PAR sensors on each of the mini towers (SQ-Series, Apogee, Logan, UT). ~~Incoming PAR reaching the understory, through the overstory vegetation, was measured with a PAR sensor installed facing upward at 5 m on each mini tower. Another sensor was installed facing downward at 5 m to record the amount of PAR reflected by the understory vegetation. The amount of PAR reaching the ground surface through the understory vegetation was recorded with a third PAR sensor facing upward at 10 cm.~~ A data logger (CR800, Campbell Scientific, Logan UT) and multiplexor (AM25T, Campbell Scientific, Logan, UT) were used to collect and store ~~PAR~~ data and to operate the phenocams. The ~~mini tower systems~~ was/were powered using a 20 W solar panel, 12 V regulator and 12 V gel cell battery. To provide a complete accounting of ~~PAR in the savanna~~ savanna PAR, two additional ~~PAR~~

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sensors (LI-190 Quantum Series, Li-COR Biosciences, Lincoln, NE) were installed on the 23 m flux tower for collection of incoming PAR and outgoing PAR reflected from the savanna ecosystem.

Changes in savanna overstory and understory vegetation greenness were assessed using consumer-grade point-and-shoot cameras (Canon Powershot A810). Each mini tower supported two cameras, one ~~to collect~~collecting upward facing images of the tree canopy and one ~~to collect~~collecting downward facing images of the understory, ~~making a total of~~(10 cameras ~~installed~~total). The cameras ~~were set to run using settings included~~ automatic exposure in aperture priority mode, with a low f/stop (focal point) value of 2.8 to ensure the entire image was used to respond to ambient light levels (Richardson et al., 2007; Ryu et al., 2012; Sonnentag et al., 2012). Automatic white balance was also used as we did not have a grey reference panel to correct for white balance manually. Images were stored ~~on SD memory cards~~ in a compressed JPEG file format, ~~to ensure the cards did not fill between site visits~~and each camera was housed in a make-shift waterproof case (Fig. 2, a & d).:-

~~Each camera was housed in a waterproof case with an aperture hole cut in the top that was sealed with a microscope slide (Fig. 2, a & d).~~ Following the concept of Ryu et al. (2012), power was delivered to the cameras through wires soldered to the battery terminals ~~and a brief pulse delivered to wires soldered to the camera 'on-button' allowed them to turn on when prompted, which received input from a 12 V relay connected with a 3.3 V regulator. A second 5 V relay was used to send a short pulse to wires soldered onto the 'on-button' of the cameras to mimic the action of turning the cameras on.~~ The Canon Hack Development Kit (<http://chdk.wikia.com/wiki/CHDK>) was used to ~~automate image capture when the camera was turned on, modify the cameras to automatically take an image when turned on,~~ which was administered via a u-Basic script saved on the memory card. Each mini tower logger was programmed to operate the cameras twice daily, once at 11:30 ACST (~~to match the~~ MODIS Terra overpass) and once at 13:00 ACST (~~approximately~~ ~ solar noon). Each camera was installed ~~on the mini towers using a metal plate angled at an angle of~~ 57.5 ° from zenith, ~~as this angle has been found~~ to minimise the effects of leaf inclination angle when calculating LAI (Weiss et al., 2004; Baret et al., 2010).

2.4 Phenocam image ~~and radiation data~~ processing

Phenocam images were ~~firstly~~ visually checked for field of view (FOV) shifts and major obstructions (i.e. water ~~on the case windows~~in image) as a first step in the image QA/QC process. Images with obstructions were removed, which accounted for between 3 - 13 % of images for each camera. However, three out of ten cameras were completely omitted from analysis due to severe FOV shifts or where an individual camera had greater than 50% of images lost, ~~leaving. This left~~ a total of four cameras for understory analysis (5031 images total) and three for the overstory (4255 images total). All remaining cameras (n = 7) experienced slight FOV shifts as a result of manual data download. However, a Student t-test of 686 analysed images, for a camera with a large visible FOV shift,

revealed no significant effect on the extracted results ($t_{686} = 0.13$, $p = 0.90$). The time series from each camera were then gap filled using the best regression relationship against another camera, most of which had an $r^2 > 0.8$.

~~For each camera, the images were analysed using code written in python that initially took the extracted Exif (Exchangeable image file format) data to rename files using a standardised (yyyy-mm-dd hh:mm:ss) format. Images were analysed in date/time succession using a region of interest (ROI) that encompassed as much of the vegetation as feasible. As a result, the ROI varied depending on the vegetation available in the overstory FOV and was the same for all understory cameras, except for a separate analysis of grass and woody green vegetation, which required individual ROI's for each understory camera (Fig. 2). In addition, we analysed a separate sky-only ROI for each overstory camera and used the sky data to filter out sky-pixel information from the calculation of each index (Fig. 2, and supplementary material). Each camera collected 8-bit depth red-green-blue (RGB) colour channel information, stored as digital numbers (DN), at a resolution of 4608 x 3456 pixels. These DN's provide a measure of colour intensity based on irradiance, so they can be highly variable when scene illumination changes (Ide and Oguma, 2010; Sonnentag et al., 2012). To reduce the effects of scene illumination, the DN's are typically used to calculate the green (GCC) chromatic coordinate, a normalised ratio of the green channel to all channels, as Eq. (1) (Gillespie et al., 1987; Woebbecke et al., 1995):~~

$$Gcc = G_{DN} / (R_{DN} + G_{DN} + B_{DN}) \quad (1)$$

~~where DN is the digital number that corresponds with the green (G), red (R) and blue (B) channels. The red (RCC) and blue (BCC) chromatic coordinates were calculated in the same way as GCC. Chromatic coordinate values were calculated for each pixel within the ROI and then averaged to give an overall GCC, RCC and BCC value for each image. In addition to the chromatic coordinates, We also calculated the excess green (ExG), red (ExR) and blue (ExB) indices in order to compare which colour index performed best in capturing savanna phenological change. The excess index is an enhancement of the respective colour channel information against the other channels and is calculated as Eq. (2) (Woebbecke et al., 1995):~~

$$ExG = 2G_{DN} - (R_{DN} + B_{DN}) \quad (2)$$

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$$ExG = 2G_{DN} - (R_{DN} + B_{DN}) \quad (2)$$

2.5 Radiation data processing

The amount of light ~~absorbed~~^{used} by vegetation over time is directly correlated with productivity (Monteith, 1972). Using the mini tower PAR data ~~collected from the mini towers~~, we calculated fPAR for the overstory (OS) Eq. (3), understory (US) Eq. (4) and ecosystem (ECO) Eq. (5) as:

$$fPAR_{OS} = (PAR_{AED} - PAR_{AEU} - PAR_{AGD}) / PAR_{AED} \quad (3)$$

$$fPAR_{US} = (PAR_{AGD} - PAR_{AGU} - PAR_{BGD}) / PAR_{AGD} \quad (4)$$

$$fPAR_{ECO} = (PAR_{AED} - PAR_{AEU} - PAR_{BGD}) / PAR_{AED} \quad (5)$$

where AED and AEU are the above ecosystem down-welling and up-welling PAR, AGD and AGU are the above grass down-welling and up-welling PAR, and BGD is the below grass down-welling PAR. ~~We did not include the reflected component of PAR in our calculations as this consistently produced negative fPAR results in the dry season. Once Using fPAR was calculated, APAR was~~ calculated for overstory, understory and ecosystem by multiplying the respective fPAR with available incoming PAR (note: this was PAR_{AGD} for the understory).

2.6 Leaf area index and biomass measurements

Variability of vegetation LAI and biomass over time is a direct result of phenology and productivity. We collected overstory LAI on each site visit (6 total) using digital hemispheric photography from a Canon digital single lens reflex (DSLR) camera (Rebel T1i) with a 185 ° super fisheye FOV (f/5.6)

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lens. The images were taken around a one-hectare plot ($n = 36$, Fig. 1) and analysed using WinScanopy (v2014a). A clumping coefficient was calculated to account for foliage clumping in the LAI estimate, which was verified using a Tracing Radiation and Architecture of Canopies (TRAC) instrument. These techniques agreed within 10-15 % of each other (0.82 to 0.94 in the wet season, 0.61 to 0.67 in the dry season). Understory biomass below 2 m in height was collected from 20 replicate 1 x 1 m quadrats along a N-S and E-W 100 m transect (10 samples each, every 5 m) over a full growing season (Dec-Apr, 4 total). Samples were separated into grass and other green biomass, weighed, then oven dried at 80 °C for 3 days to obtain dry weight. Following Chen et al. (2003), we converted the dry weight biomass into carbon content assuming it to be 43 % of grass biomass and 49 % of other green biomass.

~~The variability over time of vegetation LAI and biomass is a direct result of phenology and productivity. We collected overstory LAI on each site visit (6 total) and understory biomass samples spanning a full growing season (Dec-Apr, 4 total) to investigate how these variables changed alongside the flux and phenocam data. We used digital hemispheric photography to record overstory LAI using a Canon digital single lens reflex (DSLR) camera (Rebel T1i) with a 185 ° super fisheye FOV (f/5.6) lens attached. A one hectare plot was established around the central ecosystem flux tower and LAI measurements were recorded every 20 m within it ($n = 36$, Fig. 1). These images were analysed using WinScanopy (v2014a), where a clumping coefficient was calculated to account for foliage clumping in the LAI estimate. A Tracing Radiation and Architecture of Canopies (TRAC) instrument was used to verify the WinScanopy clumping index parameter, which agreed within 10-15 % of each other (0.82 to 0.94 in the wet season, 0.61 to 0.67 in the dry season) and gave us confidence in the hemispheric LAI estimates.~~

~~A Tracing Radiation and Architecture of Canopies (TRAC) instrument was used to verify the WinScanopy clumping index parameter, which agreed within 10-15 % of each other (0.82 to 0.94 in the wet season, 0.61 to 0.67 in the dry season) and gave us confidence in the hemispheric LAI estimates. Understory biomass below 2 m in height was collected from 20 replicate 1 x 1 m quadrats along a N-S and E-W 100 m transect (10 samples each, every 5 m) and separated in the lab into grass and other green biomass, weighed, then oven dried at 80 °C for 3 days to obtain a dry weight. The exact distance of sampling along each transect was altered by 1 m for each site visit to avoid biasing from the previous sampling period. Following the technique used by Chen et al. (2003), we converted the dry weight biomass into carbon content assuming it to be 43 % of grass biomass and 49 % of other green biomass.~~

2.7.5 Light use efficiency (LUE) models and incorporation of phenology

An alternative to estimating GPP from flux towers is to use a LUE model, where GPP is approximated by relating plant productivity to the amount of light they absorb over a growing season (Monteith, 1972). The MODIS GPP product (MOD17 A2.055/A3) is calculated using a LUE model (Eq. (6), Running and Zhao, 2015), which we use in this study, as it has been previously validated for Australian savannas (Kanniah et al., 2009):

$$GPP = APAR \times LUE_p \times T_{MINscalar} \times VPDscalar \quad (6)$$

where GPP is in $g\ C\ m^{-2}\ d^{-1}$, APAR is in $MJ\ d^{-1}$ and LUE_{maxp} is the general maximum peak light use efficiency during the wet season in $g\ C\ MJ^{-1}\ PAR^{-1}$. Because C_3 (trees) and C_4 (grasses) plants have different maximum LUE rates (Zhu et al., 2008), we calculated overstory and understory LUE_{maxp} separately following a similar approach to Kanniah et al. (2009) and Coops et al. (2007), where LUE is firstly calculated as $GPP/APAR$ and is then binned by month to obtain monthly LUE. We chose to use the months of Dec-Mar (inclusive) to provide an estimate of LUE_{maxp} for the overstory and understory, as these months ($n = 8$, across two years) have the least environmental constraints to productivity and should be close to the maximum. This gave us a LUE_{maxp} value of $1.49 \pm 0.06\ g\ C\ MJ^{-1}\ PAR^{-1}$ for the ecosystem, $1.22 \pm 0.03\ g\ C\ MJ^{-1}\ PAR^{-1}$ for the overstory and $2.41 \pm 0.23\ g\ C\ MJ^{-1}\ PAR^{-1}$ for the understory (Fig. 3). In the LUE model the LUE_{maxp} values are then down regulated on a daily basis using the $VPDscalar$ Eq. (7) and $T_{MINscalar}$ (values between 0 and 1) Eq. (8) (Running and Zhao, 2015):

$$VPDscalar = (VPD_{max} - VPD_d) / (VPD_{max} - VPD_{min}) \quad (7)$$

$$T_{MINscalar} = (T_{MIN} - T_{MINmin}) / (T_{MINmax} - T_{MINmin}) \quad (8)$$

where T_{MIN} is the minimum daily temperature for a given day, T_{MINmax} is the minimum daily temperature when LUE is at maximum and T_{MINmin} is the minimum daily temperature when LUE is 0, all of which are output in $^{\circ}C$. Likewise, VPD_d is the mean daytime VPD, VPD_{max} is the maximum VPD when LUE is 0, and VPD_{min} is the minimum VPD when LUE is at maximum, all output in Pa. These scalar values fall between the range of 0 – 1. The MOD17 GPP algorithm uses values of $-8\ ^{\circ}C$ for T_{MINmin} , $11.39\ ^{\circ}C$ for T_{MINmax} , $650\ Pa$ for VPD_{min} and $3500\ Pa$ for VPD_{max} for savannas (Running and Zhao, 2015). These values were validated for Howard Springs by Kanniah et al. (2009), so we also used them in our study, so we also used these values for Howard Springs.

The use of a soil moisture term, evaporative fraction (EF), has been argued to represent plant available moisture more reliably than VPD (Gentine et al., 2007; Yuan et al., 2007; Kanniah et al., 2009). This term is simply a fractional estimate of latent heat (LE) divided by the sum of sensible heat (H) and LE (i.e. $LE / (LE + H)$). We also used the EF term in this study to test if and how it improved

the estimation of overstory, understory and ecosystem GPP. For the overstory and ecosystem, we calculated EF using the ecosystem flux tower, whereas for the understory we calculated EF using the understory flux tower.

Another technique we tested for improving GPP estimates from the LUE model was to input phenocam greenness indices, as they have been found to correlate with ecosystem productivity in northern hemisphere forests and grasslands (Richardson et al., 2009b; Migliavacca et al., 2011; Filippa et al., 2016). We hypothesised that inclusion of GCC in the LUE model would improve the model's ability to predict savanna overstory and understory GPP, particularly given the strong phenology cycles displayed in savannas. As GCC is a fractional measure, like that of fPAR, we substituted GCC as a proxy for fPAR using the coefficients of a regression to normalise it, a similar approach to that used by Migliavacca et al. (2011). As a result, Eq. 6 was transformed to include $PAR \cdot (mGCC + c)$ in place of APAR, where m and c are the linear regression coefficients.

We repeated the above technique using MODIS EVI (Huete et al., 2002), to test if satellite indices could be used to improve estimates of ecosystem scale GPP. We chose the EVI product (MOD13Q1.005) as it has been shown to function well for identifying broad-scale phenology in Australian savannas (Ma et al., 2013; Ma et al., 2014). A 3 x 3 pixel cut out of EVI data surrounding the Howard Springs site, at 16-day and 250 m resolution, was processed in DINGO accepting the quality flags 00 (highest overall quality) and 01 (good quality) only. The 16-day data were then interpolated and smoothed, using a Savitzky-Golay technique (Savitzky and Golay, 1964) in DINGO, to create a daily time series of EVI (Beringer et al., 2016b). Daily EVI were regressed against site-based daily ecosystem fPAR and the regression was used along with incoming PAR to replace APAR in Eq. (6) ~~to estimate ecosystem GPP~~.

Finally, to test the performance of each model against tower GPP estimates, we used a Pearson correlation to provide a closeness of fit estimate (Corr) and test if the relationship was statistically significant ($p < 0.05$). We also calculated the root mean squared error (RMSE) to provide a measure of the difference between the two datasets (tower and model) and the relative predictive error (RPE) to represent the percentage difference ~~and between them, plus the~~ degree of over- (+) or under- (-) estimation ~~↔~~ of the model.

3 Results & Discussion

3.1 Phenological insights from phenocams

~~Extraction of the chromatic coordinates and excess~~ The phenocam indexes revealed expected patterns from overstory and understory vegetation over time, showing that the cameras functioned well as phenology monitors of vegetation ~~greenness~~ at the ecosystem and ~~individual~~ species level (Fig. 4, 5 &

6). Not surprisingly, both GCC and ExG were ~~at their~~ highest in the understory during the wet season and ~~gradually declined to their~~ lowest values by the late dry season (i.e. September, Fig. 4). The RCC and ExR indices showed an inverse relationship to GCC and ExG, which is ~~usually~~ symptomatic of increased red pigmentation ~~due to~~ senescing leaves and chlorophyll loss (Hoch et al., 2001; Lee et al., 2003; Wingate et al., 2015). This relationship is shown by the red-green index crossover in the understory that coincides with grass senescence and signals the end of the wet season (i.e. Mar/Apr, see Fig. 4) along with an increase in the red kandosol soil background showing through with the loss of understory biomass. At the beginning of the wet season (Oct to Nov), the red-green crossover does not occur as quickly compared with the end of the wet season (Fig. 4). Several rainfall events in November (Fig. 4, Fig. 5 for rainfall) are required to reach the crossover, which is indicative of the vegetation response to the onset of the rainy season (i.e. grasses need time to germinate). Peak GCC and ExG are not reached until February (Fig. 4), the period of highest productivity for total understory biomass (Table 1).

~~However, in this case, the crossover is likely the combined result of grass senescence (loss of green) and an increase in the red kandosol soil background showing through with the loss of understory biomass.~~

~~A different story is depicted at the beginning of the wet season (Oct/Nov), whereby the red-green crossover does not occur as quickly as it does at the end of the wet season (Fig. 4).~~

~~Here it occurs after several rainfall episodes in November (Fig. 4, Fig. 5 for rainfall). This is due to the time needed for the vegetation, particularly the grasses, to respond to the onset of the rainy season, as October and November are typically build up months where convective storms deliver rain in single events before the onset of the more consistent monsoonal rain in December (Cook and Heerdegen, 2001). Peak GCC and ExG are not reached until February (Fig. 4), which is also reflected in results from the biomass harvest (Table 1) that shows the mid wet season (February) to be the period of highest productivity for total understory biomass.~~

The understory ~~consists of~~ is a mix of annual (*S. intrans*) and perennial (*S. plumosum* & *H. triticeous*) grasses, ~~saplings of~~ overstory (*E. tetradonta* & *E. miniata*) and mid-story (*E. chlorosyachys*, *T. ferdinandiana* & *B. obovata*) ~~species saplings,~~ and cycads (*C. armstrongii*), that all have differing phenologies (Bowman and Prior, 2005). The ~~behaviour dynamic nature~~ of these phenological guilds is reflected in the temporal patterns of GCC and ExG between grasses and the non-grass woody elements (herein ~~referred to as~~ 'woody green') ~~and provides additional insight into the dynamic nature of understory savanna phenology~~ (Fig. 5). While grasses are ~~considered~~ the most abundant ~~of~~ the understory species in terms of biomass (Table 1) and LAI at Howard Springs (Hutley et al., 2000), they are only active during the wet season ~~months~~ (Andrew and Mott, 1983; Scott et al., 2010). During ~~both the early wet (October/November) and dry season (April/May) seasons, and after the first rains~~

~~of the wet season (October/November),~~ the woody green species take advantage of the lack of grass to gain biomass (Werner and Franklin, 2010; Werner and Prior, 2013).

Annual grasses typically germinate after the first 15 mm or more of rainfall, with further rainfall events required to drive leaf growth (Andrew and Mott, 1983; Cook et al., 2002). Pre-monsoonal rainfall is highly variable in ~~terms of~~ its timing and amount, therefore this phenological strategy may minimise ~~the possibility of~~ grass mortality if dry periods proceed an initial early wet season rainfall event (Moore et al., 2016b). In Fig. 5, this delay in grass greening is evident, with rapid increases in GCC ~~only~~ occurring ~~approximately a one~~ month after the first rainfall event (Fig. 5, Oct-Dec 2013). ~~Such detailed analysis of the P~~phenocam data can ~~therefore~~ tease apart composite greening signals to better understand phenological dynamics and fluxes in these ecosystems (Fig. 5 & 7). ~~Results from~~ ~~U~~nderstory biomass ~~harvests data~~ also support the GCC results, revealing that as the wet season progressed, ~~the~~ grasses ~~biomass~~ increased in dominance to account for 77 % of understory biomass by the end of the wet season (Table 1). ~~This shows that w~~While the grasses are the primary driver of understory biomass and productivity, the woody green species also make important contributions throughout the year and are likely the reason why understory GPP does not completely cease in the dry season (Moore et al., 2016a).

In contrast to the understory, ~~the~~ overstory GCC and ExG did not fluctuate much in comparison to their red and blue channel indices (Fig. 6, a). This is mostly due to the high portion of blue sky and cloud within the ROI's for the overstory images (Fig. 2, e & f), which vary depending on daily weather conditions.

However, application of a sky threshold, calculated from a sky-only ROI, improved the seasonal pattern seen in overstory GCC (see supplementary material) and contributed to removing the influence of sky pixels on the GCC calculation. These values also agreed with changes in overstory LAI (Fig. 6, b). A larger ROI was necessary for the overstory analysis due to the daily movement of trees. While there is inherent uncertainty in both the phenocam imagery (i.e. FOV, scene illumination) and LAI (i.e. leaf projection and orientation, clumping, gaps, see Ryu et al. (2010)) estimates in this study, the savanna overstory is known to experience seasonal fluctuations in LAI with the highest values in the wet season and lowest values in the late dry season (Williams et al., 1997; O'Grady et al., 2000). The same pattern is displayed in Fig. 6, giving us confidence that the phenocams were able to detect overstory cover change.

The effect on BCC/ExB is particularly strong during the wet season, where the summer monsoon varies sky conditions considerably between bright blue sky and dull grey cloud. Due to the narrow FOV and upward orientation of the overstory cameras, the trees were prone to moving in and out of smaller ROI tested (data not shown), so a larger ROI was chosen to ensure tree foliage was always present in the image, but at the cost of including a greater sky portion (Fig. 2, e & f). Nevertheless,

when viewed in isolation from the red and blue indices, temporal variation was apparent in overstory GCC and ExG, which captured variability in greenness and were consistent with changes in overstory LAI (Fig. 6, b). While there is inherent uncertainty in both the phenocam imagery (i.e. FOV, scene illumination) and LAI (i.e. leaf projection and orientation, clumping, gaps, see Ryu et al. (2010)) estimates in this study, the savanna overstory is known to experience seasonal fluctuations in LAI with the highest values in the wet season and lowest values in the late dry season (Williams et al., 1997; O'Grady et al., 2000). The same pattern is displayed in Fig. 6, giving us confidence that the phenocams were able to detect overstory cover change, despite their limitations in setup and image collection.

Nevertheless, when viewed in isolation from the red and blue indices, temporal variation was apparent in overstory GCC and ExG. These indices captured the variability in greenness and were consistent with changes in overstory LAI when compared with adhoc hemispherical LAI measurements (Fig. 6, b). While there is inherent uncertainty in both the phenocam imagery (i.e. FOV, scene illumination) and LAI (i.e. leaf projection and orientation, clumping, gaps, see Ryu et al. (2010)) estimates in this study, the savanna tree canopy is known to experience seasonal fluctuations in LAI with the highest values in the wet season and lowest values in the late dry season (Williams et al., 1997; O'Grady et al., 2000). The same general pattern is displayed in Fig. 6, giving us confidence that the phenocams are able to detect overstory cover change, despite their limitations in setup and image collection.

3.2 Phenocam and MODIS phenology in relation to GPP Integrating phenocam and MODIS phenology with GPP

The seasonality of GPP in these savannas has been found to differ between that of the overstory and understory, with understory GPP tied more closely to the duration of the wet season than that of the overstory (Moore et al., 2016a). The GCC and ExG time series approximated appeared to capture the overstory and understory GPP estimates well (Fig. 7), and so we hypothesised that they could be useful for independently predicting overstory and understory GPP. Simple linear regressions of GCC against flux tower GPP quantified the relationship between the two variables, with understory GPP ($r^2 = 0.65$) revealing a closer fit with GCC than overstory GPP ($r^2 = 0.2322$, Fig. 7). The ExG index did not perform so well compared with GCC for the overstory ($r^2 = 0.09$) but improved the relationship slightly against GCC for the understory ($r^2 = 0.729$, Fig. 7). ExG was originally developed for identifying green vegetation from images with a soil background (Woebbecke et al., 1995). This is a likely reason for why the relationship between ExG and GPP was slightly closer to 1:1 than that of GCC for the understory.

While the relationship between overstory greenness (ExG/GCC) and GPP is not as strong as that of the understory, the phenocams are still able to detect seasonality in greenness that follows GPP over

time (Fig. 7). The trees have a deeper rooting structure than the grasses, allowing them to access a larger volume of soil moisture (Eamus et al., 2002;Kelley et al., 2007) and thus maintain constant overstory transpiration throughout the year (O'Grady et al., 1999;Hutley et al., 2000). While the tree canopy is largely evergreen, the LAI will drop up to 30-40 % in order to account for the dry season water deficit (O'Grady et al., 2000;Whitley et al., 2011), which is also apparent from both our overstory LAI and GCC results (Fig. 6). Tree productivity, in contrast to transpiration, is known to decrease into the dry season (Eamus et al., 1999), and most carbon uptake is directed toward maintenance respiration rather than growth (Chen et al., 2002;Prior et al., 2004;Cernusak et al., 2006). However, the occurrence of late wet season rainfall events may benefit the productive capacity of the trees by boosting soil moisture stores, thereby supporting higher rates of productivity for longer in the dry season (Moore et al., 2016a). This effect is apparent in our overstory GCC time series, where after late April to early May rainfall events (see Fig. 5 for daily rainfall), GCC spikes in June indicate a flushing of the foliage in the dry season (Fig. 6, b).

At the ecosystem scale, the interaction of the overstory and understory with the wet and dry seasons drives variability in productivity. The MODIS greenness index, EVI, mostly captures this variability, albeit at coarser temporal resolution (Fig. 7, e) when compared with the phenocams. While the broad scale variability in savanna phenology change is captured by EVI, such as seasonality (Ma et al., 2013), it is not able to capture the finer scale details that the site based phenocams can. MODIS indices, such as EVI, do not currently have the ability to identify individual plant scale phenology patterns (Brown et al., 2016;Moore et al., 2016c), which is another advantage of the phenocam (Fig. 5). The phenocam data also provides a useful means of validating the MODIS data in that both are able to track the seasonality of savanna GPP, which is driven by a complex interaction of both meteorology and phenology (Kanniah et al., 2011;Whitley et al., 2011;Ma et al., 2013;Ma et al., 2014).

3.3 Integrating phenocam and MODIS phenology with a LUE model

~~In order to test the applicability of the phenocam indices and MODIS EVI to independently predict savanna GPP using a LUE model, peak LUE (i.e. LUE_p) needed to be calculated for the ecosystem, overstory and understory. The calculated LUE_p value~~ To use greenness phenology information for predicting GPP from the LUE model, an estimate of maximal LUE was calculated, which was higher for the understory (~~3.452 ± 0.4123~~ $g\ C\ MJ^{-1}\ PAR^{-1}$) compared to the overstory (~~1.4322 ± 0.063~~ $g\ C\ MJ^{-1}\ PAR^{-1}$, Fig. 3). The higher LUE_{maxp} for the understory is largely due to the dominance of C_4 grasses in the understory (Table 1), as their C_4 photosynthetic pathway is more energy efficient (Sage, 2004;Osborne and Beerling, 2006;Zhu et al., 2008). Our values fell within the range of LUE_{maxp} reported for African savannas, which have varied from as low as $0.33\ g\ C\ MJ^{-1}\ PAR^{-1}$ up to $3.5\ g\ C\ MJ^{-1}\ PAR^{-1}$ depending on the vegetation and season (Sjöström et al., 2013;Tagesson et al., 2015). Recent work has shown the importance of correctly applying LUE_{maxp} values to C_3 and C_4 plants

when using LUE models to calculate GPP (Yan et al., 2015). Therefore, to account for the C₃:C₄ differences, we applied these site and trait specific values to the LUE model used to estimate GPP.

The next step in our parameterisation of the LUE model was to test it in its traditional form; using the meteorological inputs of T_{MIN} and VPD that constrain LUE_{maxp}, along with APAR (Eq. 6). We found the model captured most of the seasonality of overstory GPP but underestimated the magnitude of GPP in the dry season and overestimated GPP in the wet season (Table 2, Fig. 8, a). For the understory, the LUE model appeared to overestimate and lag flux tower GPP consistently by 1-2 months (Table 2, Fig. 9, a). This resulted in a strong dry season over estimate of understory GPP (165.59 %, Table 2). For the ecosystem, the LUE model consistently overestimated GPP (Table 2, Fig. 10, a). Kanniah et al. (2009) also found the LUE model performed poorly for the Howard Springs ecosystem, so they replaced the standard VPD parameterisation with an EF term and found this to improve the relationship, which we implemented next.

Application of EF to the overstory model in this study improved its ability to predict GPP in the dry season but overestimated GPP in the wet season, causing an over prediction of annual GPP by 18 % overall (Table 2, Fig. 8, a vs. b). In contrast, the inclusion of EF in the understory LUE model slightly improved the prediction of annual GPP, with better correlation (0.6973 vs 0.567), lower RMSE (2.004.43 vs. 2.6602 g C m⁻²) and lower RPE (38.5822.27 vs. 79.6262.09 %). However, the understory model still lagged tower GPP and was still particularly poor at capturing the seasonal transitions (Fig. 9 a & b). For the ecosystem, the inclusion of EF enhanced the overestimation of GPP from 154 to 265 %, particularly in the wet season (Table 2, Fig. 10, a vs. b). EF provides a proxy measure of soil moisture as it includes a water flux component (LE) that is tightly linked with soil moisture availability (Gentine et al., 2007; Kanniah et al., 2009). In Australian savannas, soil moisture is highly seasonal and a major driver of productivity (Kanniah et al., 2010). This makes EF a useful index in the dry season, when latent heat largely comes from transpiration and is therefore tightly coupled with GPP. However, in the wet season, soil evaporation contributes a large amount to latent heat, which is not tightly coupled to GPP (Kanniah et al., 2009). This explains why EF is able to constrain the LUE model in the dry season and why it performs poorly in the wet season and transition periods.

The incorporation of phenocam GCC into the LUE model improved the estimate of understory GPP substantially (Table 2, Fig. 9, c & d). This was most apparent with the combined use of GCC and EF in the LUE model, which produced the best correlation (r = 0.865), lowest RMSE (1.420.96 g C m⁻²) and lowest RPE (39.5947.73 %, Table 2, Fig. 9). These results show that while EF is an important factor for GPP, greenness phenology is also key for estimating understory productivity. In further support of this, the inclusion of GCC also eliminated the lag in model estimated GPP, bringing the estimate closer in line with seasonal variability from the flux tower, as evidenced by the large

decrease in RMSE and RPE (Table 2, Fig. 9). As previously discussed, the understory grasses (annual species in particular) die off at the cessation of the wet season and do not contribute to the small fraction of understory GPP in the dry season (Moore et al., 2016a). This is a plant phenology response, rather than a response to meteorological conditions, as factors such as soil moisture remain high enough in the early dry season to support plant growth (Eamus et al., 2002; Kelley et al., 2007; Moore et al., 2016a). Given that these grasses dominate understory biomass at Howard Springs, it is not surprising that including greenness phenology information in the LUE model improves its output relative to the flux tower.

The inclusion of greenness indices in the LUE model for the overstory (GCC) and ecosystem (EVI) also improved the estimate of GPP. For the overstory, the combination of EF and GCC performed slightly better in the dry season than GCC alone, but was not able to capture the wet season well (Table 2, Fig. 8 d). This resulted in the incorporation of GCC into the LUE model producing the best overall result, despite the slightly lower correlation value (0.60 vs 0.72) ~~and RMSE (1.43 vs. 1.36 g C m⁻²)~~ when compared with GCC and EF combined (Table 2). For the ecosystem, the inclusion of EVI into the LUE model performed the best at predicting GPP, which was supported by the lowest values for RMSE (2.1203 g C m⁻²) and RPE (15.493.76 %, Table 2).

The greenness information clearly fills an important gap in relation to changes in overstory, understory and ecosystem greenness. The general improvement in LUE model output for overstory, understory and ecosystem with the inclusion of greenness phenology information highlights the importance of accounting for phenological variability when estimating GPP in savannas. A similar result was found for a subalpine grassland in Italy, where phenocam greenness indices improved the ability of the same LUE model to predict grassland GPP (Migliavacca et al., 2011). Likewise, in an evergreen Amazonian rainforest, Wu et al. (2016) linked phenological changes in leaf development and demography to seasonality in GPP, showing the importance of phenology as a driver of ecosystem productivity. For Australian savannas, the effect of phenology is most evident at the end of the wet season (Apr-May), where in the understory, growth ceases due to annual grass senescence even though meteorological conditions (temperature, VPD and/or EF) are still sufficient to support growth (Fig. 9 a&b vs. c&d). The original LUE model over-predicts GPP as a result of this, which is due to APAR remaining high despite the lack of green vegetation (see supplementary material). This effect is substantially reduced by the inclusion of greenness phenology indices that likely represents a type of 'green APAR' that more closely tracks the vegetation productivity over time.

~~The original LUE model over-predicts GPP as a result of this, which is substantially reduced by the inclusion of greenness phenology indices.~~

3.4 Limitations, impacts and further work

While phenocams have consistently proven to be a useful tool for phenological and productivity research (Richardson et al., 2009b; Migliavacca et al., 2011; Filippa et al., 2016; Wu et al., 2016), there still remain several limitations that require further investigation to improve their utility. Issues related to camera choice and image collection have been shown to be less problematic for simple identification of phenological transition dates and seasonal variation than first thought (Sonnentag et al., 2012), however, maintaining similar protocols for cross site comparisons remains preferable (Moore et al., 2016c). Scene illumination variability is probably the most problematic limitation of phenocams, which can be reduced by using chromatic coordinates or excess values, as well as by setting the white balance to a fixed level (Richardson et al., 2009a; Ide and Oguma, 2010; Migliavacca et al., 2011). Although white balance was not fixed for this study, we found that the GCC and ExG time series matched well with GPP estimates regardless and provided added value to that gained from using just APAR alone in the LUE model. [We suspect this is due to the highly dynamic nature of the savanna vegetation, which allows the phenology signals to be identified despite the potential for variable white balance.](#)

The wet season influence on scene illumination adds daily noise to the time series, but the indices are still useful for informing seasonal productivity estimates. This same relationship will likely not stand for other, less dynamic ecosystems in Australia (Restrepo-Coupe et al., 2015; Moore et al., 2016c), so we recommend the fixing of white balance where appropriate. The use of a grey reference panel for normalising phenocam images has also been proposed (Richardson et al., 2009a), however, this technique has issues related to panel orientation and illumination conditions that can be different to those experienced by the phenocams (Migliavacca et al., 2011). Despite these limitations, phenocams are still an important tool for both species and plot scale phenology monitoring and with further developments, will continue to provide valuable insight into Australian vegetation phenology (Moore et al., 2016c).

In addition to the phenocam issues, the light use efficiency model used in this study is also subject to limitations. This model relies on the input of meteorological information to generate an estimate of ecosystem GPP. It is often found that these models overestimate GPP in the transition periods from wet-dry or dry-wet in savanna ecosystems (Kanniah et al., 2009). The primary reason for this is that savanna GPP is not driven solely by meteorology, that plant phenology also plays an important role, as shown in our analysis. The technique for estimating LUE_{maxp} , used in the LUE model (Eq. 5), also involves a degree of uncertainty that is centred around the input parameters of LUE and APAR, as well as the scalars used to constrain it (De Bie et al., 1998; Sjöström et al., 2013).

The MODIS MOD17 A2/A3 GPP product uses a LUE_{maxp} value of 1.21 g C MJ^{-1} for savannas and 1.24 g C MJ^{-1} for woody savannas (Zhao and Running, 2010). While these values are close to the

number we calculated for the overstory (1.4326 ± 0.063 g C MJ⁻¹ PAR⁻¹), we found the understory LUE_{maxp} to be much larger (3.45244 ± 0.4123 g C MJ⁻¹ PAR⁻¹). Similarly, for African savannas, LUE_{maxp} has been found to reach up to 3.50 g C MJ⁻¹ PAR⁻¹ in the wet (growing) season (Sjöström et al., 2013; Tagesson et al., 2015). These LUE_{maxp} values are much larger than that used in the MOD17 A2/A3 algorithm, which suggests that tree-grass (C₃ vs. C₄) ratios need to be better accounted for in the LUE model. Recent work from Yan et al. (2015) has shown this to be the case, where the application of different LUE_{maxp} values to C₃ (1.8 g C MJ⁻¹ PAR⁻¹) and C₄ (2.76 g C MJ⁻¹ PAR⁻¹) plants improved global model estimates of GPP.

Finally, the flux tower estimates of GPP are not without their own limitations, as the towers measure NEE that is then partitioned into GPP and respiration most commonly by using a friction velocity (u*) threshold at night and upscaling method for the daytime (Reichstein et al., 2005; Bowman, 2000; Keith et al., 2012). Use of the u* technique has been shown to be problematic at sites with complex terrain (van Gorsel et al., 2009), where drainage flows result in horizontal loss of carbon from an ecosystem that is not accounted for by the flux instruments. While Howard Springs is a relatively flat site (slope < 1 °) that should prevent issues with using the u* technique, the flux tower estimates from this site should still be considered with an amount of uncertainty as well (Moore et al., 2016a; R Core Team, 2013). However, these issues have been addressed by previous work at this site (Moore et al., 2016a) so we have confidence in the fluxes used for this study. Despite these limitations, we were able to show that the input of phenological information into LUE models can provide a useful constraint for estimating GPP within the uncertainty limits of tower derived estimates, a similar conclusion to that found over a subalpine grassland in the Italian Alps (Migliavacca et al., 2011).

4 Conclusion

We have shown the utility of phenocams for the monitoring of tree and grass phenology in savannas and how this data can improve the quantification of productivity. Phenocams offer the ability to decipher species level phenological signals, as shown by our time series analysis of understory grasses and woody green species, as well as in the tracking of seasonal overstory leaf area change. Phenocams have also shown to be useful for improving LUE models that have traditionally failed to capture the wet-dry season transition periods well in savannas, which are characterised by phenology changes in the understory that are out of sync with meteorological variability. This approach needs to be tested in more ecosystems to determine its applicability for a wider range of ecosystem types, but promises improved results for better understanding of ecosystem GPP and phenology. Phenological information offers an important link for our understanding of ecosystem function as it provides a more accurate means of independently verifying tower derived GPP estimates in savannas. We have demonstrated that phenocams can be used in conjunction with eddy covariance flux towers to improve current

1 knowledge of savanna productivity and phenology, which will assist in our understanding of how the
2 tree-grass relationship in savannas may alter in the future.

3 **Author Contributions**

4 Field work and experimental design was executed by C. Moore, J. Beringer, L. Hutley and B. Evans.
5 Data analysis was chiefly carried out by C. Moore, with some coding assistance from B. Evans. The
6 manuscript was prepared by C. Moore with contributions from all co-authors.

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Table 1: Understory biomass harvest information for Howard Springs savanna collected across the wet seasons from 2012 to 2014.

Period	Grass biomass (t ha ⁻¹)	Other biomass (t ha ⁻¹)	Grass biomass (%)	Other biomass (%)
Start Wet – Dec	0.46	0.96	33	67
Mid Wet – Feb	1.34	1.77	43	57
Peak Wet – Mar	1.55	1.09	59	41
End Wet - Apr	1.31	0.38	77	23

Table 2: Summary of model performances against flux tower estimated GPP for overstory and understory at Howard Springs. Statistics include the Pearson Correlation coefficient (Corr), the root mean square error (RMSE, $\text{g C m}^{-2} \text{d}^{-1}$) and the relative predictive error (RPE, %) for the light use efficiency model (LUE), LUE with evaporative fraction (LUE_EF), LUE with green chromatic coordinates (LUE_GCC) and LUE with EF and GCC (LUE_EF_GCC). The * highlights that the MODIS enhanced vegetation index (EVI) is used instead of GCC for the Ecosystem analysis. Pearson p values are not included as all were significant with $P < 0.001$.

Model		Overstory			Understory			Ecosystem*		
		Corr	RMSE	RPE	Corr	RMSE	RPE	Corr	RMSE	RPE
All years	LUE	0.64	1.6445	7.50-1.79	0.567	2.6692	79.6262.09	0.80	2.184	14.823.77
	LUE_EF	0.73	1.8047	18.338.40	0.6973	2.001.43	38.5822.27	0.79	2.769	26.395.18
	LUE_GCC/EVI*	0.60	1.5643	6.39-0.85	0.8178	1.8640	80.2155.32	0.81	2.1209	15.494.85
	LUE_EF_GCC/EVI*	0.72	1.6036	16.388.44	0.865	1.420.96	39.5917.73	0.83	2.5248	26.225.51
Wet Season (15 Oct - 15 Apr)	LUE	0.61	2.001.59	24.5113.30	0.313	3.202.28	52.0030.89	0.72	2.5442	16.975.53
	LUE_EF	0.68	2.371.85	34.9322.76	0.3943	2.731.92	41.0921.60	0.66	3.3218	26.835.26
	LUE_GCC/EVI*	0.61	1.7850	22.5214.02	0.6359	2.161.43	53.8326.95	0.74	2.462	19.638.92
	LUE_EF_GCC/EVI*	0.6970	2.061.67	32.4023.13	0.676	1.9725	45.1819.33	0.71	3.1307	29.128.36
Dry Season (16 Apr – 14 Oct)	LUE	0.4037	1.2632	-10.757.97	0.564	2.091.76	165.7659.34	0.576	1.830	11.7121
	LUE_EF	0.643	1.1205	0.51-7.76	0.5248	1.050.84	30.7724.36	0.721	2.2619	25.7506
	LUE_GCC/EVI*	0.234	1.3437	-10.916.80	0.451	1.5538	162.4343.73	0.39	1.776	9.518.94
	LUE_EF_GCC/EVI*	0.567	1.063	-0.817.31	0.352	0.692	22.1712.73	0.63	1.864	22.011.38

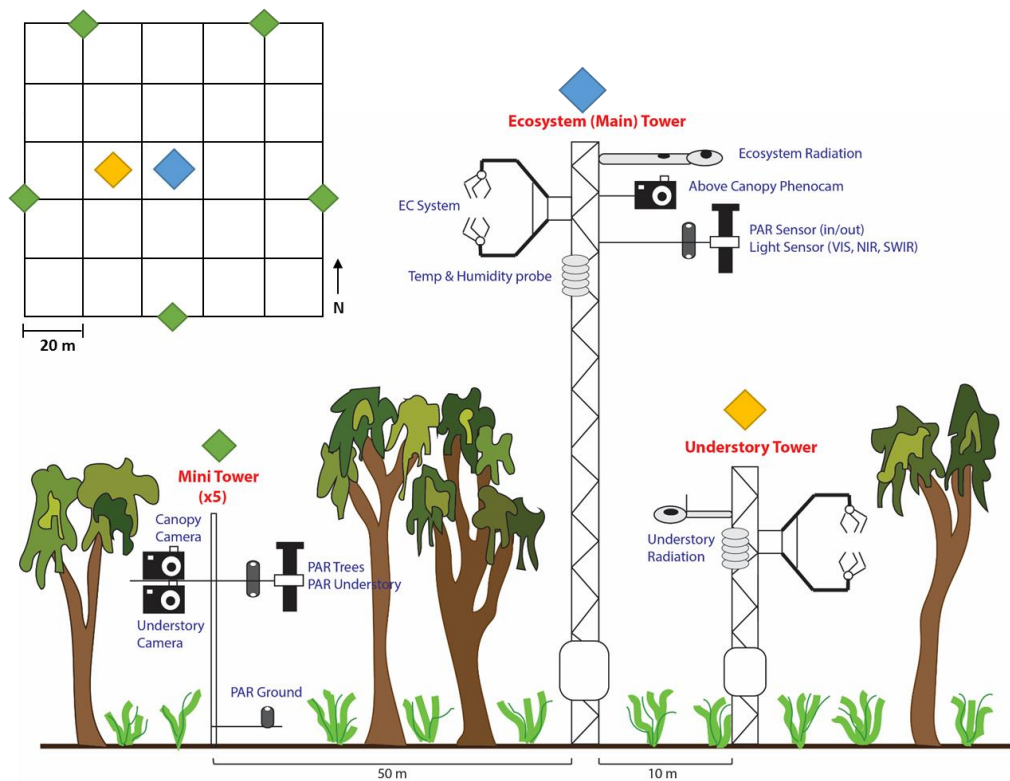


Figure 1: Diagram showing the core instrumentation supported by each flux tower and mini tower at the Howard Springs OzFlux site, as well as the layout of the monitoring plot.

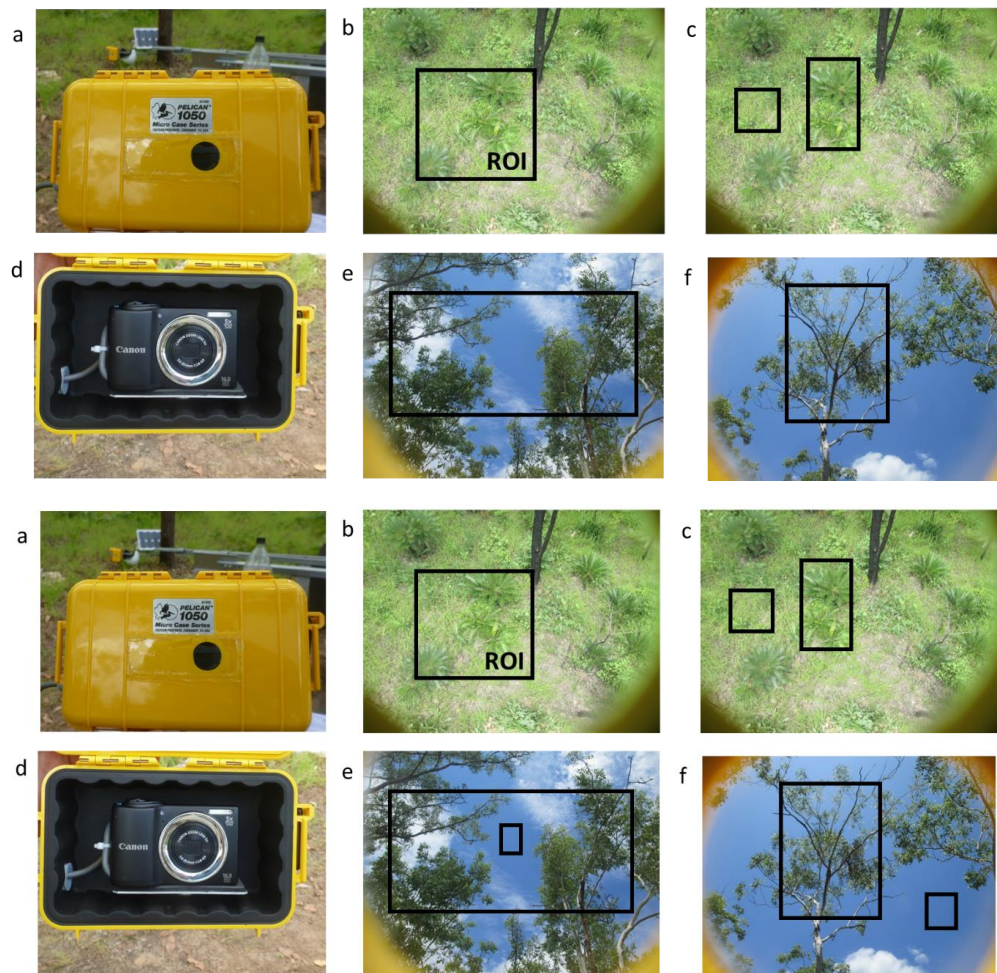


Figure 2: Camera setup (a & d) and examples of understory (b & c) and overstory (e & f) regions of interest (ROI, black box) used from phenocam images collected at the Howard Springs OzFlux site.

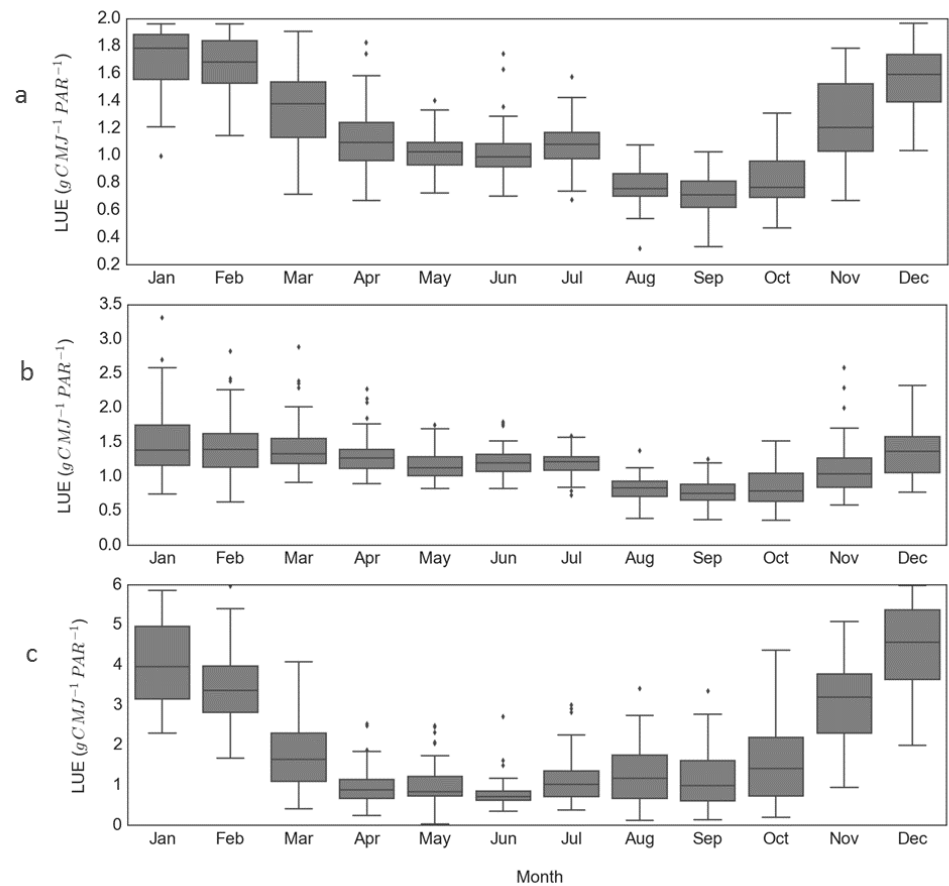
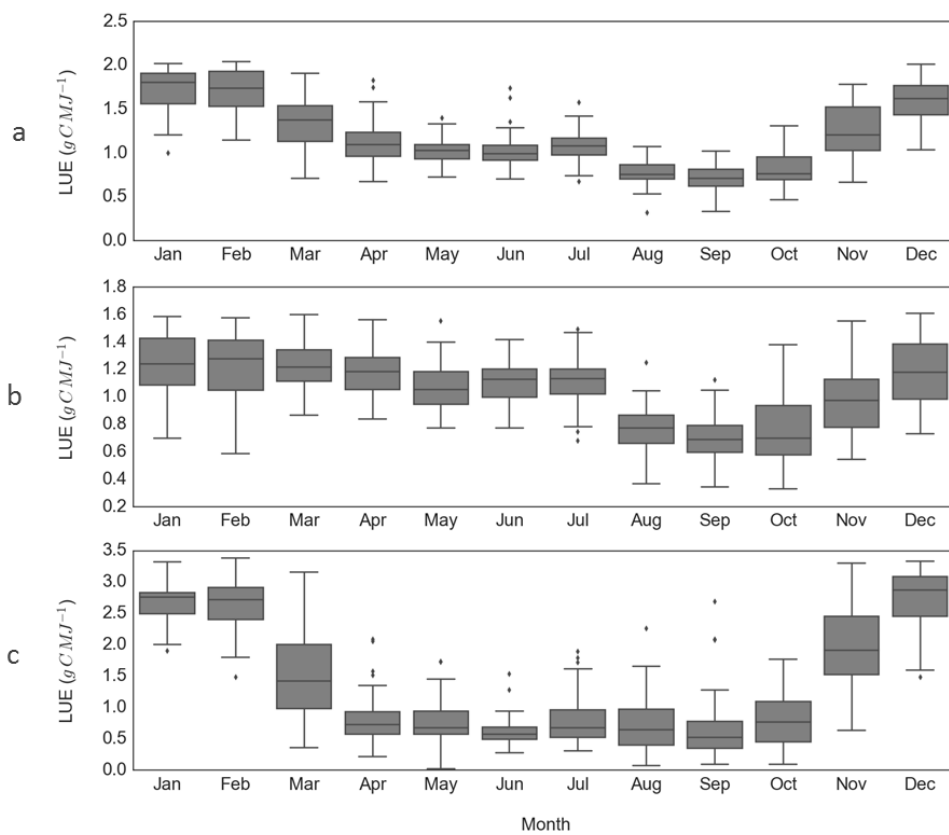


Figure 3: Monthly mean light use efficiency (LUE) \pm SE (boxes) with 95 % confidence (whiskers) for the Howard Springs OzFlux site ecosystem (a), overstory (b) and understory (c) from December 2012 to October 2014. Individual dots represent outlier values for each respective month.

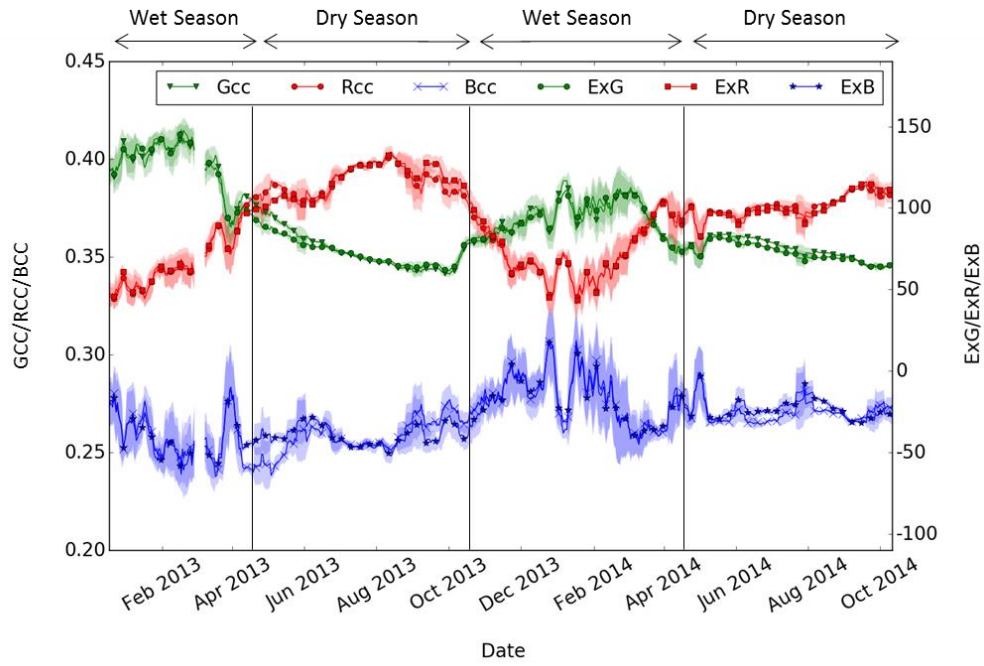


Figure 4: Daily green, red and blue chromatic coordinates (GCC/RCC/BCC) and excess indices (ExG/ExR/ExB) for the Howard Springs OzFlux site understory from December 2012 to October 2014. Daily data are shown with an 8-day centred running mean (marked every 8 days for visualisation) applied. The standard error of the mean is given by the shading.

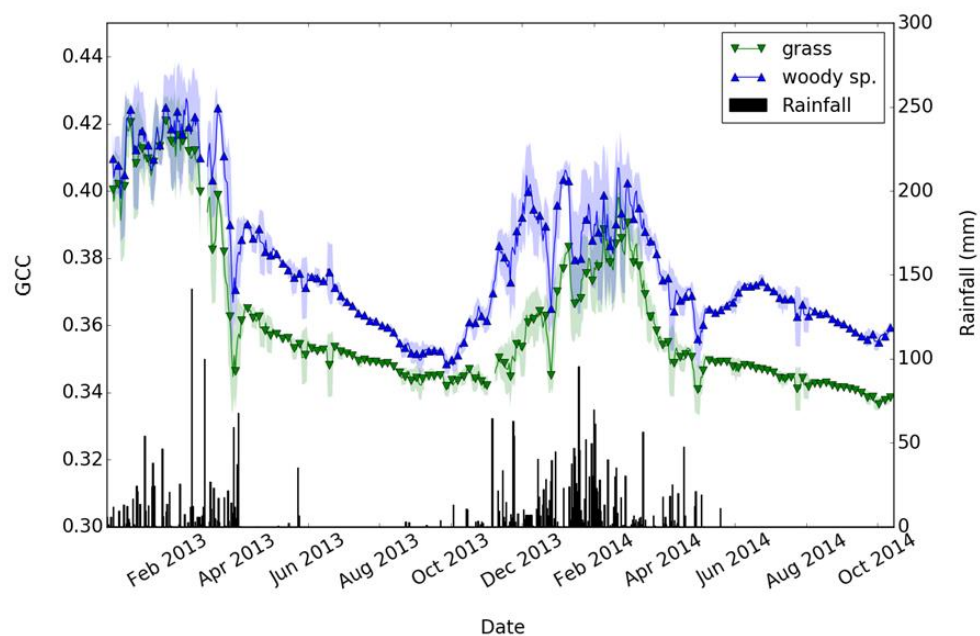


Figure 5: Daily rainfall (mm) and green chromatic coordinate (GCC) time series for grass and other woody green species (woody sp.) found in the savanna understory at the Howard Springs OzFlux site from December 2012 to October 2014. The GCC daily data are shown with an 8-day centred running mean (marked every 8 days for visualisation) applied. The standard error of the mean is given by the shading. The GCC time series represent the change in relative greenness of grass and woody species, not the absolute sum of grass versus woody species biomass in the understory.

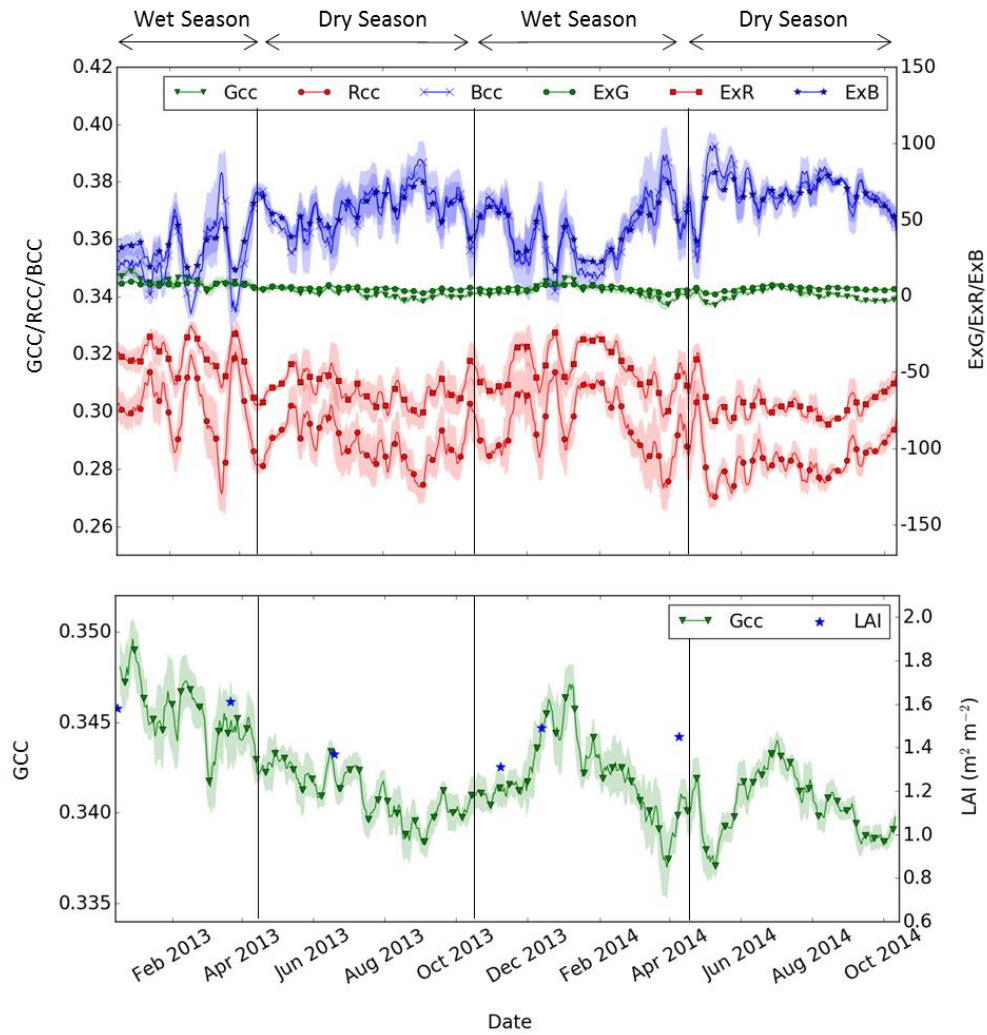
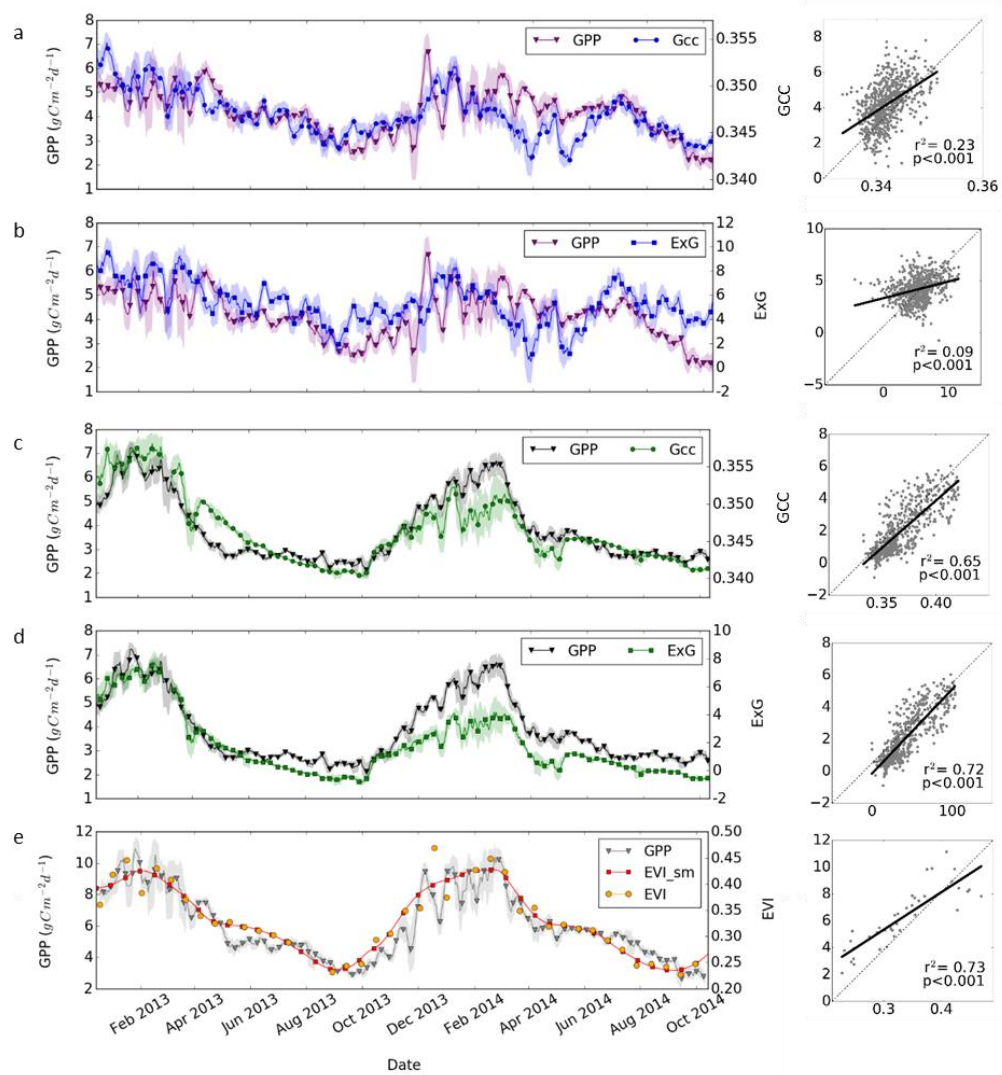


Figure 6: Daily green, red and blue chromatic coordinates (GCC/RCC/BCC) and excess indices (ExG/ExR/ExB) for the Howard Springs OzFlux site overstory (a), plus GCC and leaf area index (LAI) for the overstory (b) from December 2012 to October 2014. Daily data are shown with an 8-day centred running mean (marked every 8 days for visualisation) applied. The standard error of the mean is given by the shading.



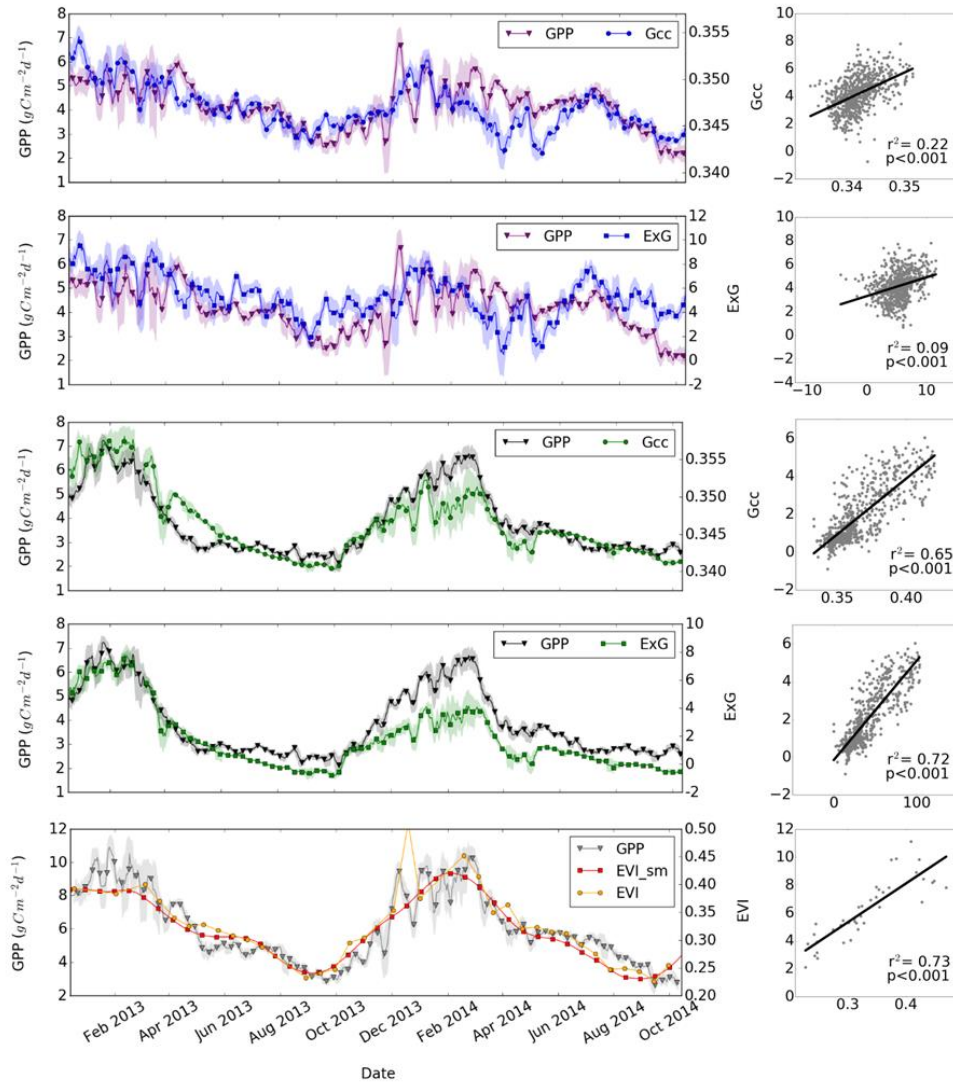


Figure 7: Overstory (a & b) and understory (c & d) flux tower GPP with green chromatic coordinate (GCC) and excess green (ExG) indices, as well as ecosystem flux tower GPP with MODIS enhanced vegetation index (EVI, e), from December 2012 to October 2014 at the Howard Springs OzFlux site. Daily data are shown with an 8-day running mean (marked every 8 days for visualisation) applied. The standard error of the mean is given by the shading. Included for each time series are the respective regression plots showing r^2 and p values for GCC/ExG/EVI (x) against flux tower GPP (y). For MODIS EVI (e) the time series plot includes raw 16 day values (EVI) and a Savitzky-Golay smoothed daily EVI product (EVI_sm), with the regression plot showing the raw 16 day EVI and the corresponding GPP for that day.

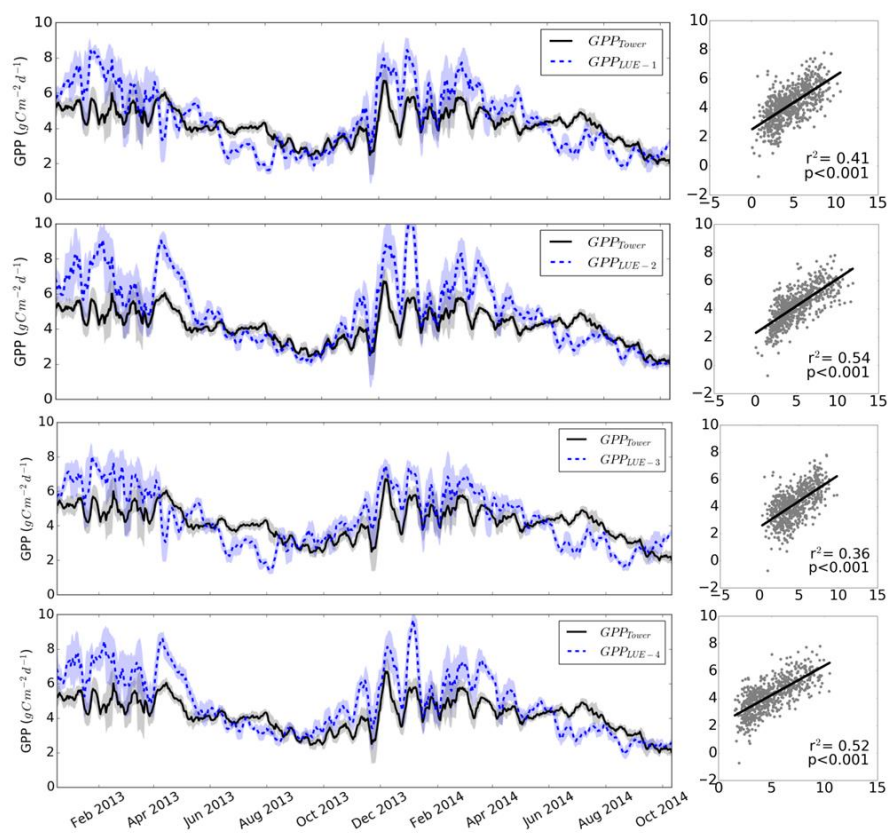
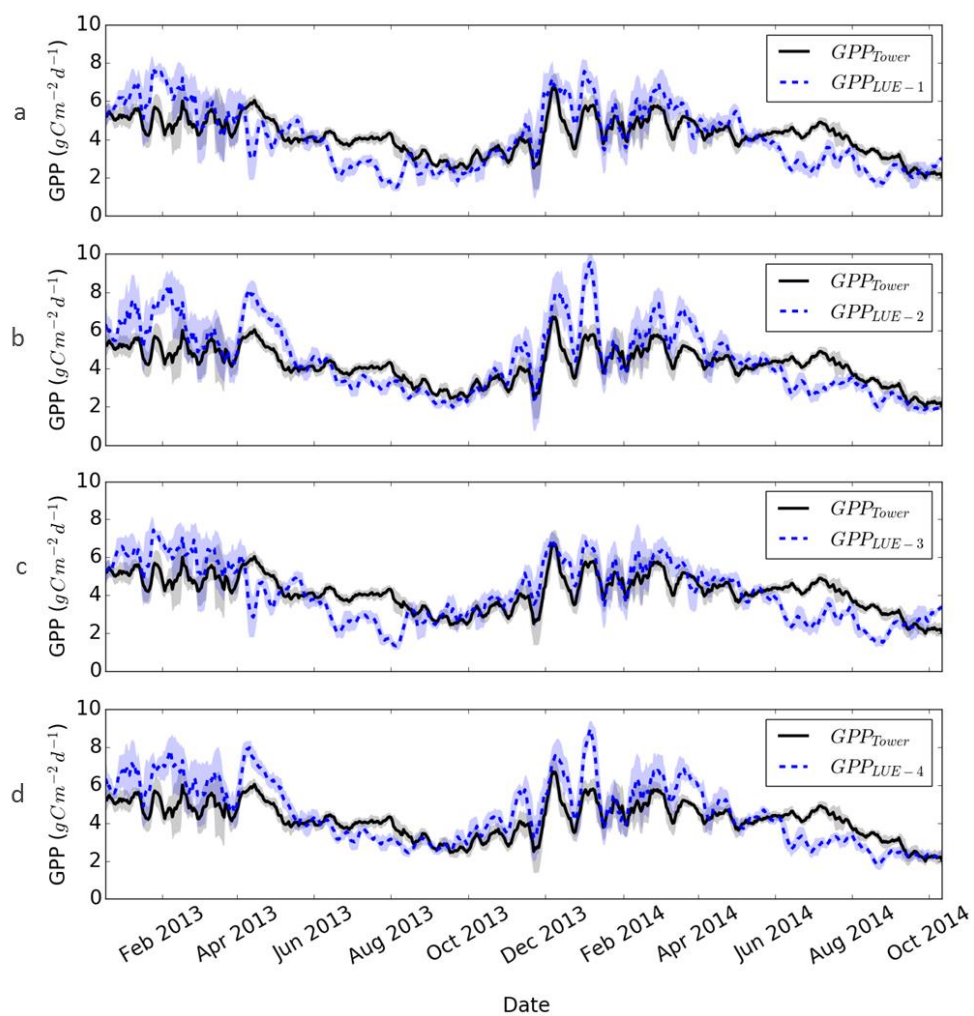


Figure 8: Overstory flux tower estimated GPP with model predicted GPP for the Howard Springs OzFlux site. Models shown are a) light use efficiency (LUE-1), b) LUE with evaporative fraction (LUE-2), c) LUE with green chromatic coordinates (LUE-3), d) and LUE with EF and GCC (LUE-4).

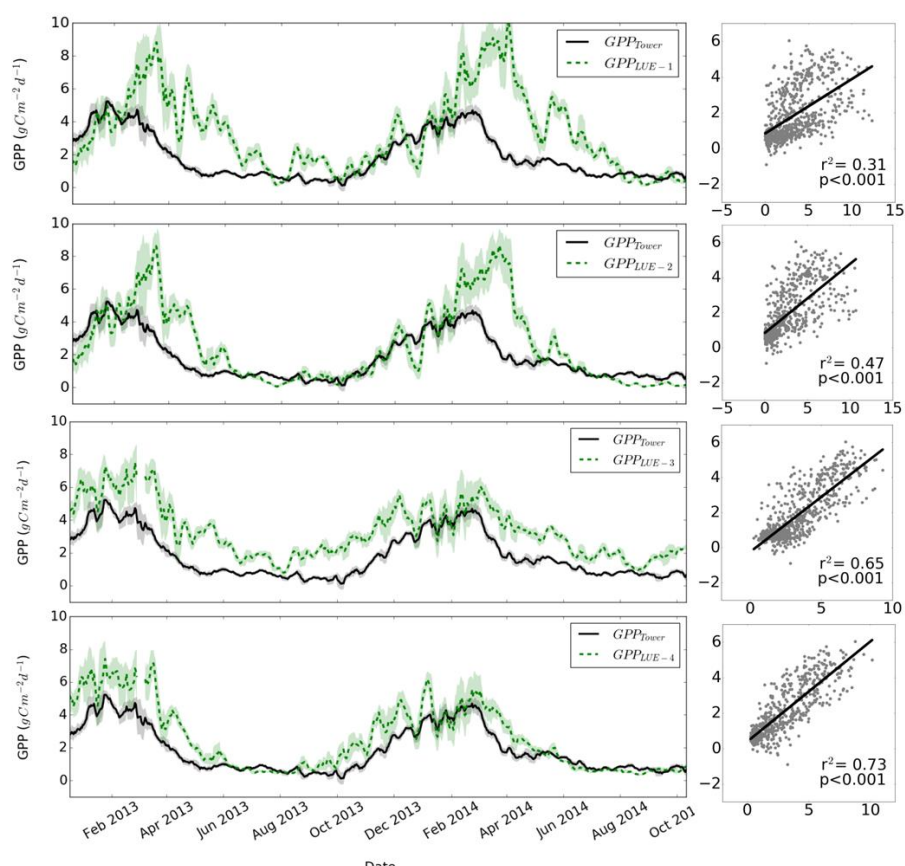
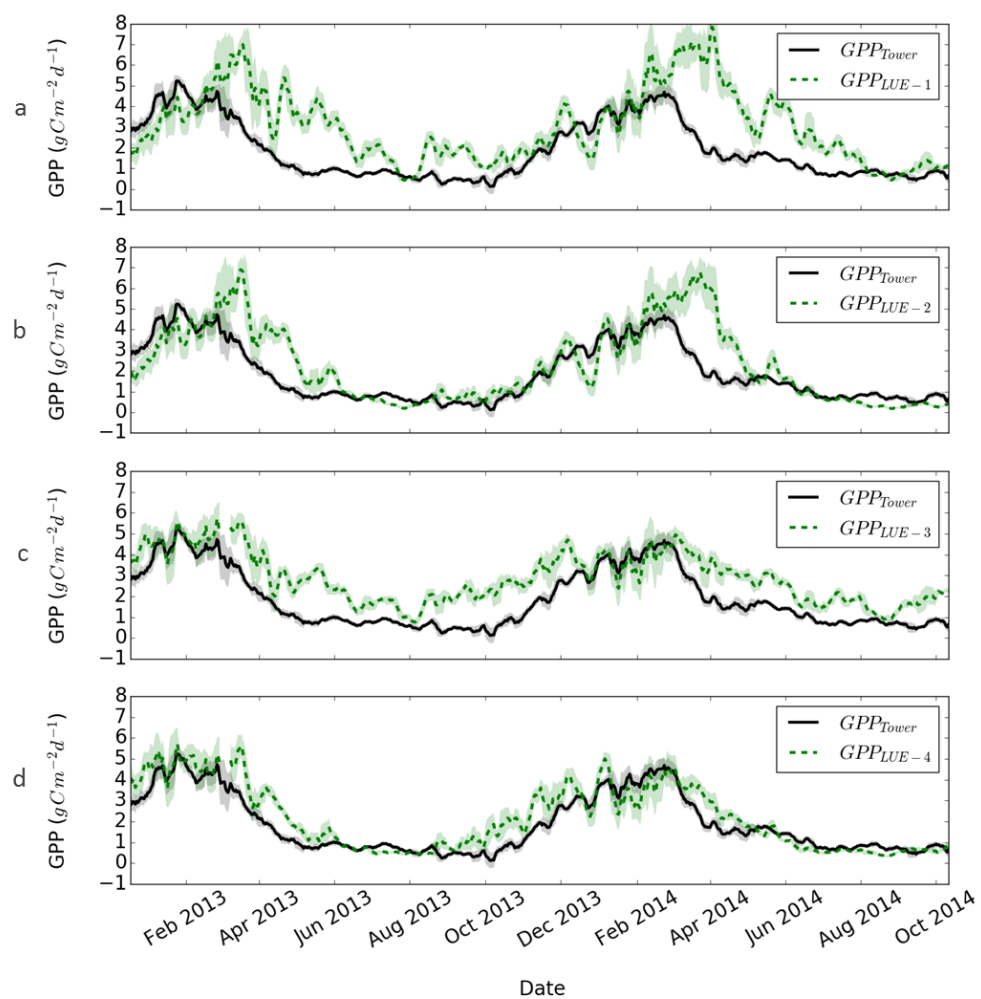


Figure 9: Understory flux tower estimated GPP with model predicted GPP for the Howard Springs OzFlux site. Models shown are a) light use efficiency (LUE-1), b) LUE with evaporative fraction (LUE-2), c) LUE with green chromatic coordinates (LUE-3), d) and LUE with EF and GCC (LUE-4).

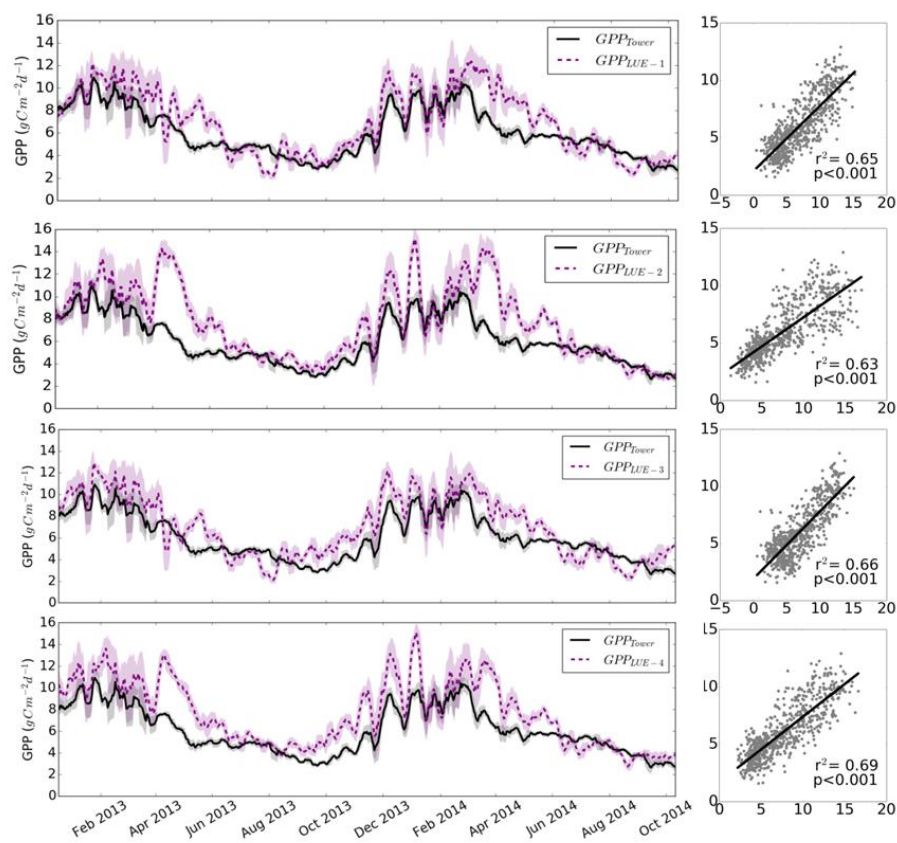
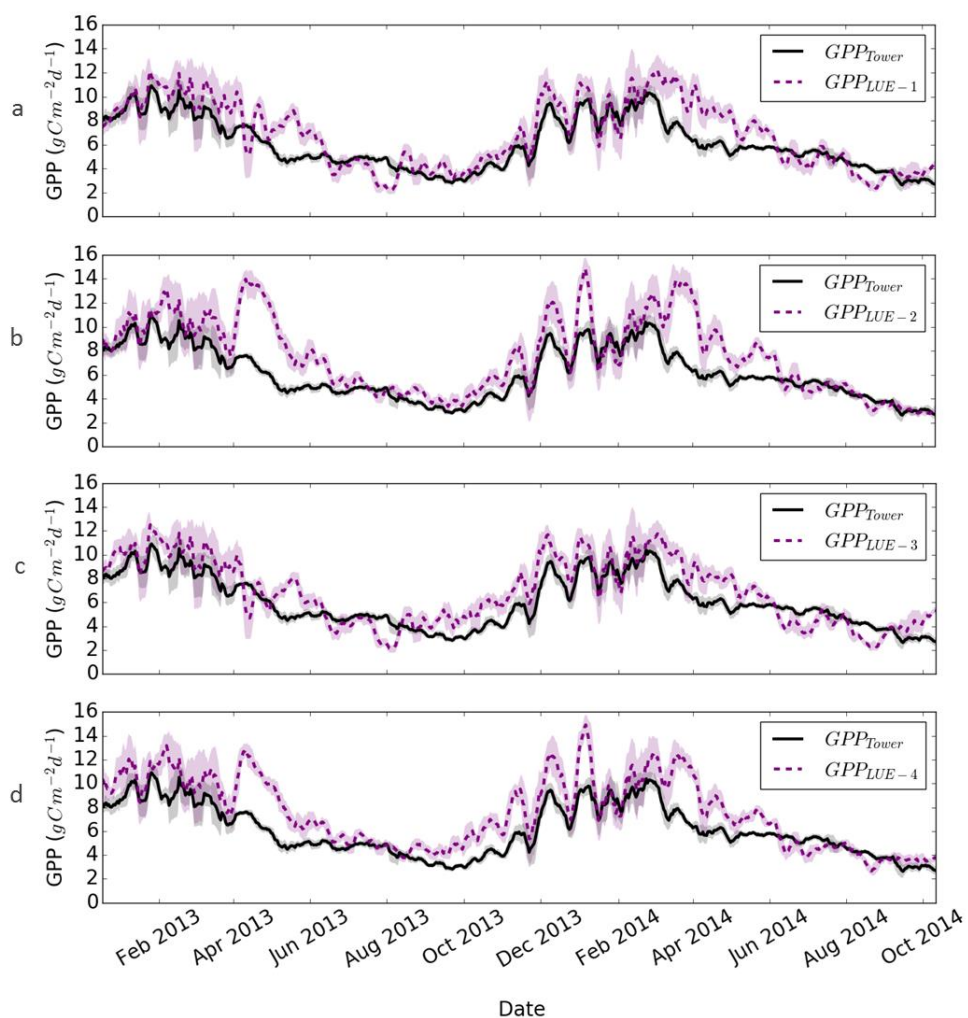


Figure 10: Ecosystem flux tower estimated GPP with model predicted GPP for the Howard Springs OzFlux site. Models shown are a) light use efficiency (LUE-1), b) LUE with evaporative fraction (EF, LUE-2), c) LUE with MODIS enhanced vegetation index (EVI, LUE-3), d) and LUE with EF and EVI (LUE-4).