

Unravelling the physical and physiological basis for the solar-induced chlorophyll fluorescence and photosynthesis relationship using continuous leaf and canopy measurements of a corn crop

Response to editor's and reviewers' comments

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Comments from the editor to the Author and our response

Dear Dr. Yang and co-authors,

As you have seen by now, your work was assessed by three reviews. All three of the reviewers are generally encouraging of this work and note that it is potentially an important contribution to the literature on the SIF-GPP relationship. However, the number of requested clarifications and comments is extensive, so I recommend revising with major revisions.

[Dear Dr. Konings, We thank you for your valuable time serving as the editor of our manuscript, and giving us the opportunity to improve our study.](#)

Based on your author responses submitted so far, here are a few things to keep in mind as you revise the manuscript:

1) In your author responses, you have addressed a number of the requests for clarification by the three reviewers only by providing clarifying statements in the review document - in most cases, these requests for clarification should also lead to changes in the text to make sure the text is made more clear for the readers.

[Response: We acknowledge the shortcomings of our response letter posted in the discussion forum. We had revised the text in the manuscript as we stated in the response letter, but did not know if it was appropriate to attach a track-change version of our revised manuscript. As suggested, we understand that the better way is to specify the changes in the response letter to make the revision more clearly for the readers, and we have modified our response letter by adding the specific changes.](#)

2) When you send a revised manuscript with response to reviewer documents, please do not just say that you have clarified something in the text as you do in the responses you have pointed to so far, but include the actual new text in your response to reviewers document. Otherwise it is quite difficult to determine that you have actually satisfactorily addressed the comments.

Response: Yes, we agree with your suggestions. We have added the specific changes to our response in the letter instead of just mentioning it. Furthermore, we have included the revised manuscript with the changes highlighted in the response letter.

3) Additionally, please make sure the abstract is consistent with the most important points in the text. For example, you plan to show the diurnal relationship between phi F and phi P only in the supplement, but this is still highlighted as a key finding in your abstract.

Response: Thanks for pointing this out. We have decided to include the diurnal correlations as the main results since they support our main findings of the study.

4) Lastly, please do pay attention to Prof. Guan's last comment. While there is nothing wrong with arguing that a reviewer suggestion is outside the scope of your manuscript, the underlying comment that the leaf-level and canopy-level results are not sufficiently well-integrated with each other in your analysis should still be addressed in your response, not just the suggestion to run SCOPE. Several other comments by Dr. Guan (#s 5 and 8, for example) are also only partially addressed in the current author responses.

Response: We acknowledge that more comprehensive responses are needed to better address several comments raised by Dr. Guan in the response letter, although we did discuss them in the revised manuscript. As we mentioned in our response to your comment #1 and #2, we have incorporated more detailed replies to all the reviewers' comments.

Please keep the above comments in mind as you prepare your revised manuscript and a final response document. I look forward to receiving the revisions.

Best regards, Alex Konings

Comments from Anonymous Referee #1 and our response

General comments

In this study Peiqi Yang and co-authors analyze observations from a corn field during one growing season, where chlorophyll fluorescence (ChlF) has been measured both actively (MONIPAM) and passively (SIF) and relate the timeseries of these variables to gross primary production (GPP) measured from a flux tower. As the title says, they aim to study the relationship between GPP and the ChlF, a very important topic for a wider research community that now is using the novel SIF observations to estimate GPP. I find this manuscript very suitable for this journal and of interest to many.

The authors find out that the correlation between GPP and SIF is small, once the effect of absorbed PAR in the canopy has been removed from the relationship. At the leaf level they found that the role of thermal dissipation was an important factor influencing the relationship between fluorescence and photosynthesis yields. Also, they show the different functionalities of sunlit vs. shaded leaves in these respects and bring up the need to take them into account in the modelling efforts.

Response: We thank the reviewer for the positive and encouraging feedback. The reviewer's comments and suggestions are constructive and have helped us to improve the manuscript substantially.

Major comments

1. I find the manuscript well-written and the figures clear. At times the text was a bit unspecific and challenging to understand (most of my comments are requirements for clarifications) and in the

Discussion it was at times difficult to know, whether it was the leaf-level or canopy-level results being discussed. I'm sure the authors can overcome these issues with a bit more work on the text.

Response: We have improved the clarity throughout the manuscript with the help of the reviewers' specific comments. Most of figures have been revised for a better readability, e.g., by adding more ticks, rearranging subpanels in a figure and adjusting size of the figures.

2. Of the things that were not discussed, I had few issues coming to my mind, that the authors might want address in the revised version. The title is very general, but the only plant being studied is corn, that is a C4 plant and might have a more linear relationship between SIF and GPP than C3 plants. Is this something worth mentioning somewhere and the possible differences related to C3 plants?

Response: Yes, it is a valid point. We only examined a corn crop, which is a C4 species. In the revised version, we have first specified that a corn crop is studied in the title and mentioned the main characteristic of corn in the introduction, and then included a short discussion on the difference between C3 and C4 crops:

“The investigated crop has a C4 photosynthetic pathway, in which dark and light reactions are separated, and the carboxylation takes place under a high CO₂ concentration. This strongly suppresses photorespiration in C4 vegetation, resulting in a higher water use efficiency and lower sensitivity to heat and higher vapour pressure deficit than C3 vegetation. Liu et al. (2017) reported that the GPP–SIF relationship was much higher for C4 crops. They showed that $\Phi_{Fcanopy}$ of the C3 and C4 crops were similar but $\Phi_{Pcanopy}$ of C4 corn was much higher than C3 wheat. Because of a different photosynthetic pathway and the contribution of photorespiration, the SIF-GPP relationship of C3 vegetation is more complicated in the corn crop examined in this study”.

3. In the discussion of light environment, it is not mentioned that the tree canopies etc will have a more complex radiative transfer. Is the sunlit-shaded -separation something that is being recommended for crop canopies or is that something you consider sufficient also for more complex canopy structures?

Response: We believe that the separation of sunlit and shaded leaves is needed for complex canopies as well. The approach for separation we used is based on a turbid medium assumption, and can be directly applied to structurally simple canopies, such as corn. However, in the revised version, we have acknowledged that for structurally complex canopies, our approach can only serve as a first-order estimation, and additional structural characteristics should be included in separating sunlit and shaded leaves. One of the most important characteristics is the clumping index, because the clumping of leaves affects the gap probability in the vegetation canopy, the light penetration, and thus the sunlit fraction of the vegetation canopy.

4. You mention, that the correlation between photosynthetic and fluorescence yields estimated from canopy level had no correlation between the variables in the leaf level. The passive and active measurements anyhow differ in the very basics, i.e. in the passive you use just one wavelength, while MONIPAM gives you a spectrally integrated signal. Maybe you could also mention this?

Response: The reviewer is absolutely right that the passive SIF is measured at one narrow band while the active fluorescence is an integral over a wide band. Although we believe that the difference between leaf and canopy measurements is mainly due to the canopy structure effects, we agree it is worth mentioning about the difference between MoniPAM and passive fluorescence measurements. Hence, we have discussed the difference as suggested in the revised version:

“It is worth noting that active fluorescence measurements are spectrally integrated signals, whereas canopy passive SIF observations are obtained at one wavelength. As a result, the leaf-level

fluorescence emission and photosynthetic light use efficiencies derived from active fluorescence measurements differ spectrally from the canopy-level efficiencies (ΦF_{canopy} and ΦP_{canopy}). This difference may also play a role in upscaling leaf-level to canopy-level relationship between ΦF and ΦP .”

Minor comments

5. 1. 20: You mention, that the link between GPP and SIF is much weaker after taking into account iPAR and fAPAR. The correlation is below 0.30, so it is maybe even negligible. Maybe you could write this number here (because now it sounds, like there would still be definitely a functional link).

Response: Agreed. We have revised it accordingly.

“the remaining correlation between far-red SIF and GPP due solely to the functional link between fluorescence and photosynthesis at the photochemical level was much weaker ($\rho = 0.30$).”

6. 1. 20-22: Actually the positive correlation was present for sunlit leaves in well illuminated conditions, whereas it was negative in the low-light conditions, was it? Maybe you could add that here.

Response: Agreed. We have revised it accordingly.

“Active leaf-level fluorescence measurements revealed a moderate positive correlation between the efficiencies of fluorescence emission and photochemistry for sunlit leaves in well-illuminated conditions but a weak negative correlation in the low-light condition, and which was negligible for shaded leaves.”

7. 1. 32: Eddy covariance measures the net flux, not GPP. This is not now obvious from the text.

Response: We have specified that eddy covariance flux towers provide point measurements of net carbon flux in the revision.

8. 1. 83: Sorry, what is ‘fluorescence quenching’? And what maximum level are you referring to here? Maybe this sentence could be rephrased.

Response: Fluorescence quenching refers to any process that decreases the fluorescence of a sample. The maximum level refers to the status when the photochemical pathway is completely inhibited (e.g. by using a saturating light). We have rephrased the sentence in the revised version.

“The relationship between the photochemical-level photosynthetic light use efficiency (ΦP) and fluorescence reduction (i.e., quenching) was described with the Genty equation as $(F_m - F_s)/F_m$ (Genty et al., 1989) which compares the relative fluorescence change from a steady state (F_s) to its maximal level (F_m) when the photochemical pathway is completely inhibited (e.g., by using a saturating light).”

9. 1. 116: Should it be ‘carbon fluxes’ instead of ‘crop fluxes’?

Response: Yes. We have corrected the mistake.

10. 1. 138: Not exactly clear, how the interpolation goes above the maximum observed value.

Response: We used both extrapolation and interpolation. It has been clarified in the revision.

11. 1. 144: Sometimes ‘MoniPAM’, few times ‘MONIPAM’. The writing could be uniform throughout the text.

Response: We have revised accordingly by consistently using MoniPAM.

12. 1. 161, section 2.4: Later you use PRI also, but you don’t introduce its calculation.

Response: We introduced its calculation in section 3.4, but we agree that it is better to mention the calculation of PRI in the method section. Hence, we have added a sentence about its calculation in section 2.4.

13. 1. 215: Maybe you could show the equation for photosynthetic LUE here. It is not necessarily clear to which variable you're referring to here, so that would help. This is unclear, because in line 223 you say you calculate variables using only leaf temperature and radiation intensity as input, but here you say that this variable is dependent on many different input variables.

Response: We agree this requires further clarification. We meant that all the input variables were required, but we have field measurements of the two most important variables (leaf temperature and radiation). For the remaining variables, the model default values were used. The photosynthesis model (the FvCB model) is relatively simple, but still requires some efforts to explain. Instead of providing a set of equations of the photosynthesis model, we have rephrased the text on the model simulation to make our simulation settings clear.

“The two most influential model input variables, leaf temperature and incoming radiation, were measured by using the field measurements MoniPAM. $V_{c_{m0}}$ was set to $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 25°C , a recommended value for the corn crop (Houborg et al., 2013; Wullschleger, 1993; Zhang et al., 2014).”

14. 1. 224: Would you have a reference for the crops $V_{c_{m0}}$ value? Which temperature response are you using for it?

Response: The value of $V_{c_{m0}}$ varies with temperature. In Zhang et al (2014), the estimated $V_{c_{m0}}$ values of corn range from 11 to 75 with an average of $37 \mu\text{mol m}^{-2} \text{s}^{-1}$. In Houborg et al. (2013), the reported $V_{c_{max}}$ at 25°C (i.e., $V_{c_{m0}}$) of 11 to $48 \mu\text{mol m}^{-2} \text{s}^{-1}$ for corn during the growing season.

$V_{c_{m0}}$ refers to the $V_{c_{max}}$ at 25°C . For the temperature response of $V_{c_{max}}$, we use Collatz et al. (1992), namely $V_{c_{max}} = V_{c_{m0}} \times 2.1^{((\text{temperature}-25)/10)}$. Additional constraints for extreme low and high temperature condition are considered but not shown in the equation, which can be found in Collatz et al. (1992).

15. Section 3.1. Are there changes in the LAI values during the growing season and is there an increase in the senescent material in the field of view during the last development stage? The seasonal cycle of the observations is not shown. Therefore it is a bit difficult to judge, from which time period certain points in the e.g. Fig. 1 are.

Response: Yes, there are changes in LAI and as well as increase of the senescent material during the last developmental stage. We have retrieved the values of LAI and senescent material from TOC reflectance by inverting a radiative transfer model. The results, however, are not directly related to the topic of the present manuscript. Therefore, we only show the retrieved values in the response letter to address the reviewer's comment. Please find them in the figure below.

As for the seasonal variation of observations, we have provided all the measurements of GPP, SIF, and MoniPAM measurements in a supplement. The link to the data is on the same page with the manuscript below the manuscript pdf icon (<https://bg.copernicus.org/preprints/bg-2020-323/bg-2020-323-supplement.zip>).

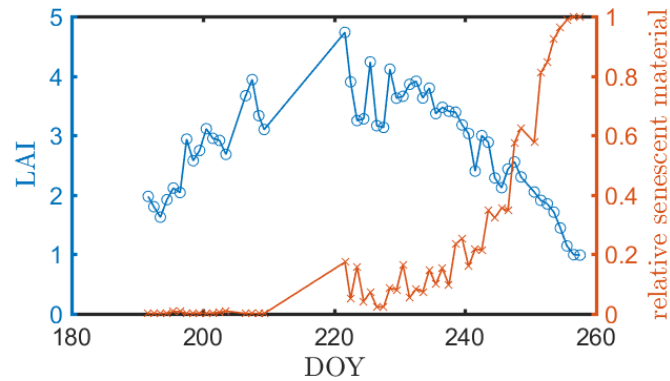


Fig. retrieved values of LAI and relative senescent material from TOC reflectance by inverting a radiative transfer model.

16. Fig. 3: I miss having ticks in this figure. Especially, as the subplots don't have numbers. Adding ticks would help readability.

Response: We have added the ticks to the figure as suggested.

17. l. 278: "an order of magnitude improvement of 13%" - just wondering, if a higher correlation between SIF and GPP is necessarily 'an improvement', I'd tend to think it is just a higher correlation. Also, is increase of 13% 'an order of magnitude' size?

Response: We agree with the reviewer's interpretation of the results and with the comment on the magnitude, and have revised it by removing the statement "an order of magnitude improvement of 13%".

"As for the different times of a day, we found that their correlations were the strongest in the afternoon ($\rho = 0.89$) while ρ was only 0.76 when the data were acquired in the morning (Figs 3d vs. 3f).

18. Fig. 4: A suggestion for this figure would be to make the panels bigger and include both sunlit and shaded in the same figure, shaded e.g. in dashed line. This would make comparison between the two easier (if it doesn't get far too busy plot).

Response: We have enlarged and merged the two panels in the revised revision.

19. l. 298: Is this midday dip of FiiN more occurring only in the sunlit leaves? Overall, when discussing Fig. 4 you don't mention differences between sunlit and shaded leaves. If they are similar in their dynamics, that's also maybe worth noting. There anyhow seems to be differences, that might be interesting, e.g. FiiPshade maybe goes lower fast during senescence, FiiFshade has lower values than FiiFsunlit, even though other components are perhaps on pretty similar levels.

Response: We found that this midday dip occurred in both sunlit and shaded leaves. This is a nice suggestion. We have added a paragraph about the comparison of sunlit and shaded leaves in section 3.2.

"Although the sunlit and shaded leaves had similar seasonal and diurnal patterns, some interesting differences are observed. As expected, the radiation levels were higher for the sunlit leaves than for the shaded leaves, which produced higher ΦF^ for the sunlit leaves and slightly lower ΦP at the young and mature stages. In comparison to the difference in ΦF^* , the difference in ΦP was less pronounced. At the senescent stage ΦP of the shaded leaves was substantially lower than sunlit leaves despite receiving lower radiation, which normally would lead to higher ΦP . This could be attributed*

to the different leaf ages and functionality of sunlit and shaded leaves; for example, shaded corn leaves senesce earlier than sunlit leaves. Additionally, ΦD^ of sunlit leaves was higher than the shaded leaves while ΦN of the sunlit and shaded leaves was similar.*”

20. 1. 305-306: Maybe you can share some numbers about nighttime FiiF, as I find it difficult to see ‘clear’ decrease in these values. Is your sentence referring to this picture or the whole timeseries? For the sunlit leaves, it seems that during the young and mature stages there are nights with some higher values, but the overall level (at least as far as I can try to read the figure) is not that different. I’m not arguing your claim, but maybe you can back that up a bit.

Response: We have included some numbers of PhiF to justify the reduction of nighttime PhiF. At the young stage, its value was around 60, while in the senescent stage it was 50.

21. 1. 313: So, is the Fig. 5 for the sunlit or shaded leaves?

Response: This figure is for sunlit leaves. We have clarified in the caption of the figure.

22. 1. 314: ‘evident: : : increased through the growing season’: to me this sentence sounds that there is increase between all young – mature – senescence -stages. For the nighttime, yes, there is a definite change during senescence compared to other stages. But the daytime values during senescence don’t then seen lower, and then if there is a change in daytime values between young and mature stages is not so clear, as there is daily variation. For the Fig. 5 you chose ‘representative’ day for the pie chart. Could you tell on what conditions you chose this day? Did it have certain meteorological conditions or was it just similar as most other days?

Response: The reviewer is right. The diurnal variation should have been considered. Nevertheless, we think the argument is valid for daytime as well, because the daytime and nighttime sustained heat dissipations are the same, and an increase of PhiD is observed for both daytime and nighttime, which leads to a decrease of PhiP in a seasonal cycle. That is to say, because of the increase of PhiD from young and mature to senescent stage, it is expected that both nighttime and daytime PhiP decreases despite of its diurnal variation. The three ‘representative’ days were selected on the condition that clouds effects are negligible according to the iPAR measurements, so they were representative for clear sky conditions

23. I find it a bit annoying that you show days 193-197 in Fig. 4 and 192-196 in Fig. 5. It doesn’t help in comparison. Was there a special reason you chose to show differing time periods?

Response: Sorry for our mistake. They should have been the same. We have revised Fig. 5 to make them consistent.

24. 1. 325-327: Are these numbers for the contributions correct? Based on numbers on the pie chart, I’d say different (but as mentioned below, I cannot read them clearly).

Response: Sorry for the slight inconsistency between the figure and the text. We have revised the numbers in the text accordance with the values in the figure. The differences were small (less than 2%) and did not affect our arguments in the text.

25. 1. 341: Sorry, what does your ‘seasonally averaged’ means?

Response: ‘Seasonally averaged’ is reductant and misleading here. We have deleted it.

26. 1. 345: A bit confusing, that you are here referring to subplots 6a and b, but the values are from the averaged plot 6c (and your point also).

Response: The reviewer is right and it should be Fig. 6c. We have revised the text accordingly.

27. 1. 349: Should this be 6a (for FiiP and FiiF relationship)?

Response: Yes. We have revised the text accordingly.

28. 1. 350: You write in response to incoming light, but the color code here is for FiiN? If you want to emphasize ‘to incoming light’, maybe you can say something about that how it is related to this.

Response: As the reviewer suggested, we have clarified that PhiN increased with increasing incoming PAR as shown in Fig. 4.

29. 1. 351-353: Actually the arrow for the shaded leaves doesn’t necessarily show the response to sustained heat dissipation so well, as the highest FiiD levels are not on the lowest levels (Fig. 7b). Also, yes, the responses between sunlit and shaded seem pretty similar, but just by looking, maybe the slopes (FiiP vs FiiN) in sunlit leaves change between the colored groups and not so in shaded leaves.

Response: The reviewer is correct on the difference between sunlit and shaded leaves. We have acknowledged this difference in the revised version. Please see our response to your comment #19.

30. 1. 363: Do you get the value 65% from the Fig. 7c? If so, you could clearly state which value you are referring to. (These larger variations in FiiP are also more present in lower FiiN values, logically: : :)

Response: Yes, the values are from Fig. 7c. PhiP can vary from 0.37 to 0.61 when PhiN was around 0.05. We have included this additional information in the revised version to improve the clarity.

31. 1. 376: Sorry, not clear what you mean by ‘these trends’. The mentioned values were from half-hourly values and you mean that similar behavior is visible in seasonal and diurnal values?

Response: We were referring to the observed reduction of the correlation between PhiF and PhiP. We have revised this sentence as

“The reduction of the correlation between PhiP and PhiF was caused by diurnal variations in PhiN as well as seasonal variations in both PhiN and PhiD.”

32. 1. 391: So, did you exclude measurement points from drought conditions from the dataset? Based on what conditions was that made? Or was the plot irrigated to start with, and you didn’t have to worry about drought?

Response: Sorry for the confusion. We meant that the drought effects were not included in the simulation but were very likely present in the field measurements. We have clarified this in the revision.

“Furthermore, we did not include changes in leaf display geometry induced by low water stress (i.e., drought) in the simulations, but it is a common phenomenon in corn plants in the field.”

33. 1. 394: So, did you find any ways that you could parameterize sustained heat dissipation, so that you could model it during the growing season?

Response: At this point, we have not found a convincing way to parameterize the sustained heat dissipation, because its controlling factors are still not clear. Our study only shows the seasonal variation, which is related to the change of pigment pools, but we don’t have a certain answer on this.

34. 1. 454: Your point here is that heat dissipation is more directly connected to photosynthetic lue than fluorescence emission to what.. heat dissipation? This sentence is a bit unclear, please rephrase. Are you here referring to Fig. 7a or 7b, are you talking about leaf or canopy level?

Earlier you mentioned that give some doubt to PRI and show its correlations with a question mark. So this would be more about leaf level?

Response: Yes, it is about leaf level. We have rephrased this part by stating the role of sustained and reversible heat dissipation on the diurnal and seasonal variation of leaf photosynthetic light use efficiency, respectively.

“Compared to the relationship between leaf fluorescence emission efficiency, total heat dissipation (both D and N) provided a robust and direct indicator of leaf photosynthetic light use efficiency (Fig. 7). In particular, the variation of reversible heat dissipation better explains the diurnal variation of leaf photosynthetic light use efficiency, whereas the sustained heat dissipation contributes to the seasonal variation.”

35. 1. 456: ‘photosynthetic energy’, what do you actually mean by this? Is this the absorbed light energy in the photosynthetically active region?

Response: Yes, we have changed it to ‘absorbed photosynthetically active radiation’.

36. 1. 456: So are you now only referring to the study by Heber et al, or what did you see in your diurnal results? Or is the diurnal scale visible in 6c (but the relationship is not positive for shaded leaves)? To my understanding the review by Heber concentrates on mosses and lichens, quite different plants than corn. Maybe you could better clarify what is the meaning for you of this reference and how it related to your results?

Response: We have added several more relevant papers showing the dominant role of reversible heat dissipation in various vegetation. Our study confirms this with field measurements and finds Φ_N is responsible for regulating the correlation between Φ_P and Φ_F . The reviewer is right that the positive relationship exists for sunlit leaves. We have addressed this in the revision.

“Reversible heat dissipation is the main regulating mechanism for the dissipation of absorbed photosynthetically active radiation (Adams et al., 1989; Demmig-Adams et al., 1996; Heber et al., 2006; Huang et al., 2006). Our study confirms its dominant role for the corn crop with field measurements and finds that the reversible heat dissipation is responsible for the positive relationship between Φ_F and Φ_P of sunlit leaves at diurnal scales, though less so at seasonal scales when sustained heat dissipation is dominant (Fig. 6)”

37. 1. 482: Sorry, what is the LUE-GPP relationship mentioned here?

Response: It should be the relationship of photosynthetic light use efficiencies at both leaf and canopy levels.

38. 1. 502: Often, when a model separates the canopy into sunlit and shaded fractions, it is called a two-leaf model (such a BEPS, e.g. Qiu et al 2019). Not ‘two-big-leaf’, even though to my understanding the idea is pretty much the same as you’re here proposing.

Response: We are aware that both ‘two-leaf’ and ‘two-big-leaf’ models are used interchangeably (Dai et al, 2004; Luo et al., 2018; Parazoo et al, 2020), and agree with the reviewer’s suggestion. In the revised version, we have used ‘two-leaf’ models and noted that ‘two-big-leaf’ was also used in literature.

39. 1. 504: Sorry, is the a word missing in this sentence? Was shown what?

Response: Yes, the missing part is ‘an improved correlation with LUE’.

40. 1. 502-509: In this paragraph you talk about LUE models and then mention SCOPE as an example of a more detailed model, but there are also large scale models of with varying degree of

complexity (e.g. Parazoo et al, 2020), located between SCOPE and LUE models. Just mentioning, since now this paragraph offers maybe a quite narrow view.

Response: Thanks for the nice review article. We have incorporated a more compressive discussion of the existing models, such as SCOPE, BEPS-SIF, BETHY-SCOPE and DART.

“Qiu et al, (2019) incorporated a fluorescence simulation in the Boreal Ecosystem Productivity Simulator (BEPS, Liu et al., 1997), which is a two-leaf process-based model. More classes of leaves with varying ambient temperatures and incident radiation levels can be examined using more explicit models, such as SCOPE (Soil-Canopy-Observation of Photosynthesis and Energy fluxes, Van Der Tol et al., 2009), BETHY-SCOPE (the Biosphere Energy Transfer Hydrology model coupled with SCOPE, Norton et al., 2018) or DART (the Discrete Anisotropic Radiative Transfer model, Gastellu-Etchegorry et al., 2017).”

41. l. 521: You mean that they (sunlit FiiF and FiiP) are more tightly connected than the FiiFshaded and FiiPshaded?

Response: Yes, we have clarified as suggested.

42. l. 560: So, you mean that the physiological traits of shade/light -adapted leaves would be good to be taken into account in SCOPE and other such models? It is not that clear how the above examination about the sunlit fraction depending on LAI and zenith angles really ties with the discussion. Could you maybe tie that better to the context?

Response: Yes, the examination of the sunlit fraction changing with canopy structure and zenith angles provides a prediction at a single moment. To account for the different physiological traits of shade/light -adapted leaves, we could predict the light distribution inside the canopy with varying sun positions (e.g., a diurnal cycle). In this way, sun-adapted and shade-adapted leaves can be differentiated according to the probability of being illuminated for a longer period instead of assuming a steady state. A leaf is considered as sun-adapted when it is almost always illuminated at various sun positions or different time in a day. Furthermore, different physiological traits of sun-adapted and shade-adapted can be taken into account in the model.

Technical/typos

43. l. 68: ‘improved the correlation’, the correlation of SIF?

Response: Yes. It has been clarified in the revision.

“improved the correlation between SIF and APAR but not GPP”

44. Table 1: Also add here how you measure the PRI.

Response: We have added the calculation of PRI in section 2.4 in the revision.

45. Fig. 1: The a) and b) seem to be flipped.

Response: The reviewer is right. We have swapped their positions in the revision.

46. l. 279: Why do you talk about ‘mid-morning’? Your morning seems to end at midday, not to ‘late morning’: : :

Response: We have changed mid-morning and mid-afternoon to morning and afternoon.

47. Fig. 4: Maybe change some y-axis labels for the right side for better readability?

Response: We have moved all the y-axis labels to the right side to improve the readability.

48. Fig. 5: At least in my version the numbers in the pie charts are challenging to read. Could you improve the figure in that respect?

Response: Yes, we have changed the figure from 1.5 column width to double column (full width). Additionally, we have increased the resolution of the figure.

49. Fig. 6: Would you like to add a legend box? At first, the dot belonging to the legend might seem to be in the plot. Please, add ticks to subplots a and b.

Response: Yes, it is a nice suggestion. We have added a legend box and ticks to the figure in the revised version.

50. l. 348: ‘linear relationship’?

Response: Agreed and revised accordingly.

51. l. 355: Is ‘expressed’ the best word to use in this context?

Response: We have used ‘fully manifest’ for a clearer meaning.

52. Fig. 8c : The plotted symbols are below the subpanel name.

Response: We have moved the subpanel names to the other side to avoid overlapping with the symbols.

53. Fig. 10 caption: Do you mean in the second last sentence, that the values of FiiNcanopy are unknown or what?

Response: Yes, there was a typo in FiiFcanopy and it should be FiiNcanopy.

54. Fig 10: Show the values with the same number of decimals, even if 0.1 is 0.10.

Response: Yes. We have revised it accordingly.

55. Fig. 11. In my copy it is not easy to differentiate the lines with zenith angle 30 and 0. At least in subpanel c) the legend also looks suspicious. If you want to have a w/b –figure here, could you maybe differentiate the lines with different widths or styles?

Response: Yes. In the revised version, we have used different line styles and linewidths to improve the readability.

56. l. 444: So, are these now leaf level values?

Response: These statements refer to leaf-level results. We have specified this in the revision.

References:

Parazoo, N. C., Magney, T., Norton, A., Raczka, B., Bacour, C., Maignan, F., Baker, I., Zhang, Y., Qiu, B., Shi, M., MacBean, N., Bowling, D. R., Burns, S. P., Blanken, P. D., Stutz, J., Grossmann, K., and Frankenberg, C.: Wide discrepancies in the magnitude and direction of modeled solar-induced chlorophyll fluorescence in response to light conditions, *Biogeosciences*, 17, 3733–3755, <https://doi.org/10.5194/bg-17-3733-2020>, 2020.

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Zhang, Y., Guanter, L., Berry, J. A., Joiner, J., van der Tol, C., Huete, A., Gitelson, A., Voigt, M. and Köhler, P.: Estimation of vegetation photosynthetic capacity from space-based measurements of chlorophyll fluorescence for terrestrial biosphere models, *Glob. Chang. Biol.*, 20(12), 3727–3742, doi:10.1111/gcb.12664, 2014.

Comments from Anonymous Referee #2 and our response

Yang et al. used a unique dataset comprising both active and passive measurements of fluorescence to explore the physical and physiological relationship between SIF and GPP. Considering the large amount work on the SIF-GPP relationships during the last few years, the work conducted is therefore relevant and it will be of interest for the scientific community working on remote sensing of GPP using SIF. The manuscript is a nice addition to the current body of literature and I think it is worth publishing. A few minor suggestions may be taken into account to improve the manuscript.

Response: We thank the reviewer for the encouraging feedback. We have revised the manuscript according to both reviewers' comments.

Line 167: Are the coefficients in Equation 2a obtained from Vina and Gitelson (2005)? If not, please add correct reference.

Response: The coefficients are not explicitly given in Vina and Gitelson (2005), but they can be obtained from the linear regression line on Fig. 3C in Vina and Gitelson (2005). We obtained these coefficients from Vina and Gitelson (2005) and also from Miao et al., (2018), in which the exact coefficients are given. The difference of the two sets of coefficients is very small (1.373 RededgeNDVI-0.172 vs. 1.37 RededgeNDVI-0.17). In the revised version, we have added this reference Miao et al., (2018) apart from Vina and Gitelson (2005).

Lines 277-279 (Figure 3d-f): The data points are more disperse in the morning than in the afternoon. Please briefly discuss the possible reasons.

Response: More disperse data points suggest lower correlation between SIF and GPP in the morning. We have discussed one possible reason in section 4.3, which is the fraction of diffuse light. However, we also believe that there are other possible reasons. For example, LUEp is generally more variable in the morning due to the quicker change of environmental conditions, such as air temperature and humidity, whereas LUEf may not change correspondingly. The different response of LUEp and LUEf to the rapidly changing environment may have caused the lower correlation.

Figure 9: Shaded leaves exhibit higher light use efficiency of sustained heat dissipation than sunlit leaves, which is inconsistent with measured results (Figure 7). Briefly discuss the difference.

Response: Thank you for this comment. The model does not simulate a different response to environmental variables between sunlit and shaded leaves (it considers just one type of leaf). The very small difference in simulated heat dissipation is because the sunlit leaves have a higher temperature than the shaded leaves. This affects the sustained heat dissipation in the model. We made a mistake in using the color map and have corrected it.

Line 464 (Figure 10b): The correlation coefficient between PRI and APARcanopy is 0.28, not -0.28 in Figure 10b, right?

Response: The correct value is 0.28. We have revised Fig. 10b in the revision.

In addition, many sentences can be improved, for example: Line 452: per leaf unit area → per unit leaf area

Response: We have checked and improved the overall quality of our writing.

Short comment from Dr. Kaiyu Guan and our response

Review for “Unravelling the physical and physiological basis for the solar-induced chlorophyll fluorescence and photosynthesis relationship” by Yang et al.

General comments

This manuscript used field measured leaf and canopy fluorescence and photosynthesis and investigated the physical and physiological basis of SIF-GPP relationship at a corn field. They found that APAR dominated the positive SIF-GPP relationship. They further used the continuous active fluorescence measurements from the MoniPAM system to analyze the relationship between fluorescence yield and photochemical yield at leaf scale and found a moderate correlation between the efficiencies of fluorescence emission and photochemistry for sunlit leaves but a weak correlation for shaded leaves. The manuscript has some strength.

The major strengths are: (1) The author combined leaf-scale active fluorescence measurements to fully investigate the physiological basis of the SIF-GPP relationship which is lacking in many studies. (2) The authors are on top of the most recent literatures in this topic. The references used are up to date, and the authors had a very thorough summary of the past literatures. The manuscript is also well-written. However there are several unclear points which should be addressed:

Dear Dr. Guan, Thank you for your positive and encouraging feedback, as well as the clear summary and constructive suggestions. We have revised our manuscript according to your and the other two reviewers' comments.

(1) The reliability of relative efficiency of the sustained heat dissipation (ΦD^*) calculation. In L210, the author claims that “Because Fm was measured during the night in the absence of both reversible heat dissipation and photochemistry, a change in Fm must be caused by a change in the sustained heat dissipation”. But during night, there are still ΦN and ΦF from Fig. 5. I am concerned about the reliability of ΦD^* calculation since to my knowledge, this calculation hasn't been used in previous studies. The author should provide more literature to back up this method.

Response: You are absolutely right that, as far as we know, the derivation of ΦD^* has not been reported in other places. It is also correct that ΦF is still present in the night because ΦF is derived from MoniPAM F_t measurements, which are induced by the measuring light. The values are below 100 in the night since leaves are dark-adapted and have maximal ΦP . The nighttime ΦN is not at the absolute zero, but it is very small (<0.05 , and $<1\%$ from the pie chart), which is most likely due to the uncertainties in the MoniPAM measurements.

Our idea is that Φ_N is negligible in the night and Φ_P is zero when saturating light is applied. Hence, the change of Φ_F (i.e., F_m) represents the change of Φ_D , since $\Phi_N + \Phi_P + \Phi_D + \Phi_F = 1$, where $\Phi_N \approx 0$ and $\Phi_P = 0$. We hope our explanation makes the issue clear.

(2) The data availability across the whole growing season is not provided. In L154, the author mentioned that they excluded 29 days rainy and cloudy data, but the whole period of available canopy data is not provided. The author could provide a time series of the SIF, GPP, APAR data in the supplementary. Also, the availability of the active PAM measurements is also not explicitly provided.

Response: We had provided all the measurements of GPP, SIF, and MoniPAM measurements in a supplement. The link to the data is on the same page with the manuscript below the manuscript pdf icon (<https://bg.copernicus.org/preprints/bg-2020-323/bg-2020-323-supplement.zip>).

(3) The author reported the overall correlation between Φ_P canopy and Φ_F canopy. It would be good that they provide the scatter plot and compare this with the leaf scale relationship.

Response: We have included the suggested plot in the appendix (Fig. A1). We agree that such a plot can give more detailed information to the reader and allow a more informative comparison with the correlation at the leaf-level. Thank you for the suggestion.

(4) L423 They found no clear relationships between Φ_P canopy vs. Φ_P or Φ_F canopy vs. Φ_F^* . This result needs more explanation, such as this poor correlation is for sunlit leaves or for shaded leaves or both and what causes this poor correlation. Of course, they are from different levels (leaf vs canopy) and canopy structure plays a role here. Although fesc calculation still has large uncertainty, there are several methods proposed to quantify this term (e.g., NIRv/fPAR). The author should try to correct fesc effect and get canopy total Φ_F canopy and compare with leaf Φ_F^* .

Response: Thank you for this comment. We have included scatter plots of the leaf and canopy efficiencies in the appendix for (both sunlit and shaded) as shown in Fig. A2. Furthermore, we have added a section discussing about the role of fesc on the SIF-GPP relationship. We found that the accuracy of fPAR is crucial to estimate fesc and total emitted SIF when using either FCVI or NIRv. Although we did not find an improvement in GPP estimation after correction TOC SIF for fesc, we believe that canopy total emitted SIF is a better indicator of GPP compared with TOC SIF. With either a better estimation or measurement of fPAR or i_0 , we can improve the relationship between SIF and GPP by accounting the fesc effects.

(5) L440. They found progressive increase of sustained heat dissipation (Φ_D^*) during senescence. In contrast with no seasonal variation of Φ_N . Why there is no seasonal variation of Φ_N ? What factor determined the seasonal variation of Φ_N .

Response: As shown in the Figs. 4 and 5 (i.e., the seasonal variation of energy partitioning at the leaf level), there was some seasonal variation of Φ_N , but its variation has no clear pattern. We think that Φ_N is mainly determined by the radiation levels, which is more pronounced in a diurnal cycle. As in a seasonal course, the pigment pool of the leaf certainly plays a role since Φ_N or NPQ is related to the carotenoid content. However, as far as we know, the relationship between carotenoid and NPQ is still not clear yet. The challenge is to eliminate the effects of absorbed radiation levels on NPQ. Because the absorbed radiation is also related the pigment pool (e.g., Chl and carotenoid content), it is difficult to separate the effects of pigment content on NPQ from the effects of absorbed radiation. The data we have in this study are not sufficient to give an answer to what factor determined Φ_N . To further investigate, we think dedicated laboratory experiments are needed.

(6) L455. The author mentioned that reversible heat dissipation is responsible for the positive relationship between Φ_F and Φ_P at diurnal scale, but there is no diurnal relationship between Φ_F and

ΦP in the current manuscript. The author only provided the seasonal and seasonal+diurnal relationships.

Response: Thanks for this comment. Indeed, we did not provide the diurnal relationships between ΦF and ΦP separately. We have included a figure for their diurnal relationship in the revised manuscript in the appendix (Fig. 8). More positive diurnal correlation between ΦF and ΦP are found for sunlit leaves than for shaded leaves. For the correlation ΦN and ΦP , positive correlations are found for both sunlit and shaded leaves.

(7) L520. The author claimed that a stronger relationship between SIF and GPP for dense canopies is expected since ΦF sunlit and ΦP sunlit are moderately correlated. I am not convinced that dense canopy means the fraction of sunlit leaves is larger. Also, the poor correlation between SIF and GPP at senescent stage is probably due to the less data points and more uncertainty of the SIF retrieval.

Response: We agree that the less data points and larger uncertainties of the SIF retrieval are also possible reasons for the lower correlation between SIF and GPP at the senescent stage. We believe that leaves in the upper layer absorb a major part of the incoming PAR, and thus contribute more to TOC SIF and GPP for dense canopies. These leaves are normally sunlit, for which ΦF and ΦP are moderately correlated. Dense canopy does not mean that the fraction of sunlit leaves is larger. In fact, the simulations (Fig. 13 in the revised manuscript) show that larger LAI leads to lower sunlit fraction. However, the relevant quantity is $fPAR_{sunlit}/fPAR_{tot}$, which supposes to be higher for dense canopies.

(8) L528. The author claimed that under cloudy conditions, SIF-GPP relationship becomes worse. But this is opposite to the previous study from Yang et al. (2018) in a rice paddy. They found similar relationship under sunny and cloudy conditions. Why will diffuse condition lead to a worse SIF-GPP relationship?

Response: Thanks for pointing this out. Indeed, Yang et al. (2018) reported that an identical correlation between SIF and GPP for sunny and cloudy days as indicated by the R^2 and $rRMSE$ values (Fig. 4 in Yang et al, 2018). We think that this is not opposite to our results, but suggests that the relationship between SIF and GPP changes under various environmental conditions. The possible cause of a worse SIF-GPP relationship under diffuse (or cloudy) condition, we think, are 1) the higher contribution to TOC SIF from shaded leaves, in which a very weak ΦF - ΦP relationship occurs, and 2) measurements of TOC SIF are more likely to be more noisy under diffuse illumination in cloudy days.

Yang, K., Ryu, Y., Dechant, B., Berry, J. A., Hwang, Y., Jiang, C., ... & Yang, X. (2018). Sun-induced chlorophyll fluorescence is more strongly related to absorbed light than to photosynthesis at half-hourly resolution in a rice paddy. *Remote Sensing of Environment*, 216, 658-673.

(9) Overall, I feel that the link between MoniPAM active fluorescence and canopy SIF is weak and the author analyzed these two datasets separately. Although they used to SCOPE but only to model the leaf scale relationship. It would be good if the author can use the leaf measurements to run SCOPE and get canopy SIF and GPP and compare with observations.

Response: We agree with the importance of the link between leaf and canopy measurements. We think that leaf measurements gives the physiological information while canopy measurements are strongly affected by canopy structure. Of course, leaf physiological traits have an impact on the relationship between SIF and GPP on canopy scale. In section 4.3 (i.e., physically and physiologically joint effects on the SIF-GPP relationship), we discuss the link between leaf and canopy measurements by using the two-leaf model. Because we don't have the measurements or estimation of the fraction of sunlit canopy, it is difficult to link the measurements in this study quantitatively. Nevertheless, we discuss the possibility to estimate this fraction once we know some canopy structural parameters.

As for the SCOPE simulation, it is indeed a good way to link leaf and canopy observations. However, to run SCOPE, many more properties of the leaf and canopy structure are required. We have done such an experiment: i) retrieving leaf and canopy structural parameters from canopy reflectance measurements, ii) using the measured leaf physiological traits, and the estimated leaf and canopy structural properties as input to drive the SCOPE model and iii) simulating canopy GPP, SIF and comparing with the measured GPP and SIF. Because many details are required to interpret correctly the experiment and results, we think it is better to present in a separated paper, since

Finally, I want to provide encouragements for this work. The general goal that this work aims to achieve is worth praising. I enjoyed the reading of this manuscript and it clearly shows the authors have been putting lots of efforts into the literature review. I can see that this work could have a good impact and contribution to this field if all the above concerns can be properly addressed. Thus I fully encourage moderate revision of this work. Meanwhile, please understand that a rigorous scrutiny is necessary here as this topic that you are addressing is very important and your conclusion can have a large impact for the general public's understanding about SIF and photosynthesis.

Response: We agree totally with your recommendation and appreciate the constructive comments. We hope that the additional figures and section we added have addressed your concerns. Thank you again!

Revised manuscript with the changes marked

Unravelling the physical and physiological basis for the solar-induced chlorophyll fluorescence and photosynthesis relationship using continuous leaf and canopy measurements of a corn crop

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Abstract. Estimates of the gross terrestrial carbon uptake exhibit large uncertainties. Sun-induced chlorophyll fluorescence (SIF) has an apparent near-linear relationship with gross primary production (GPP). This relationship will potentially facilitate the monitoring of photosynthesis from space. However, the exact mechanistic connection between SIF and GPP is still not clear. To explore the physical and physiological basis for their relationship, we used a unique dataset comprising continuous field measurements of leaf and canopy fluorescence and photosynthesis of corn over a growing season. We found that, at canopy scale, the positive relationship between SIF and GPP was dominated by absorbed photosynthetically active radiation (APAR), which was equally affected by variations in incoming radiation and changes in canopy structure. After statistically controlling these underlying physical effects, the remaining correlation between far-red SIF and GPP due solely to the functional link between fluorescence and photosynthesis at the photochemical level was much weaker ($\rho = 0.30$). Active leaf-level fluorescence measurements revealed a moderate positive correlation between the efficiencies of fluorescence emission and photochemistry for sunlit leaves in well-illuminated conditions but a weak negative correlation in the low-light condition, and which was negligible for shaded leaves. Differentiating sunlit and shaded leaves in the light use efficiency (LUE) models for SIF and GPP facilitates a better understanding of the SIF-GPP relationship at different environmental and canopy conditions. Leaf-level fluorescence measurements also demonstrated that the sustained thermal dissipation efficiency dominated the seasonal energy partitioning while the reversible heat dissipation dominated the diurnal leaf energy partitioning. These diurnal and seasonal variations in heat dissipation underlie, and are thus responsible for, the observed remote sensing-based link between far-red SIF and GPP.

1 Introduction

For our understanding of the Earth's climate, estimates of the gross carbon uptake by terrestrial ecosystems are crucial. Despite considerable progress in measurement systems and models, contemporary estimates of the gross terrestrial carbon uptake still exhibit large uncertainties (Ryu et al., 2019). On the one hand, eddy covariance flux towers provide point measurements of net
 35 carbon flux at selected locations on all continents, but such *in situ* measurements are sparse. On the other hand, optical remote sensing provides spatially continuous and dense data, but these observations are only indirectly related to the carbon flux. In this respect, the development of sun-induced chlorophyll fluorescence (SIF) measurement techniques from satellites has raised expectations. This is because chlorophyll fluorescence (ChlF) as a by-product of photosynthesis has long been used as a probe of photochemistry in laboratory and field studies (Mohammed et al., 2019). Ever since satellite SIF data products related to
 40 the far-red fluorescence peak became available during the past decade, numerous studies have reported a strong correlation between far-red SIF and gross primary production (GPP) at the local, regional and global scales (e.g., Campbell et al., 2019; Damm et al., 2015; Guanter et al., 2014; He et al., 2017; Wieneke et al., 2016). This SIF-GPP link has been employed to estimate photosynthetic capacity (Zhang et al., 2014) and crop yield (Guan et al., 2016).

45 The rising expectations of far-red SIF rely on a contestable closer relationship with GPP than other optical remote sensing signals, such as well-chosen reflectance indices. In order to make use of SIF quantitatively, it is necessary to understand the physical and physiological meaning of SIF, and to establish mechanistic understanding of its relation to GPP (Gu et al., 2019; Magney et al., 2019; Miao et al., 2018; Yang et al., 2015). In recent studies, the light use efficiency (LUE) model of Monteith (1977) has been the common starting point for describing GPP and SIF as a function of the absorbed photosynthetically active
 50 solar radiation (APAR):

$$\text{GPP} = \text{iPAR} \cdot \text{fAPAR} \cdot \Phi_{P_{canopy}} \quad (1a),$$

$$\text{SIF} = \text{iPAR} \cdot \text{fAPAR} \cdot \Phi_{F_{canopy}} \cdot f_{esc} \quad (1b),$$

where iPAR denotes the available incoming photosynthetically active radiation for a vegetation canopy; fAPAR is the fraction of APAR absorbed by green vegetation; and $\Phi_{P_{canopy}}$ and $\Phi_{F_{canopy}}$ describe the canopy-scale light use efficiencies for
 55 photochemistry and fluorescence, respectively, which are related to the plant physiological status. f_{esc} is the fraction of the emitted far-red fluorescence that escapes the canopy in the viewing direction (per solid angle), which depends on the viewing and illumination geometries and canopy structure (Porcar-Castell et al., 2014; Yang et al., 2020; Yang and Van der Tol, 2018).

From the LUE model, it is evident that the common terms iPAR and fAPAR are primarily responsible for the often-reported
 60 linear relationship between SIF and GPP (Campbell et al., 2019; Dechant et al., 2020; Miao et al., 2018; Rossini et al., 2010; Yang et al., 2018). The combined contribution of $\Phi_{F_{canopy}}$ and f_{esc} to the SIF-GPP relationship is much less clear. It has been

argued that $\Phi_{F_{canopy}}$ may also contribute to the positive correlation between GPP and far-red SIF, while f_{esc} is viewed as an interfering factor. Guanter et al. (2014) implicitly assumed that a positive relationship between $\Phi_{F_{canopy}}$ and $\Phi_{P_{canopy}}$ exists and that f_{esc} in the near-infrared region is isotropic and close to unity when explaining the SIF-GPP relationship. However, these assumptions need to be verified, and we still lack a clear conclusion on the physical and physiological basis for the relationship between far-red SIF and GPP.

Dechant et al. (2020) explored the relationship between SIF and GPP for three in situ crop datasets. They found that correcting SIF for canopy scattering (f_{esc}) improved the correlation ~~between SIF to and~~ APAR but not ~~to~~ GPP. Furthermore, they reported that their estimates of physiological SIF yield ($\Phi_{F_{canopy}} = \text{SIF}/\text{APAR}/f_{esc}$) showed no clear seasonal patterns and were unlikely to contribute to the positive correlation between GPP and far-red SIF. In contrast, Qiu et al. (2019) reported that the similar correction of SIF for canopy scattering resulted in a better correlation to GPP, and Yang et al. (2020) showed that the estimates of canopy-scale light use efficiency of fluorescence ($\Phi_{F_{canopy}}$) were clearly higher in young and mature stages than for the senescent stages, and were correlated with $\Phi_{P_{canopy}}$. The inconsistent findings could partly be caused by considerable uncertainties in the estimates of f_{esc} and $\Phi_{F_{canopy}}$, especially since the physiological indicators ($\Phi_{F_{canopy}}$ and $\Phi_{P_{canopy}}$) are still contaminated by canopy structural effects (Yang et al., 2020).

More fundamental understanding can be obtained by returning to the established physiological methods of *in vivo* active fluorescence measurements to discern the relative energy distribution among the four pathways in plants via photosynthesis, fluorescence and heat losses (both sustained and reversible). At the photochemical level in leaves, it is clear that a change in fluorescence emission efficiency can be attributed to a change in the combined efficiencies of photochemistry and heat dissipation, expressed as photochemical quenching (PQ) and non-photochemical quenching (NPQ) of fluorescence (Baker, 2008; Maxwell and Johnson, 2000). The relationship between the photochemical-level photosynthetic light use efficiency (Φ_p) and fluorescence reduction (i.e., quenching) was described with the Genty equation as $(F_m - F_s)/F_m$ (Genty et al., 1989) which compares the relative fluorescence change from a steady state (F_s) to the its maximal level (F_m) when the photochemical pathway is completely inhibited (e.g., by using a saturating light) to a steady state was described with the Genty equation (Genty et al., 1989). Semi-empirical generalized relationships have further been developed to model these maximal and steady-state fluorescence levels as a function of photosynthetic light use efficiency and temperature (Rosema et al., 1991; Van Der Tol et al., 2014). However, the universal applicability of the latter models has not been validated, and continuously collected field measurements of active fluorescence at the leaf level along with canopy photosynthesis and SIF measurements are rare, which limits our understanding of their relationship in natural conditions.

The present study aims to assess the drivers of the apparent SIF-GPP relationship using independent measurements of all terms in the light use efficiency model (Eq. 1), collected under different illumination conditions and at different growth stages, at the

95 leaf and canopy levels. We chose a corn crop (*Zea mays* L.), also referred to as maize, because it provides a relatively simple canopy, typically a row crop with plants nominally having a spherical shape. As a C4 species, corn does not lose carbon through photorespiration, which makes GPP observations from flux towers more representative to the actual photosynthesis of the canopy. Maize is also a globally important crop that comprises the “bread-basket” to feed the world. Some have claimed (e.g., Guanter et al., 2014) that the observed far-red SIF obtained from space reveals that the US cornbelt achieves the highest
100 carbon sink of any of Earth’s ecosystems. On that basis alone, and because of the importance of agricultural surveys from space for food security reasons, we are justified to conduct a more comprehensive examination of the photosynthetic function and associated fluorescence activity of this crop.

We drew upon a unique dataset comprising growing season-long continuous measurements of a corn crop for leaf active
105 fluorescence, canopy SIF, hyperspectral reflectance, and GPP. With partial correlation analysis we evaluated the contributions of iPAR, fAPAR and APAR to the SIF-GPP relationship at the canopy scale. In parallel, we used active fluorescence measurements to investigate the energy partitioning in leaves to reveal the relationship between fluorescence and photosynthesis at the photochemical level.

2 Materials and methods

110 2.1 Study site

Field measurements were collected in 2017 at the Optimizing Production inputs for Economic and Environmental Enhancement (OPE³) field site (De Lannoy et al., 2006) at the US Department of Agriculture’s (USDA) Agricultural Research Service (USDA-ARS) in Beltsville, MD, USA (39.0306° N 76.8454° W, UTC-5). The site is instrumented with a 10 m eddy-covariance tower and a height-adjustable tower (i.e., 1.5-4 m tall) supporting the optical spectral measurements and surrounded
115 by corn (*Zea mays* L.) fields. The two towers were located within the same field that was provided the optimal (100%) nitrogen application for this climate zone, separated by approximately 120 m. Three distinct growth phases of the corn canopy were discerned: Young stage (Y) from DOY 192 to 209, Mature stage (M) from DOY 220 to 235 and Senescent stage (S) from DOY 236 to 264.

2.2 Field measurements

120 The field measurements included active fluorescence observations made on individual leaves, as well as canopy reflectance and SIF retrievals. These were supplemented by erap-carbon fluxes and meteorological data from the site’s instrumented tower. These measurements cover the 2017 growing season from day-of-year (DOY) 192 to DOY 264, except for the period from DOY 210 to DOY 219. The main field measurements used in this study are listed in Table 1. In what follows, we briefly introduce the measurements used in the present study (the field campaign was described in detail in Campbell et al., 2019).

125 *[Insert Table 1 here]*

The site's eddy covariance tower-based system provided 30-minute GPP fluxes continuously collected throughout the growing season. An infrared gas analyzer (Model LI-7200, LI-COR Inc., Lincoln, NE, USA) measured net ecosystem productivity (NEP), which was further partitioned into GPP and ecosystem respiration (R_e) using a standard approach (Reichstein et al., 2005) which extrapolated nighttime values of R_e into daytime values using air temperature measurements.

Canopy spectral measurements were collected by using a field spectroscopy system, the FLoX (JB Hyperspectral Devices UG, Germany), between 7:00 and 20:00 (local time) with a time sampling interval from 1-3 minutes. The system consists of two spectrometers: a QEpro spectrometer (Ocean Optics, Dunedin, FL, USA) and a FLAME-S spectrometer (Ocean Optics, Dunedin, FL, USA). The QEpro measured down-welling irradiance and up-welling radiance with a 0.3 nm spectral resolution at Full Width at Half Maximum (FWHM) between 650 and 800 nm, which were used to retrieve SIF. The FLAME-S measured the same up-welling and down-welling fluxes but between 400 to 1000 nm with a lower spectral resolution (FWHM of 1.5 nm), which were used to compute canopy values for reflectance (R) and to estimate incident PAR ($iPAR_{canopy}$) and $fAPAR_{canopy}$.

Leaf $fAPAR$ ($fAPAR_{leaf}$) was measured on six days spaced across the growing season ($n= 18$ samples per day). The leaf absorbance spectra between 350 and 2500 nm for nine leaves were measured in the laboratory with an ASD FieldSpec 4 spectrometer (Malvern Panalytical, Longmont, CO, USA) and an ASD halogen light source coupled with an integrating sphere. The mean $fAPAR_{leaf}$ values per date were computed: 0.92 ± 0.007 (i.e., mean \pm stdv) on DOY 192; 0.92 ± 0.01 on DOY 199; 0.91 ± 0.01 on DOY 221; 0.90 ± 0.03 on DOY 222; 0.82 ± 0.03 on DOY 240; and 0.75 ± 0.05 on DOY 263. Finally, $fAPAR_{leaf}$ on the rest of the days was linearly interpolated/extrapolated from those measurements. Therefore, $fAPAR_{leaf}$ values ranged from 0.93 to 0.70 across the growing season.

Leaf-level active fluorescence measurements were collected by using an automated MoniPAM fluorometer system (Walz, Germany) and five MoniPAM emitter-detector probes, which were operated using a MoniPAM Data Acquisition system (Porcar-Castell et al., 2008). Three probes were positioned to measure sunlit leaves in the upper canopy and the remaining two probes collected measurements on shaded leaves within the lower canopy. The fluorometer collected continuous steady state fluorescence (F_s) and maximal fluorescence (F_m) every 10 minutes during the day and night. The MoniPAM measured chlorophyll fluorescence induced by an internal, artificial light source, which produces modulated light with constant intensity (Baker, 2008; Schreiber et al., 1986). In addition to leaf fluorescence measurements, the MoniPAM also measured leaf temperature by an internal temperature sensor and incident PAR ($iPAR_{leaf}$) by a PAR quantum sensor. Leaf APAR ($APAR_{leaf}$) was computed as the product of $iPAR_{leaf}$ and $fAPAR_{leaf}$.

2.3 Data quality control and sampling

Data quality control of canopy reflectance, SIF and GPP measurements was conducted prior to the analysis. First, measurements collected on 29 rainy or densely clouded days were excluded. Second, a window-based outlier detection was applied to incident PAR data collected by the FLoX to identify unrealistic short-term fluctuations in atmospheric conditions leading to unreliable SIF retrievals. The fluctuations were detected by finding the iPAR_{canopy} measurements that were not within ± 3 times the standard deviation for the mean of seven consecutive measurements. Once all cases with fluctuating atmospheric conditions were identified, the reflectance, GPP and SIF measurements acquired within \pm half hour of their occurrence were excluded from the analysis. Finally, the remaining FLoX measurements were re-sampled into the 30-minute temporal resolution of the eddy covariance measurements.

2.4 Calculation of canopy SIF, fAPAR and APAR

The QEpro spectral measurements were used to compute Top-of-Canopy (TOC) SIF in the O₂-A absorption feature at around 760 nm (F_{760}). SIF was retrieved using the spectral fitting method (SFM) described in Cogliati et al. (2015). Canopy iPAR (iPAR_{canopy}) was computed from the irradiance spectra collected with the FLAME-S spectrometer as the integral of irradiance over the spectral region from 400 to 700 nm. Canopy fAPAR was approximated by using the Rededge NDVI (Normalized Difference Vegetation Index) (Miao et al., 2018; Viña and Gitelson, 2005):

$$fAPAR = 1.37 \cdot RededgeNDVI - 0.17 \quad (2a),$$

where

$$RededgeNDVI = \frac{R_{750} - R_{705}}{R_{750} + R_{705}} \quad (2b),$$

where reflectance at specific wavelengths is utilized (R_{λ} : 705 and 750 nm). Rededge NDVI is a widely used index for estimating fAPAR, and Viña and Gitelson (2005) suggest it as an optimal index for fAPAR among various other vegetation indices in corn canopies. We, however, have tested several other indices for estimating fAPAR, including the enhanced vegetation index (EVI) (Huete et al., 2002; Xiao et al., 2004) and the green NDVI (Viña and Gitelson, 2005), and found that the choice among the three indices had little impact on the results in section 3.1. We also computed the photochemical reflectance index PRI=

$\frac{R_{531} - R_{570}}{R_{531} + R_{570}}$ (Gamon et al., 1992), as an indicator of diurnally reversible canopy heat dissipation efficiency $\Phi_{Ncanopy}$.

2.5 Quantifying energy partitioning from leaf fluorescence measurements

The continuous MoniPAM measurements offered a way for assessing the dynamics of energy partitioning in photosystem II (PSII). The pathways include photochemistry (P), fluorescence emission (F) and heat dissipation (H). H is further categorized as a sustained thermal dissipation (D) and a reversible energy-dependent heat dissipation (N). N is controlled by mechanisms that regulate the electron transport of the photosystems and is related to photo-protection mechanisms and NPQ (Baker, 2008).

Relative fluorescence emission efficiency (Φ_F^*) was derived from the MoniPAM steady state fluorescence measurements F_s , with a correction for time-varying leaf absorption in the growing season. The correction is needed because F_s responds to the absorbed measurement light rather than the incident measurement light:

$$190 \quad \Phi_F^* = \frac{F_s}{fAPAR_{\text{leaf}}} \quad (3)$$

MoniPAM maximal fluorescence measurements (F_m), together with the steady state fluorescence (F_s), allows the assessment of the absolute efficiencies of absorbed light energy for photochemistry (Φ_P) and the reversible energy-dependent heat dissipation (Φ_N) of PSII. The usual approach to obtain Φ_P is to ‘switch off’ photochemistry by applying a saturating light to
 195 leaves, so that the fluorescence measurements in the presence and absence of photochemistry (F_s and F_m), can be estimated (Maxwell and Johnson, 2000). A generic expression of Φ_P proposed by Genty et al. (1989) was used:

$$\Phi_P = 1 - \frac{F_s}{F_m} \quad (4)$$

Unlike photochemistry, it is difficult to fully inhibit heat dissipation. Nevertheless, long duration dark-adaptation can reduce
 200 reversible heat dissipation to zero. Then, fluorescence measurements acquired in the presence and absence of reversible heat dissipation can be estimated. We took the expression proposed by Hendrickson et al. (2004) for Φ_N :

$$\Phi_N = \frac{F_s}{F_m} - \frac{F_s}{F_m^o} \quad (5)$$

where F_m^o is the highest (or maximal) value obtained for dark-adapted leaf fluorescence measurements in the absence of reversible heat dissipation; the pre-dawn value of F_m is typically used as an estimate of true maximal dark-adapted fluorescence
 205 (Maxwell and Johnson, 2000). Alternative expressions of Φ_N can be found in the literature, but they are equivalent and convertible to each other. For example, Eq. 5 can be rewritten as $\Phi_N = (1 - \Phi_P)(1 - \frac{F_m}{F_m^o})$. Furthermore, it can be expressed as a function of a commonly used fluorescence parameter NPQ, which is defined as $\frac{F_m}{F_m^o} - 1$ (Baker, 2008). In that formulation, $\Phi_N = (1 - \Phi_P) \frac{NPQ}{NPQ+1}$.

210 The expression of the sum of Φ_F and Φ_D (symbolized as Φ_{F+D}) is straightforward, because the sum of the efficiencies of the four pathways (Φ_F , Φ_P , Φ_D and Φ_N) is always unity and $\Phi_{F+D} = 1 - \Phi_N - \Phi_P$, and

$$\Phi_{F+D} = \frac{F_s}{F_m^o} \quad (6)$$

Further separation of Φ_F and Φ_D from Φ_{F+D} is difficult, because neither can be inhibited. However, relative efficiency of the
 215 sustained heat dissipation (Φ_D^*) across the growing season can be inferred from the pre-dawn values of F_m (i.e., F_m^o). Because F_m^o was measured during the night in the absence of both reversible heat dissipation and photochemistry, a change in F_m^o must

be caused by a change in the sustained heat dissipation. Therefore, we can take the maximal pre-dawn $\Phi_{F_m}^* = \frac{F_m^0}{fAPAR_{leaf}}$, (when Φ_D^* is minimal) as a reference and express Φ_D^* across the growing season as:

$$\Phi_D^* = 1 - \frac{F_m^0 / fAPAR_{leaf}}{\max_{192 \leq DOY \leq 264} [F_m^0 / fAPAR_{leaf}]} \quad (7)$$

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Photosynthetic light use efficiency can be predicted as a function of leaf temperature, ambient radiation levels, intercellular CO₂ concentrations C_i , and other leaf physiological parameters (e.g., photosynthetic pathways, maximum carboxylation rate at optimum temperature - V_{cmo}) by using a conventional photosynthesis model of Collatz et al., (1992; 1991). Van der Tol et al., (2014) established empirical relationships between fluorescence emission efficiency and photosynthetic light use efficiency under various environmental conditions by using active fluorescence measurements. With these relationships, the fraction of the absorbed radiation by a leaf emitted as fluorescence and dissipated as heat can be simulated. The MoniPAM system measured leaf temperature and incoming radiation intensity. We reproduced the efficiencies of photochemistry, fluorescence, and reversible and sustained heat dissipation by using the biochemical model of Van der Tol et al., (2014). The two most influential model input variables, leaf temperature and incoming radiation, were measured by using the field measurements MoniPAM. V_{cmo} was set to $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ at $25 \text{ }^\circ\text{C}$, a recommended value for the corn crop (Houborg et al., 2013; Wullschlegel, 1993; Zhang et al., 2014). of leaf temperature and incoming radiation intensity were used for the model input. We set V_{cmo} to $30 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is a recommended value for C4 crops, and T the rest of the model parameters (e.g., C_i) to their default values. In this way, we simulated the efficiencies for the temporal resolution of the MoniONIPAM measurements (i.e., 10 minutes) and examined the relationship among the efficiencies as predicted by the biochemical model.

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2.6 Statistical analysis

Pearson correlation coefficients (ρ) were computed to evaluate the relationships between pairs of observations, such as Φ_p and Φ_F^* , or GPP and SIF. In addition to the correlation coefficients, partial correlation coefficients were computed to measure the degree of association between GPP and SIF, where the effect of a set of controlling variables was removed, including fAPAR, iPAR and APAR. Partial correlation is a commonly used measure for assessing the bivariate correlation of two quantitative variables after eliminating the influence of one or more other variables (Baba et al., 2004). The partial correlation between x and y given a controlling single variable z was computed as

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$$\rho_{x,y(z)} = \frac{\rho_{x,y} - \rho_{x,z}\rho_{y,z}}{\sqrt{1-\rho_{x,z}^2}\sqrt{1-\rho_{y,z}^2}} \quad (8)$$

where $\rho_{x,y}$ is the Pearson correlation coefficient between x and y.

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Partial correlation can be calculated to any arbitrary order. $\rho_{x,y(z)}$ is a first-order partial correlation coefficient, because it is conditioned solely on one variable (z). We used a similar equation to calculate the second-order partial coefficient that accounts

for the correlation between the variables x and y after eliminating the effects of two variables z and q (de la Fuente et al., 2004).

$$\rho_{x,y(zq)} = \frac{\rho_{x,y(z)} - \rho_{x,q(z)}\rho_{y,q(z)}}{\sqrt{1-\rho_{x,q(z)}^2}\sqrt{1-\rho_{y,q(z)}^2}} \quad (9)$$

250 3 Results

3.1 Relationship between canopy SIF and GPP observations

Fig. 1a confirms the linear SIF-GPP relationship reported in previous studies and shows that F_{760} and GPP were strongly correlated with an overall correlation $\rho = 0.83$. This correlation was slightly stronger than the relationship between $\text{APAR}_{\text{canopy}}$ and GPP (an overall $\rho = 0.80$, Fig. 1b). The $\text{APAR}_{\text{canopy}}$ -GPP relationship was apparently comprised of parallel groups of responses (colors) with large variation in GPP exhibited for the same levels of $\text{APAR}_{\text{canopy}}$ (Fig. 1b). This relationship complies with the common understanding of the response of photosynthesis to light showing the well-known saturation with irradiance as photosynthesis of the whole canopy gradually shifts from light limitation to carbon limitation, while the unexplained (by light intensity) variation in GPP can be attributed to stomatal aperture responses and a time-varying carboxylation capacity, especially in the upper sunlit canopy, which experienced larger variations of light intensity. SIF, which is affected by both light and carbon limitations, shows a more linear response to GPP than $\text{APAR}_{\text{canopy}}$ (Figs. 1a vs. 1b).

[Insert Figure 1 here]

Incoming radiation (i.e., $\text{iPAR}_{\text{canopy}}$) had a strong, positive linear relationship with SIF, GPP and $\text{APAR}_{\text{canopy}}$ (as shown in Figs. 1 and 2). We investigated these canopy-scale relationships with partial correlation analysis as diagrammed in Fig. 2, where for simplicity's sake, the subscripts denoting “canopy” variables were omitted in the diagram. Our team (Yang et al., 2020) and others (Miao et al., 2018; Migliavacca et al., 2017) have previously demonstrated that in addition to incoming radiation intensities, the energy available for photochemistry and fluorescence (i.e., $\text{APAR}_{\text{canopy}}$) is strongly affected by canopy structure and leaf biochemistry. As a result, there were cases of low SIF, GPP and/or $\text{APAR}_{\text{canopy}}$ values at high $\text{iPAR}_{\text{canopy}}$ (Fig. 1, red and orange dots), and *vice versa* high SIF, GPP and/or $\text{APAR}_{\text{canopy}}$ values at low $\text{iPAR}_{\text{canopy}}$ (Fig. 1, blue and violet dots). This is shown in the correlation diagram as well (Fig. 2) which indicates that SIF, GPP and $\text{APAR}_{\text{canopy}}$ were all moderately dependent on leaf biochemistry as well as on canopy structure according to their correlations with $\text{fAPAR}_{\text{canopy}}$, i.e., $\rho_{\text{SIF},\text{fAPAR}} = 0.60$, $\rho_{\text{GPP},\text{fAPAR}} = 0.58$ and $\rho_{\text{APAR},\text{fAPAR}} = 0.70$ (i.e., numbers in bold, blue text, Fig. 2). Compared with either $\text{iPAR}_{\text{canopy}}$ or $\text{fAPAR}_{\text{canopy}}$, $\text{APAR}_{\text{canopy}}$ as their product (located in center, Fig. 2) can better explain the variations in SIF and GPP observations, with Pearson correlations of $\rho = 0.92$ and 0.80 , respectively.

275 *[Insert Figure 2 here]*

After removing the effects of this important controlling variable that affects both SIF and GPP, namely $\text{APAR}_{\text{canopy}}$, the correlation between GPP and SIF was weak ($\rho_{\text{SIF,GPP}(\text{APAR})} = 0.27$; refer to results below the triangle's baseline). In contrast, the correlation between SIF and GPP remained significant after controlling for the effects of the components of canopy APAR, either $\text{fAPAR}_{\text{canopy}}$ or $\text{iPAR}_{\text{canopy}}$, i.e., $\rho_{\text{SIF,GPP}(\text{fAPAR})} = 0.72$, $\rho_{\text{SIF,GPP}(\text{iPAR})} = 0.66$ (equations below the triangle, Fig. 2).

We further investigated how the SIF-GPP relationship varied seasonally with growth stage and diurnally with time of the day (Fig. 3). The SIF-GPP correlation was significantly lower (by 22-27%) for the senescent canopy than for the young and mature canopy. The Pearson correlation coefficient was highest when the canopy was fully developed with the underlying surface covered in the mature stage ($\rho = 0.77$, Fig. 3b). As for the different times of a day, we found that their correlations were the strongest in the afternoon ($\rho = 0.89$) while ρ was only 0.76 when the data were acquired in the morning, ~~representing an order of magnitude improvement of 13% from mid-morning to mid-afternoon observations~~ (Figs 3d vs. 3f).

[Insert Figure 3 here]

290 3.2 Dynamics of energy partitioning in photosystems

The continuously acquired active fluorescence measurements offered a way to assess the dynamics of energy partitioning in photosystems and facilitated the understanding of the relationship between fluorescence and photosynthesis before aggregation to the canopy, at the photochemical level. We investigated how the partitioning evolved over time.

295 During the nighttime, as can be seen from the responses in the dark-bars in Figs. 4a and 4b, the photosystem energy partitioning was stable for all leaves, whether they were designated as sunlit or shaded during the day. Three efficiencies (Φ_P , Φ_F^* and Φ_D^*) showed little overnight change, and the reversible heat dissipation Φ_N was always close to zero. This null response for Φ_N agrees with the known status/behavior of the most important driver of reversible heat dissipation, the xanthophyll pigment cycle, which reverts overnight to the energy-neutral form violaxanthin, and then converts during the day to antheraxanthin in moderately high light levels and subsequently to zeaxanthin at high light levels by chemical de-epoxidation (Middleton et al., 300 2016; Müller et al., 2001).

[Insert Figure 4 here]

During the daytime, there were dramatic day-to-day changes in energy partitioning to photochemistry, fluorescence and reversible heat dissipation (Figs. 4a and 4b). Generally, both Φ_F^* and Φ_N increased during mornings to midday and decreased afterwards, except that Φ_N exhibited unexplained midday dips during the senescent stage. On the other hand, Φ_P decreased during mornings to midday lows and increased afterwards (i.e., Φ_P diurnals were bowl-shaped, as shown in many studies).

The changes in Φ_N and Φ_P corresponded closely with the changes in incident radiation, while Φ_F^* changes corresponded closely with the dynamics in incident radiation in the morning but not at midday when the radiation level was high.

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At the seasonal scale (Fig. 4), however, the nighttime energy partitioning over the three other pathways (Φ_P , Φ_F^* and Φ_D^*) displayed substantial variations. The nighttime Φ_P was about 0.82 on all days during the young and mature stages, which is close to the theoretical maximal value (Zhu et al., 2008), but it was only about 0.64 during the senescent stage. Similarly, the nighttime relative light use efficiency of fluorescence Φ_F^* clearly decreased as the canopy development progressed from the physiologically robust (young and mature) stages to the senescent stage. For example, the nighttime Φ_F^* for both the sunlit and shaded leaves was above 60 in the young stage but was around 50 in the senescent stage. The seasonal/growth stage decreases during nighttime in both Φ_F^* and Φ_P were attributed to an increase of sustained heat dissipation Φ_D^* since nighttime Φ_N was always close to zero. In extrapolating Φ_D^* to daytime, we assumed that the sustained heat dissipation remained unchanged within any full day (from 0:00 to 24:00), but noticeable changes in Φ_D^* sometimes occurred between two consecutive days, e.g., between Φ_D^* on DOY 194 and DOY 195, and between DOY 230 and DOY 231, as indicated in Fig. 4.

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Although the sunlit and shaded leaves had similar seasonal and diurnal patterns, some interesting differences are observed. As expected, the radiation levels were higher for the sunlit leaves than for the shaded leaves, which produced higher Φ_F^* for the sunlit leaves and slightly lower Φ_P at the young and mature stages. In comparison to the difference in Φ_F^* , the difference in Φ_P was less pronounced. At the senescent stage Φ_P of the shaded leaves was substantially lower than sunlit leaves despite receiving lower radiation, which normally would lead to higher Φ_P . This could be attributed to the different leaf ages and functionality of sunlit and shaded leaves; for example, shaded corn leaves senesce earlier than sunlit leaves. Additionally, Φ_D^* of sunlit leaves was higher than the shaded leaves while Φ_N of the sunlit and shaded leaves was similar.

325

330

It is evident that the contribution to the photosynthetic process by the combined nighttime fluorescence and sustained heat dissipation group (Φ_{F+D} , red color in Fig. 5) increased through the growing season, to competitively reduce photochemical efficiency (Φ_P , green color), especially during senescence. The increase of sustained heat dissipation (Fig. 4) also resulted in a decrease of Φ_P in the daytime as the young and mature stages progressed through the senescent stage, although Φ_P can vary substantially during the daytime. Additionally, the diurnally reversible heat dissipation (Φ_N , gold color) was generally higher at the senescent stage than at the young and mature stages, which contributed to the reduction in photochemical efficiency as well. In the pie charts, we focus on the energy partitioning in both nighttime and midday since they ~~portray~~represent the potential maximal Φ_P (i.e., the photosynthetic reaction centers in the nighttime are mostly open) and the steady-state Φ_P at the most common time of day for satellite observations, respectively.

335

[Insert Figure 5 here]

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The pie charts (Fig. 5) clearly show how these the partitioning of the relative efficiency pathway contributions changed with growth stage on the three representative clear sky days. The nighttime Φ_p was reduced by 2017% between the young and senescent stages, while Φ_{F+D} increased by 4619% during senescence. The pie charts also clearly show the very strong role of reversible heat dissipation in limiting midday photosynthesis throughout the growing season. For example, the per cent contribution for the pathways from the young crop (DOY 196) was 353% for Φ_p , 232% for Φ_N , and 425% for Φ_{F+D} . The corresponding values for leaves in the mature crop (DOY 232) were 310%, 142%, and 569%. And for the leaves in the senescing crop (DOY 254), the corresponding values were 143%, 26%, and 61%. Combining these together, Fig. 5 further highlights the complexity of energy efficiency dynamics underlying the photosynthetic process.

3.3 Relationships among photosynthesis, fluorescence and heat dissipation at leaf level

350 Next, we examine the leaf-level efficiency terms obtained from *in situ* measurements, in terms of their combined responses. The first set compares Φ_F^* and Φ_p , in the context of variable $iPAR_{leaf}$ (Figs. 6a, b). This figure clearly shows that the relationship between Φ_F^* and Φ_p during daylight (9:00 - 17:00) was different for the sunlit (sun adapted) vs. shaded (shade adapted) leaves, since the sunlit leaves were more often exposed to $iPAR$ above $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. The higher Φ_p values were obtained for relatively low $iPAR_{leaf}$, whether sunlit or shaded. For sunlit leaves, Φ_F^* and Φ_p were positively correlated overall 355 ($\rho = 0.53$, Fig. 6a) and in conditions with moderate to high light intensity ($iPAR_{leaf} > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$, excluding blue and teal colored dots), $\rho = 0.60$. In contrast, at low light intensity ($iPAR_{leaf} < 500 \mu\text{mol m}^{-2} \text{s}^{-1}$, blue dots), correlation between Φ_F^* and Φ_p was weak and negative for $\Phi_p > 0.4$. These two efficiency terms were uncorrelated in shaded leaves (Fig. 6b), and Φ_F^* was much lower in the shaded than in sunlit leaves. The correlations on individual days are presented in Fig. 8a, which shows that positive correlations between Φ_F^* and Φ_p are more often for sunlit leaves than shaded leaves.

360 *[Insert Figure 6 here]*

At the seasonal scale, the midday Φ_F^* and Φ_p values (the average of all values acquired between 11:00 and 14:00) had a quasi-linear, positive relationship for both the sunlit and shaded leaves when $iPAR_{leaf} > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 6c). In contrast, at low average midday light intensities, the relationships were clearly negative. The Φ_p values tended to decrease with the increasing 365 light intensities while the relationship between Φ_F^* and $iPAR_{leaf}$ was not definite. However, the seasonally averaged-ranges for Φ_F^* in sunlit and shaded leaves clearly represent two populations: Φ_F^* shaded was < 110 (Fig. 6**cb**) whereas Φ_F^* sunlit > 100 (Fig. 6**ac**). These results could have implications for interpreting canopy-scale measurements.

The linear relationship obtained between Φ_p and Φ_N was considerably stronger for both sunlit and shaded leaves (Figs. 7a, b) 370 than the correlation between Φ_F^* and Φ_p previously shown for sunlit leaves (Fig. 6**7a**). Here, both sunlit and shaded leaves showed consistent and strong linear decreases in Φ_p as Φ_N increased (Figs. 7a, b) in response to variations-increase in the intensity of incoming light ($iPAR_{leaf}$, Fig. 4) (Figs. 7a, b). Furthermore, the Φ_p and Φ_N relationships definitely varied in

response to the sustained heat dissipation (Φ_D^* , levels represented in the color bar) in a similar fashion for both sunlit and shaded leaves, although higher Φ_D^* values (orange and red dots) were obtained in sunlit leaves. The efficiency of photochemistry obviously declined at higher Φ_D^* , as indicated with the arrows in Fig. 7, especially pronounced in sunlit leaves. For shaded leaves, there were cases with higher Φ_D^* that did not result in lower Φ_P (the orange dots in Fig. 7b). -When both thermal dissipations were strongly fully manifested expressed, the Φ_P was greatly reduced; in sunlit leaves, this reduction was ~40%. The correlations on individual days are presented in Fig. 8b, which shows Φ_N and Φ_P are negatively correlated for both sunlit and shaded leaves.

375
380 *[Insert Figure 7 here]*

[Insert Figure 8 here]

At the seasonal scale, as can be seen from Figs. 4 and 5, Φ_P decreased while Φ_D^* increased as the canopy progressed through its growth stages. Their seasonal relationship is depicted in Fig. 7c, showing a same-day comparison of the midday Φ_P value (the average between 11:00 and 14:00), as a function of Φ_N across the growing season noting that Φ_D^* remained unchanged within any full day. Generally, Φ_N and Φ_P exhibited an overall negative correlation, but clearly their relationship was regulated by Φ_D . This is seen in the different midday Φ_P responses at high vs. low Φ_D^* values. At the same level of Φ_N (around 0.05), the magnitudes of midday Φ_P varied by up to 0.45 (65%, from 0.37 to 0.61 in Fig. 7c) due to variations in the efficiency of the sustained heat dissipation which varied between 0.1 and 0.6.

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We have shown that Φ_P was regulated by heat dissipation (Figs. 5 and 7), and was moderately correlated with Φ_F^* for the sunlit leaves (Fig. 6). With the dynamics of energy partitioning within the photosystem now quantified, we interpret the emerging relationship between photochemical and fluorescence efficiencies, namely Φ_P and Φ_F^* (Table 2), in the context of thermal dissipation efficiencies (Φ_N , Φ_D^*). After eliminating the effects of both sustained and reversible heat dissipation, Φ_P and Φ_F^* were negatively and equally correlated ($\rho = -0.75$) for both sunlit and shaded leaves. As surprising as this is, the presence of either sustained or reversible heat dissipations changed this underlying negative relationship (Φ_P vs. Φ_F^*) into an observed apparent positive relationship at leaf scale, which contributes to the positive relationship of GPP and SIF at canopy scale. In fact, accounting for the effects of either Φ_N or Φ_D^* reduced the correlation coefficients between Φ_P and Φ_F^* . For sunlit leaves, controlling for only Φ_N reduced the correlation from 0.53 to 0.05 (by ~0.48 units); after controlling for only Φ_D^* , the correlation dropped by 0.45 units to 0.08. For shaded leaves this reduction was from 0.10 to -0.31 after controlling for Φ_N , or to -0.35 after controlling for Φ_D^* . ~~The These results represent reduction of the correlation between Φ_P and Φ_F^* , trends that include were caused by both~~ diurnal variations in Φ_N and seasonal variations in both Φ_N and Φ_D^* .

400

[Insert Table 2 here]

405 Results of model simulations are presented in Figs [98](#) and [109](#). In comparison with Figs. 6 and 7 that describe our *in situ* measurements, these two figures show that the biochemical model outputs were more successful in describing photosynthetic efficiency as a function of reversible heat dissipation (Φ_N) than fluorescence efficiency (Φ_F). Specifically, for the Φ_P - Φ_F relationships, the Fig. [8-9](#) simulation shows some similarity to the Fig. 6 measurements, but clearly does not capture the different responses we obtained for sunlit versus shaded leaves. However, Fig. [109](#) does generally replicate the general responses expected based on *in situ* measurements (Fig. 7), portraying the strong negative impact of Φ_N on Φ_P , but it doesn't convey the variability captured under field conditions. These differences occurred in the simulations because we did not consider the physiological (i.e., enzyme activity) or physical (i.e., thickness, pigment ratios) differences among leaves at different growth stages. Neither did we consider the physical differences or photochemical potential differences (e.g., total chlorophyll content and Chl a/b ratios; rubisco activity) between sunlit and shaded leaves in this modelling experiment.

415 Therefore, it is to be expected that the simulations for sunlit and shaded leaves would be similar, and not displaying the differences observed in field measurements. Furthermore, we did not include changes in leaf display geometry induced by low water stress (i.e., drought) in the simulation, but it is a common phenomenon in corn plants in the field, in either measurements ~~or the~~ simulations. Another likely reason contributing to the differences between simulations and observations is that in using the model of Van der Tol et al. (2014) to derive Φ_F from Φ_P , Φ_D is assumed to be a constant and Φ_N is empirically estimated

420 as a function of Φ_P/Φ_{P0} . The observations shown in Figs. 4 and 5 prove that Φ_D varied over the growing season, and therefore, cannot be considered as a constant. These findings may help improve the modelling of Φ_F at the biochemical level and thus improve our understanding of the relationship between SIF and GPP at the canopy scale.

[Insert Figure [98](#) here]

425 *[Insert Figure [109](#) here]*

3.4 Comparison of light use efficiencies at leaf and canopy levels

The responses of the efficiencies to APAR and the relationships between these efficiencies are diagrammed in Fig. 10, showing the Pearson correlation coefficients between pairs of variables, for leaves (Fig. [10a11a](#)) that were either sunlit or shaded (indicated in bold, blue text), and for canopy (Fig. [10b11b](#)).

430 *[Insert Figure [10-11](#) here]*

At the leaf level, we see that Φ_F^* showed moderate correlation to Φ_P for sunlit leaves ($\rho = 0.53$) but very low correlation to Φ_P for shaded leaves ($\rho = 0.10$). The highest correlations were negative, denoting inverse relationships between Φ_N and Φ_P (-0.74 sunlit and -0.87 shaded), whereas similar positive correlations (0.64 sunlit and 0.68 shaded) were obtained between

435 Φ_N and $\text{APAR}_{\text{leaf}}$ (located in center, Fig. [10a11a](#)), as expected since Φ_N is well known to be light-level sensitive when invoking the xanthophyll cycle. Notice that all of the high correlations (>0.64 or <-0.74), whether positive or negative, are located on the left-hand side of Fig. [10a11a](#), which compares efficiencies of photochemistry with efficiencies of reversible thermal

dissipation (Φ_N) and their connection through $\text{APAR}_{\text{leaf}}$. The remaining correlations on the right-hand side, between Φ_F^* and either Φ_P , Φ_N , or $\text{APAR}_{\text{leaf}}$, are significantly lower (from -0.33 to 0.53).

440

At the canopy level, $\Phi_{F\text{canopy}}$ also showed moderate correlation to $\Phi_{P\text{canopy}}$ with $\rho = 0.37$ (Fig. ~~10b11b~~, for the scatter plot between $\Phi_{P\text{canopy}}$ and $\Phi_{F\text{canopy}}$, see Fig. A1), which falls between the values for sunlit and shaded leaves (Fig. ~~10a11a~~). An inverse relationship between $\Phi_{P\text{canopy}}$ and $\text{APAR}_{\text{canopy}}$ (-0.41) was found at the canopy level, but this correlation was much weaker than that at the leaf level (-0.75 for both sunlit and shaded leaves). The photochemical reflectance index $\text{PRI} = \frac{R_{531} - R_{570}}{R_{531} + R_{570}}$ (Gamon et al., 1992), as an indicator of $\Phi_{N\text{canopy}}$, appeared to have no correlations with either $\text{APAR}_{\text{canopy}}$ or $\Phi_{P\text{canopy}}$, while at the leaf level these three variables had strong correlations (located on the left-hand side of Fig. ~~10a11a~~). Comparing the efficiencies obtained from the leaf- and canopy-level measurements (i.e., $\Phi_{P\text{canopy}}$ vs. Φ_P or $\Phi_{F\text{canopy}}$ vs. Φ_F^*), no clear relationships were found ($\rho < 0.1$, data are ~~not~~ shown in Fig. A2).

450 *[Insert Figure 12 here]*

[Insert Table 3 here]

Comparison of Fig 11a with Fig. 12a reveals that the strength of correlations between pairs of variables describing energy partitioning for both sunlit and shaded leaves increased for most pairs when evaluated at midday vs. diurnal measurements (Table 3). For example, three pairs showed notable correlation enhancements for sunlit leaves in midday across the growing season: the negative correlations between Φ_N and Φ_F^* (from -0.33 to -0.45) and between $\text{APAR}_{\text{leaf}}$ and Φ_F^* (from -0.10 to -0.27), and the positive correlation between Φ_P and Φ_F^* (from 0.53 to 0.62). Shaded leaves showed similar but even stronger responses than sunlit leaves overall at midday, and especially for these same three pairs: Φ_N vs. Φ_F^* (shaded, from -0.23 to -0.45), and Φ_N vs. Φ_F^* (from 0.10 to 0.27). In addition, for shaded leaves, the midday positive correlation between $\text{APAR}_{\text{leaf}}$ and Φ_N also was higher (from 0.68 to 0.77) as was the negative correlation between Φ_N and Φ_P (from -0.87 to -0.92), while the positive correlation between $\text{APAR}_{\text{leaf}}$ and Φ_F^* became a weak negative association (from 0.25 to -0.14). No noticeable correlation changes occurred for sunlit leaves at midday vs. daily measurements for these two pairs: Φ_N - Φ_P ($\rho \approx -0.75$) or $\text{APAR}_{\text{leaf}}$ - Φ_N ($\rho \approx 0.61$). The negative correlations were equal for sunlit and shaded leaves between Φ_N and Φ_P whether determined for daily or at midday, but the midday correlation was stronger (from -0.75 to -0.81). Especially noteworthy are the strong negative correlations that were observed (Table 3) in sunlit and shaded leaves for Φ_N and Φ_P (between -0.74 and -0.92) and $\text{APAR}_{\text{leaf}}$ and Φ_P (between -0.75 and -0.81).

Comparison of Fig. 11b and Fig. 12b reveals that at the canopy scale all correlations between variable pairs were relatively modest (e.g., $\rho \leq \pm 0.55$) but were higher at midday than for daily observations across the growing season, except for $\Phi_{N\text{canopy}}$ (as estimated with the PRI) vs. $\Phi_{F\text{canopy}}$ (≤ -0.07 , indicating no relationship). For the remaining five pairs, the strongest and

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most improved responses at midday were between $\Phi_{P_{canopy}}$ and $\Phi_{F_{canopy}}$ (from 0.37 to 0.53) and between $APAR_{canopy}$ and $\Phi_{P_{canopy}}$ (from -0.41 to -0.55), with a stronger association also seen for $APAR_{canopy}$ vs. $\Phi_{F_{canopy}}$ (from -0.25 to -0.32). It is apparent that the canopy responses based on remote sensing, without including critical information on the sunlit/shaded canopy illumination fractions (Figs 11b, 12b), were less successful in describing the energy partitioning that was provided at the leaf level (Figs. 11a, 12a).

4 Discussion

4.1 Physical basis for the SIF-GPP relationship

Incoming radiation intensity, leaf biochemistry, leaf and canopy structure all affect $APAR_{canopy}$, the energy source for photosynthesis, SIF and heat dissipation. We found an equal contribution of $iPAR_{canopy}$ and $fAPAR_{canopy}$ to the observed SIF-GPP canopy relationship. The correlation coefficients between SIF and GPP remained relatively high after controlling either term. In stark contrast, after holding $APAR$ (their product, $iPAR_{canopy} \times fAPAR_{canopy}$) constant, the SIF-GPP canopy correlation coefficient was reduced from 0.83 to 0.27. This demonstrates the dominance of $APAR_{canopy}$ in determining the relationship between SIF and GPP. Compared to $APAR_{canopy}$, SIF was slightly better correlated with GPP (Fig. 1). The physiological information implied in GPP was seemingly better expressed with SIF than $APAR_{canopy}$.

The interfering effects of f_{esc} at canopy scale have not been considered explicitly. They are implicit in the relations of $\rho_{SIF,GPP(APAR)}$ (Qiu et al., 2019). When accounted for, they may provide a better estimate of the correlation attributable to the physiological response of photosystems (i.e., $\rho_{SIF,GPP(APAR,f_{esc})} > 0.27$). The magnitude and sign of $\rho_{SIF,GPP(APAR)}$ are nevertheless consistent with the moderate correlation we found between leaf Φ_F^* and Φ_P for sunlit leaves and the weak correlation for shaded leaves (Figs. 6 and 10a11a). In addition, we found that the positive relationship between Φ_F^* and Φ_P at the seasonal time scale is dominated by the progressive increase of sustained heat dissipation (Φ_D^*) during senescence. In contrast, there was significant diurnal but no clear seasonal variation of Φ_N .

4.2 Physiological basis for the SIF-GPP relationship

Clear differences between the responses of sunlit and shaded leaves influence the correlation for the canopy as a whole. The Φ_F and Φ_P of sunlit leaves exposed to moderate or high $iPAR_{canopy}$ exhibited a moderately strong linear relationship, while no such relationship existed for leaves at low $iPAR_{canopy}$ (independent of whether the leaves were classified as sunlit or shaded leaves). Leaves regularly receiving sunlight during development (sunlit leaves) differ structurally and biochemically from leaves in lower light positions in the canopy. Shaded leaves are often thinner, smoother, and larger in surface area (Dai et al., 2004). The larger shaded leaves provide a larger area for absorbing light energy for photosynthesis where light levels are lower. In contrast, smaller sunlit leaves provide less surface area for the loss of water through transpiration which is higher due to

direct exposure to solar radiation. The greater mesophyll thickness of sunlit leaves produces more inter-cellular spaces to facilitate increased carbon dioxide conductance into their smaller chloroplasts, producing greater rates of photosynthesis per unit leaf area in sunlit leaves (Givnish, 1988; Jackson, 1967).

505 The investigated crop has a C4 photosynthetic pathway, in which dark and light reactions are separated, and carboxylation takes place under a high CO2 concentration. This strongly suppresses photorespiration in C4 vegetation, resulting in a higher water use efficiency and lower sensitivity to heat and high vapour pressure deficit than for C3 vegetation. Liu et al. (2017) reported that the GPP-SIF relationship was much stronger for a C4 crop (corn) than a C3 crop (wheat). They showed that while $\Phi_{Fcanopy}$ of the C3 and C4 crops were similar, the $\Phi_{Pcanopy}$ of corn was much higher than for wheat. Because of
510 different photosynthetic pathway and the contribution of photorespiration, the SIF-GPP relationship of C3 vegetation is more complicated in the corn crop examined in this study.

Compared to the relationship between leaf fluorescence emission efficiency, total heat dissipation (both D and N) provided a robust and direct indicator of leaf photosynthetic light use efficiency (Fig. 7). In particular, the variation of reversible heat
515 dissipation better explains the diurnal variation of leaf photosynthetic light use efficiency, whereas the sustained heat dissipation contributes to the seasonal variation. –Reversible heat dissipation is the main regulating mechanism for the dissipation of absorbed photosynthetically active energy radiation energy (Adams et al., 1989; Demmig-Adams et al., 1996; Heber et al., 2006; Huang et al., 2006). –and Our study confirms its dominant role for the corn crop with field measurements and finds that the reversible heat dissipation is responsible for the positive relationship between Φ_F and Φ_P of sunlit leaves at
520 diurnal scales, though less so at seasonal scales when sustained heat dissipation is dominant (Fig. 6) (Heber et al., 2006). Remote sensing monitoring at the canopy/landscape scale of the reversible efficiency of heat dissipation is still challenging. It is well known that changes in Φ_N are often associated with changes in leaf green reflectance due to changes in the de-poxidation state (DEPS) of xanthophyll cycle pigments. The photochemical reflectance index (PRI) utilized the link between the biochemical changes within xanthophyll cycle expressed with a narrow-band green reflectance, providing a way to
525 remotely assess photosynthetic light use efficiency (Gamon et al., 1992; Garbulsky et al., 2011), but the link becomes partially obscured at canopy scale due to the effects of canopy structure and sun-observer geometry (Hilker et al., 2009; Middleton et al., 2009). Because of these interfering effects, canopy PRI showed very weak overall relationship with $APAR_{canopy}$ ($\rho=0.28$, Fig. ~~40b11b~~), which clearly differed from the connection between Φ_N and $APAR_{leaf}$ at the leaf level ($\rho \geq 0.64$, Fig. ~~40a11a~~).

530 Since the reversible heat dissipation pathway is such a strong competitor to photochemistry, especially in the sunlit canopy fraction, it seems very important to fully understand the green reflectance link to the energy regulation via the xanthophyll cycle, and then develop radiative transfer modelling approaches to translate this link to the canopy level. In this regard, Vilfan et al. (2018) extended the Fluspect leaf radiative transfer model to simulate xanthophyll driven leaf reflectance dynamics. Further efforts on implementing this extended model in canopy radiative transfer models will connect efficiencies of

535 photochemistry and reversible heat dissipation to canopy reflectance observations. This may open new opportunities to estimate photosynthetic light use efficiency and improve GPP estimation using remote sensing methods *in situ* and from space.

4.3 Physically and physiologically joint effects on the SIF-GPP relationship

The canopy equivalent efficiencies ($\Phi_{Fcanopy}$ and $\Phi_{Pcanopy}$) are composed of integrals of the efficiencies of leaves of the sunlit and shaded canopy fractions. The correlation between the canopy effective equivalents of Φ_F and Φ_P may be expected to take a value between the equivalent correlation of leaf-level Φ_F and Φ_P for sunlit leaves ($\rho = 0.53$) and for shaded leaves (540 $\rho = 0.10$). This means that the ability to view the SIF and reflectance hot spots (whether they occur together or not) from sunlit leaves varies with viewing angle and time of day (e.g., illumination angle, diffuse light). We suggest that these factors strongly affect f_{esc} . Therefore, they must, in turn, affect the success of remote sensing relationships for SIF-GPP (Yang and Van der Tol, 2018). Likewise, these factors also affect the variability of the APAR-GPP relationship (Dechant et al., 2020; Qiu et al., 2019), and the relationship of photosynthetic light use efficiencies at leaf and canopy levels (i.e., Φ_P and $\Phi_{Pcanopy}$) (e.g., Middleton et al., 2019). However, it is worth noting that active fluorescence measurements are spectrally integrated signals, whereas canopy passive SIF observations are obtained at one wavelength. As a result, the leaf-level fluorescence emission and photosynthetic light use efficiencies derived from active fluorescence measurements differ spectrally from the canopy-level efficiencies ($\Phi_{Fcanopy}$ and $\Phi_{Pcanopy}$). This difference may also play a (550 role in upscaling leaf-level to canopy-level relationship between Φ_F and Φ_P .

The exact correlation between $\Phi_{Fcanopy}$ and $\Phi_{Pcanopy}$ at canopy scales depends on both the relative contributions of sunlit and shaded leaves to the canopy equivalents and the native correlation of the efficiencies at leaf level (Köhler et al., 2018; Mohammed et al., 2019). Canopy structure dictates the relative abundance and thus the relative weights of these contributing (555 factors to the canopy equivalent Φ_F and Φ_P . The weight is not only determined by leaf class abundance, but also by the relative magnitude of the SIF and GPP response of the leaf classes. Sunlit leaves during daytime usually constitute a greater contribution to the effective canopy efficiencies than shaded leaves, simply because sunlit leaves tend to emit a higher SIF signal and, at the same time, produce a higher GPP. This suggests that the correlation between the canopy effective equivalents of Φ_F and Φ_P tends to be closer to the correlations of leaf-level Φ_F and Φ_P for sunlit leaves ($\rho = 0.53$) than for shaded leaves.

(560 The LUE models as shown in Eq. 1 are, essentially, one-big-leaf models. The one-big-leaf approach assumes that canopy photosynthesis or SIF have the same relative responses to the environment as any single leaf, and that the scaling from leaf to canopy is therefore linear (Friend, 2001). However, sunlit and shaded leaves clearly showed a different Φ_F - Φ_P relationship (Figs. 6 and 4011). In order to better interpret the SIF-GPP relationship, we recommend a revision of the LUE model of SIF and GPP (Eq. 1) by separating the contributions of sunlit and shaded leaves:

$$\text{GPP} = \sum_{n=\text{sunlit,shaded}} \text{iPAR} \cdot \text{fAPAR}^n \cdot \Phi_P^n \quad (10a),$$

$$\text{SIF} = \sum_{n=\text{sunlit,shaded}} i\text{PAR} \cdot f\text{APAR}^n \cdot \Phi_F^n \cdot f_{esc}^n \quad (10b),$$

This approach updates the existing one-big-leaf LUE models into two-big-leaf (or two-big-leaf) LUE models. The idea of differentiating sunlit and shaded leaves in vegetation modelling has been applied in predicting canopy temperature and photosynthesis, and an improved ability of PRI to track canopy light use efficiency was shown ~~for the canopy PRI response~~ when including both sunlit and shaded leaves in model simulations of field results (Dai et al., 2004; Luo et al., 2018; Wang and Leuning, 1998; Zhang et al., 2017), ~~but has not been implemented in the LUE model for SIF. Qiu et al. (2019) incorporated a fluorescence simulation in the Boreal Ecosystem Productivity Simulator (BEPS, Liu et al., 1997), which is a two-leaf process-based model. More classes of leaves with varying ambient temperatures and incident radiation levels can be examined using more~~ ~~More~~ explicit models, such as SCOPE (Soil-Canopy-Observation of Photosynthesis and Energy fluxes, Van Der Tol et al., 2009), BETHY-SCOPE (the Biosphere Energy Transfer Hydrology model coupled with SCOPE, Norton et al., 2018) or DART (the Discrete Anisotropic Radiative Transfer model, Gastellu-Etchegorry et al., 2017), ~~consider more classes of leaves with varying ambient temperature and radiation levels. Although the concept of differentiating sunlit and shaded leaves is implemented in these model, the functional variation of the two categories of leaves is not considered. Moreover, the role of sunlit fraction in explaining SIF-GPP relationship has not been explored. ,but they require many parameters as input.~~ The two-big-leaf LUE models consider the major difference of leaves in a canopy, and are relatively simpler compared with SCOPE and DART (Parazoo et al., 2020) but more realistic compared with one-big-leaf LUE models in linking SIF and GPP.

The fraction of sunlit canopy is determined by canopy structure and the direction of incoming light as well as the fraction of diffuse light. Hence, it is expected that these factors will affect the contribution of sunlit and shaded leaves to the canopy SIF-GPP correlation. Furthermore, the instantaneous sun-view angle geometry affects where the sunlit leaves occur during the day and the likelihood of their being viewed at particular angles (e.g., nadir). This means that the ability to view the SIF hot spot emitted from sunlit leaves varies with viewing angle and time of day. We suggest that these factors strongly affect f_{esc} which must, in turn, affect the SIF-GPP remote sensing relationship (Yang and Van der Tol, 2018).

Intuitively, in fully contiguous vegetation canopies the leaves in the upper layer (which are often sunlit) contribute a major fraction to the whole canopy of APAR, whereas $f\text{APAR}_{\text{shaded}}$ is small. Therefore, Φ_F^{sunlit} and Φ_P^{sunlit} have much larger relative contributions to $\Phi_{F\text{canopy}}$ and $\Phi_{P\text{canopy}}$, respectively. Hence, a stronger relationship between SIF and GPP for dense canopies is expected since Φ_F^{sunlit} and Φ_P^{sunlit} are more tightly connected than Φ_F^{shaded} and Φ_P^{shaded} ~~moderately correlated~~. This insight can provide some explanation for the seasonally varying results describing canopy SIF and GPP (Fig. 3 a-c), where the SIF-GPP relationship varied with the growth stages: for the Young crop ($\rho = 0.72$); Mature crop ($\rho = 0.77$); and the Senescent crop ($\rho = 0.50$).

600 Furthermore, the effects of diffuse light (the diffuse/direct iPAR ratio) on the relationship between SIF and GPP can be explained by the revised equation (Eq. 10). When the fraction of diffuse light is higher (e.g., a hazy, or cloudy day), there is greater iPAR penetration into lower canopy layers (the shaded leaves). As a result, $fAPAR_{\text{shaded}}$ increases while $fAPAR_{\text{sunlit}}$ decreases. This leads to a higher contribution of shaded leaves to the SIF-GPP relationship at canopy level, and weakens the SIF-GPP correlation. This was indeed observed in earlier field measurements reported in Miao et al. (2018), which showed
 605 that both the SIF-GPP correlation and the correlation between the SIF/APAR and GPP/APAR ratios were significantly weaker under cloudy conditions than sunny conditions. The relative fraction of diffuse light is also a possible cause for the diurnally varying correlation between SIF and GPP (Fig. 3 d-f), where the SIF-GPP relationship varied at different times of day: for the data acquired in the morning ($\rho = 0.76$); for the data acquired in the midday ($\rho = 0.83$); and for the data acquired in the afternoon ($\rho = 0.89$). This highlights the unique physiological information of SIF for monitoring GPP, and the joint effects of
 610 incoming radiation, canopy structure and leaf physiology on the SIF-GPP relationship. We suggest that the canopy structure, illumination and viewing conditions, and especially the foliage thermal dissipation must be taken into account to accurately represent the physiological underpinnings of the observed SIF-GPP relationships.

A simple model was used to examine the sensitivity of the fraction of sunlit canopy to LAI, leaf angle distribution function
 615 (LIDF) and solar zenith angles (θ_s). Considering a vegetation canopy as a turbid medium consisting of leaves, the instantaneous sunlit fraction can be estimated as a function of the direction of incoming light, canopy LAI (L) and leaf angle distribution. In stochastic models describing the transfer of radiation in plant canopies, the probability of the leaves being sunlit at a specified vertical height x (i.e., $x=0$ referring to top of canopy, $x=-1$ referring to bottom of canopy) can be estimated as $P_s = \exp(kLx)$, where L is canopy LAI and k the extinction coefficient, which is determined by the solar direction and leaf angle distribution
 620 (He et al., 2017; Stenberg and Manninen, 2015). The computation of k is explicitly given in Verhoef (1984) by projecting the leaf area into the direction of the sun. In the model SCOPE (Van Der Tol et al., 2009), the total fraction of sunlit canopy LAI is the integral of P_s in the vertical direction given as:

$$P_{sun} = \frac{1}{kL}(1 - \exp(-kL)) \quad (11)$$

625 The effects of LAI, leaf angle distribution function (LIDF) and solar zenith angles (θ_s) on the instantaneous sunlit canopy fraction are presented in Fig. 4+13. In line with our intuitive understanding, the fraction of sunlit canopy decreases with increasing canopy LAI in denser canopies. This fraction also decreases with increasing solar zenith angle, which are also affected by the leaf angle distribution. The important quantity for our purposes is the relative (not absolute) angular difference between the sun and leaf positions. Eq. 11 gives the prediction for the total fraction of sunlit canopy, but the fraction of sunlit LAI at a given height and thus the vertical variation of P_{sun} can be predicted in a similar way. The calculation of the fraction of sunlit canopy LAI shown in Eq. 11 is based on a turbid assumption of the vegetation canopy. Corn has a simple canopy architecture and a corn canopy can be considered as turbid medium. However, for forests or other more complex canopies,
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635 other structural characteristics, e.g., the clumping of foliage (Liu et al., 1997; Qiu et al., 2019), affect the gap probability of a vegetation canopy layer and the associated light penetration, and should be considered when separating sunlit and shaded leaves in the canopy.

[Insert Figure 13~~1~~ here]

640 A limitation of the current SCOPE capability for describing physiological responses is related to capturing the changing light environments that affect estimates of the sunlit/shaded fractions. This is because SCOPE and most radiative transfer models for vegetation assume steady state conditions and lack temporal memory of state variables at different times. SCOPE predicts the sunlit/shaded fractions at one moment while the shaded and sunlit leaves discussed in this paper are a result of long-term adaption to the light conditions (i.e., sun-adapted and shade-adapted leaves). Nevertheless, we can gain insights into relationships under specified conditions, which can serve as new information to be used in updating the models. A possible
645 way is to predict the light distribution inside the canopy with varying sun positions (e.g., a diurnal cycle). In this way, sun-adapted and shade-adapted leaves can be differentiated according to the probability of being illuminated for a longer period instead of for a single moment in time. A leaf is sun-adapted when it is almost always illuminated at various sun positions or different time in a day. In contrast, a shade-adapted leaf is rarely or occasionally illuminated for various sun positions. Furthermore, different physiological traits of sun-adapted and shade-adapted can be taken into account in the model.

650 4.4 Combined use of TOC reflectance and SIF for GPP estimation

SIF observed at the top of a canopy is a fraction of total emitted SIF by all the leaves in the canopy due to the reabsorption and scattering effects. In section 4.1, we inferred that the correction of TOC SIF for f_{esc} can result in a better correlation to GPP, and in section 4.3 we discussed the difference between leaf- and canopy-level efficiencies caused by the canopy structural and sun-observer geometry. Apart from separating sunlit and shaded leaves in the LUE models proposed in section 4.3, employing corrections to SIF for interfering structural and angular effects are possible ways to enhance understanding of the relationship between SIF and GPP.

660 Several studies have been conducted to convert TOC SIF to total emitted SIF by the canopy (SIF_{tot}) for a better estimation of GPP (e.g., Lu et al., 2020; Qiu et al., 2019). A direct way to estimate f_{esc} or SIF_{tot} is by using a radiative transfer model (e.g., SCOPE and DART), but this approach requires leaf and canopy characteristics to drive the models and has obvious limitations in applications. Because TOC reflectance and TOC SIF are similarly determined by leaf biochemistry, canopy structure and sun-observer geometry, we can use TOC reflectance to explain vegetation biochemical and structural, and bidirectional effects on TOC (Yang et al., 2019, 2020; Yang and Van der Tol, 2018). This can be achieved by retrieving required leaf and canopy characteristics for running the radiative transfer model from TOC reflectance (Yang et al., 2019). Alternatively, we can
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establish a direct link between TOC reflectance and f_{esc} skipping the retrieval of vegetation properties by inverting a radiative transfer model. This can be achieved by exploring the similarity of radiative transfer of intercepted incident light and emitted SIF. We established such a link, which states that the ratio of far-red reflectance (R) to the product of canopy interception (i_0) and leaf albedo (ω) is an accurate estimate of canopy scattering of far-red SIF (i.e., $f_{esc} = R/i_0\omega$) (Yang and Van der Tol, 2018). Furthermore, we found that the product of f_{esc} and $fAPAR_{canopy}$ can be well approximated by a reflectance index, which is called fluorescence correction vegetation index (FCVI) and is given as the difference of near-infrared (NIR) and broadband visible (VIS) reflectance acquired under identical sun-canopy-observer geometry of the SIF measurements (i.e., $FCVI = R_{nir} - R_{vis} \approx f_{esc} \times fAPAR_{canopy}$) (Yang et al., 2020). With the above mentioned link and index, it is possible to estimate f_{esc} and canopy total emitted SIF at 760 nm F_{760}^{tot} .

$$f_{esc} = FCVI/fAPAR_{canopy} \quad (12)$$

$$F_{760}^{tot} = \pi F_{760}/f_{esc} \quad (13)$$

[Insert Figure 14 here]

We estimated F_{760}^{tot} using Eqs. 12 and 13 and found that F_{760}^{tot} is not better correlated with GPP compared with F_{760} as indicated by the similar correlation coefficients and RMSEs (Fig. 1a vs Fig. 14). For F_{760}^{tot} and GPP, the Pearson correlation coefficient was 0.82 and RMSE was $0.29 \text{ mg m}^{-2} \text{ s}^{-1}$, while the values were 0.83 and $0.28 \text{ mg m}^{-2} \text{ s}^{-1}$ for F_{760} and GPP. The reason is likely to be the uncertainties in the f_{esc} estimation. The accuracy of f_{esc} estimation with FCVI is largely determined by $fAPAR_{canopy}$, which is difficult to accurately estimate from TOC reflectance alone. In most studies including the present study, $fAPAR_{canopy}$ is usually estimated by using vegetation indices and the accuracy is not always guaranteed. Because SIF is a weak signal, the uncertainties in $fAPAR_{canopy}$ estimation may have a considerable impact on estimating f_{esc} and F_{760}^{tot} . Similar problems also exist when using the NIRv (near infrared vegetation index, $NDVI \times R_{nir}$) to correct TOC SIF for f_{esc} , since $fAPAR_{canopy}$ is required (i.e., $f_{esc} = NIRv/fAPAR_{canopy}$) (Zeng et al., 2019). Nevertheless, Lu et al. (2020) found that canopy GPP was better correlated with F_{760}^{tot} and F_{760} . Instead of $fAPAR_{canopy}$ and either FCVI or NIRv, they used the original link we established (Yang and Van der Tol, 2018) between TOC far-red reflectance and f_{esc} when estimating f_{esc} (i.e., $f_{esc} = R/i_0\omega$). The important variables i_0 and ω for applying this link were estimated by using field measurements of leaf and canopy characteristics (e.g., leaf chlorophyll content and LAI). The study of Lu et al. (2020) not only confirms that canopy total emitted SIF is a better estimate of GPP than TOC SIF, but also supports the importance of $fAPAR_{canopy}$ in estimating f_{esc} when using either NIRv or FCVI. We, therefore, recommend that canopy interception i_0 be included into measurement protocols in future field campaigns to better monitor GPP based on SIF remote sensing retrievals.

5 Conclusions

We have used a unique dataset to explore the relationship between fluorescence and photosynthesis at leaf and canopy levels over a growing season in a corn canopy. We have quantified the contribution of incoming radiation, canopy structure and plant physiology to the SIF-GPP relationship by using partial correlation analysis.

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We demonstrate that the observed positive relationship between SIF and GPP is largely due to the fact that both of them are dependent on APAR (i.e., not on iPAR). Incoming radiation and canopy structure had comparable contributions to the SIF-GPP relationship. After eliminating the effects of variable APAR on the SIF-GPP relationship, the apparent positive relationship between SIF and GPP became much weaker. However, there is still some remaining connection due to the functional link between fluorescence and photosynthesis at the leaf level, which is confirmed by active fluorescence measurements.

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We also confirm that heat dissipation is responsible for the positive relationship between the efficiencies of fluorescence and photochemistry. Sustained (i.e., diurnally stable) heat dissipation increased through the crop's growth into the senescent stage, which caused the late season decrease in photosynthetic light use efficiency. The seasonal variation in sustained heat dissipation contributed to a moderate positive relationship between the efficiencies of fluorescence and photochemistry at the seasonal scale. At the diurnal scale, the reversible heat dissipation is responsible for the change of photosynthetic light use efficiency.

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We propose to use a two-big-leaf LUE model instead of the commonly used one-big-leaf LUE model for interpreting the SIF-GPP relationship. This is because of clearly different relationships between fluorescence emission and photochemical light use efficiencies for sunlit and shaded leaves. The use of the two-big-leaf LUE model leads to a better understanding of the SIF-GPP relationship and its responses to weather conditions, such as clouds and fraction of diffuse light, as well as its responses to canopy structure, such as canopy openness and growth stages. We also suggest to include measurements of canopy interception or fAPAR in future field campaigns to allow estimating canopy total emitted SIF from TOC SIF for a better estimation of GPP.

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~~We also confirm that heat dissipation is responsible for the positive relationship between the efficiencies of fluorescence and photochemistry. Sustained (i.e., diurnally stable) heat dissipation increased through the crop's growth into the senescent stage, which caused the late season decrease in photosynthetic light use efficiency. The seasonal variation in sustained heat dissipation contributed to a moderate positive relationship between the efficiencies of fluorescence and photochemistry at the seasonal scale. At the diurnal scale, the reversible heat dissipation is responsible for the change of photosynthetic light use efficiency.~~

730 **Appendix A**

[Insert Figure A1 here]

[Insert Figure A2 here]

735 *Author contributions:* P.Y., E.M., C.vdT and P.C. designed and performed research; P.Y. analyzed the data and prepared the original draft; P.Y., E.M., C.vdT and P.C. reviewed and edited the paper.

Data availability: The data is provided as a supplement.

Competing interests: The authors declare no conflict of interest.

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Tables and figures

Table 1: Summary of the main canopy and leaf field measurements used in the analyses.

Variable	Description	Measuring system	Unit	Temporal resolution
GPP	gross primary production	eddy covariance system	mg m ⁻² s ⁻¹	30 minutes

Canopy	F_{760}	canopy SIF at 760nm	QEpro (in FLOX)	$\text{mW m}^{-2} \text{s}^{-1}$	1-3 minutes
	$i\text{PAR}_{\text{canopy}}$	TOC incoming PAR	FLAME-S (in FLOX)	$\mu\text{mol m}^{-2} \text{s}^{-1}$	1-3 minutes
	$f\text{APAR}_{\text{canopy}}$	canopy fraction of absorbed PAR	FLAME-S (in FLOX)	-	1-3 minutes
Leaf	$i\text{PAR}_{\text{leaf}}$	leaf incoming PAR	MoniONIPAM system	$\mu\text{mol m}^{-2} \text{s}^{-1}$	10 minutes
	$f\text{APAR}_{\text{leaf}}$	leaf fAPAR	ASD spectrometer	-	-
	F_m	maximal fluorescence levels	MoniONIPAM system	-	10 minutes
	F_s	steady-state fluorescence levels	MoniONIPAM system	-	10 minutes

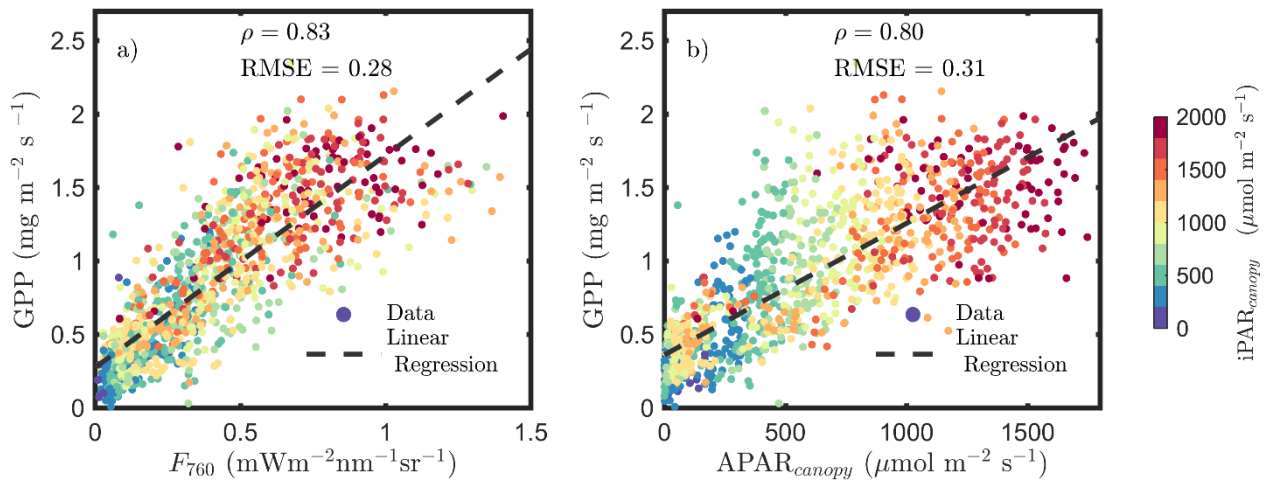
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Table 2: Correlation coefficients and partial correlation coefficients (i.e. controlling for or eliminating separate effects) between fluorescence and photosynthesis.

Φ_F^* vs. Φ_P	Sunlit leaves	Shaded leaves
Without controls	0.53	0.10
Controlling Φ_N	0.05	-0.31
Controlling Φ_D	0.08	-0.35
Controlling both Φ_N and Φ_D	-0.75	-0.75

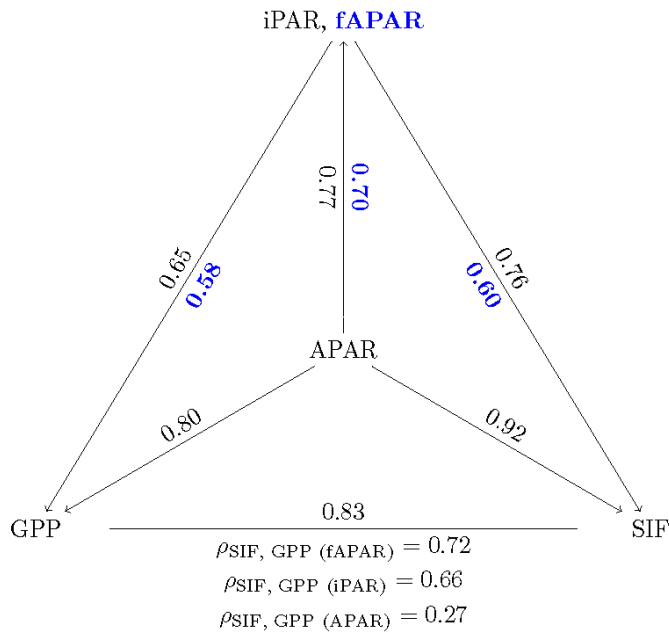
Table 3. Correlations between variables describing energy partitioning at leaf and canopy scales

Scale	Time	Types	Φ_N vs. Φ_F	Φ_P vs. Φ_F	Φ_N vs. Φ_P	APAR vs. Φ_F	APAR vs. Φ_N	APAR vs. Φ_P
Leaf	All	Sunlit	-0.33	0.53	-0.74	-0.10	0.64	-0.75
		Shaded	-0.23	0.10	-0.87	0.25	0.68	-0.75
	Midday	Sunlit	-0.45	0.62	-0.76	-0.27	0.60	-0.81
		Shaded	-0.45	0.27	-0.92	-0.14	0.77	-0.81
Canopy	All		-0.04	0.37	-0.16	-0.25	0.28	-0.41
	Midday		-0.07	0.53	-0.25	-0.32	0.41	-0.55



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Figure 1: Relationships between far-red SIF (F_{760}) and GPP, and between $APAR_{canopy}$ and GPP of a corn canopy in the 2017 growing season with half-hour temporal resolution during daylight hours. F_{760} and $APAR_{canopy}$ were retrieved from FLoX canopy measurements. GPP was obtained from the site's flux tower measurements.



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Figure 2: Pearson correlation coefficients among the canopy variables $iPAR_{canopy}$, $APAR_{canopy}$, $fAPAR_{canopy}$ (indicated in bold, blue text), GPP, and SIF for a corn canopy across the 2017 growing season, based on the dataset shown in Fig. 1 (a, b). The partial correlation coefficients between SIF and GPP (listed at the base of the triangle) were determined by removing the effects of the controlling variables, $fAPAR$, $iPAR$ and $APAR$, respectively. Measurements had a half-hour resolution.

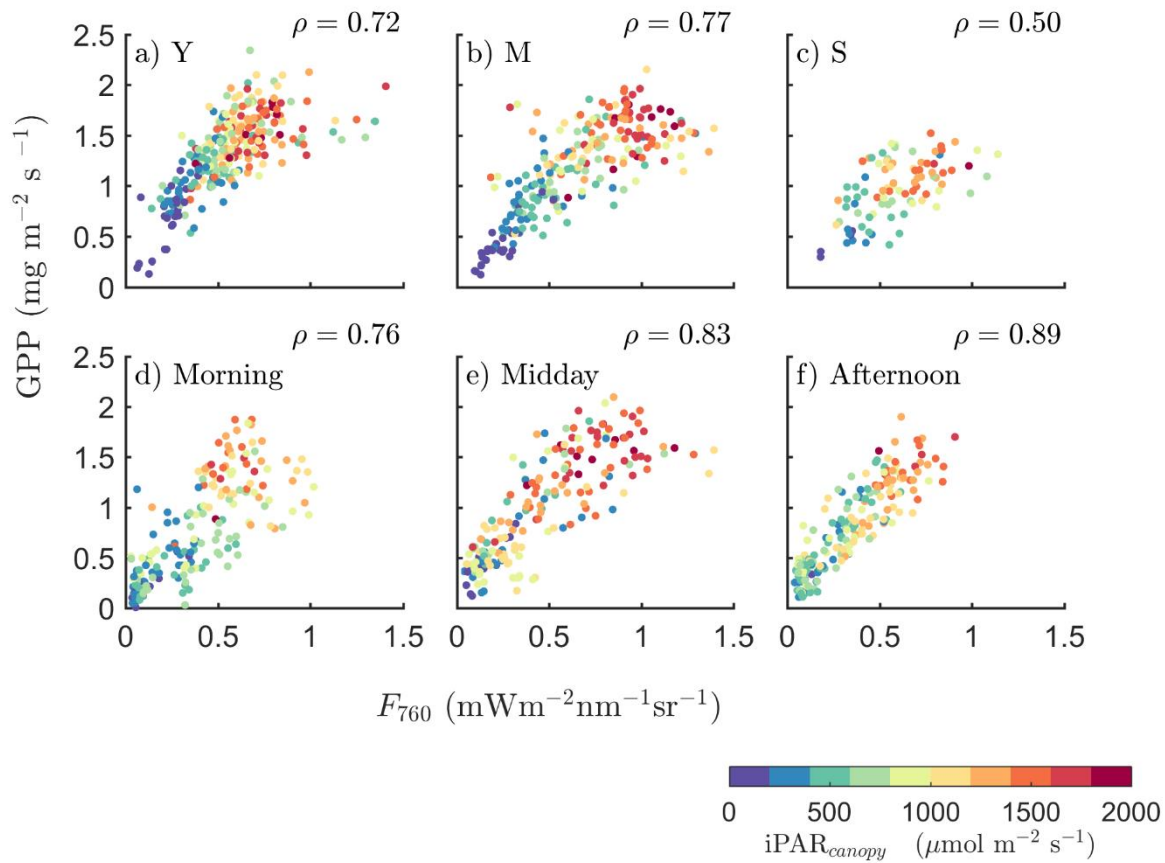


Figure 3: Relationships between far-red SIF (F_{760}) and GPP of a corn canopy in-across the 2017 growing season with half-hour temporal resolution during daylight-daytime hours for three growth stages (a-c): young (Y), mature (M) and senescent (S); for three times of a day (d-f): morning (9:00-11:00), midday (11:00-14:00) and afternoon (14:00-17:00). Colors refer to the $iPAR_{canopy}$ values obtained in conjunction with the GPP and SIF observations, as shown in the legend bar.

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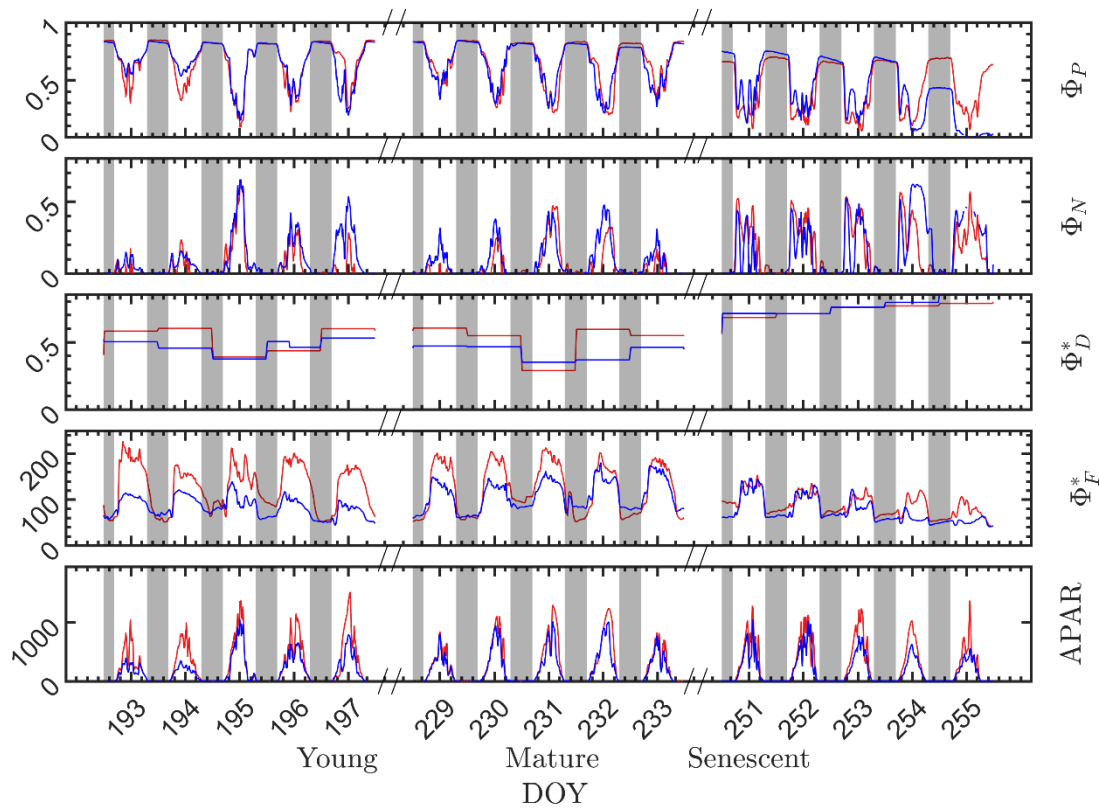
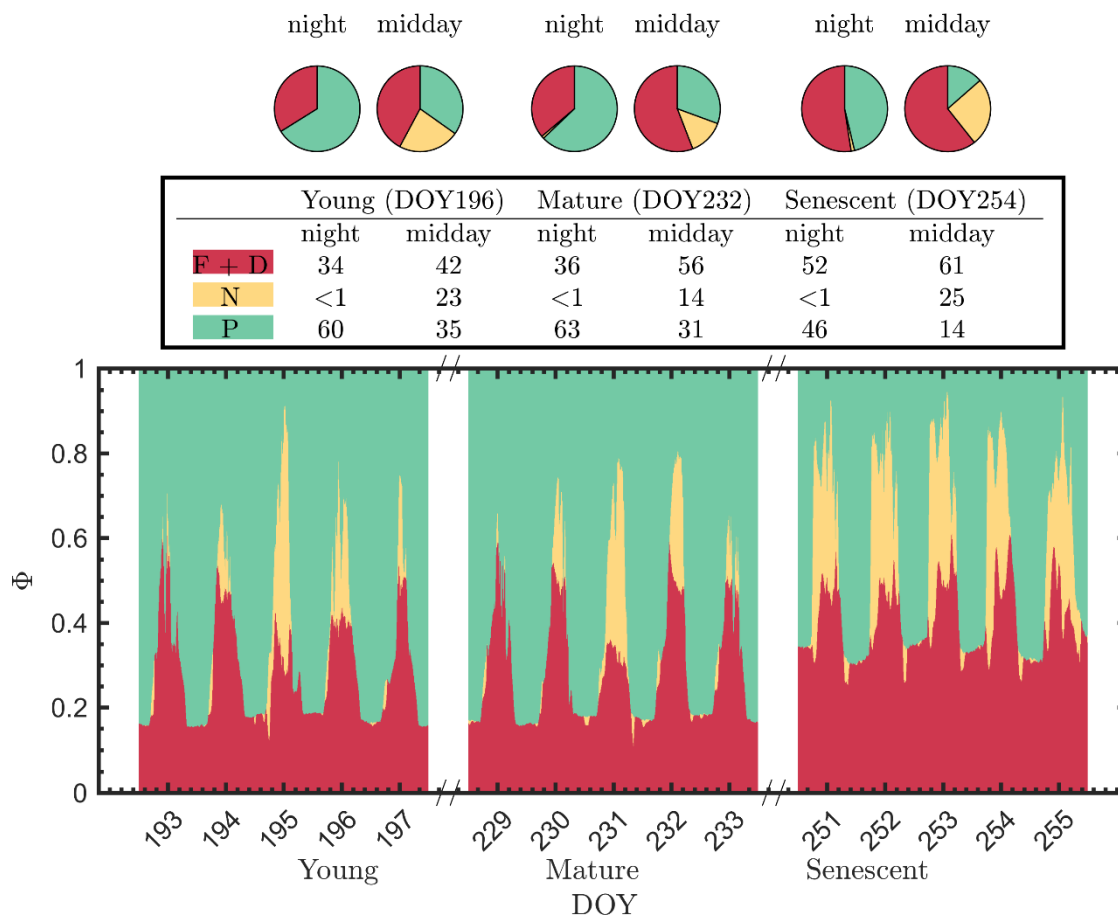


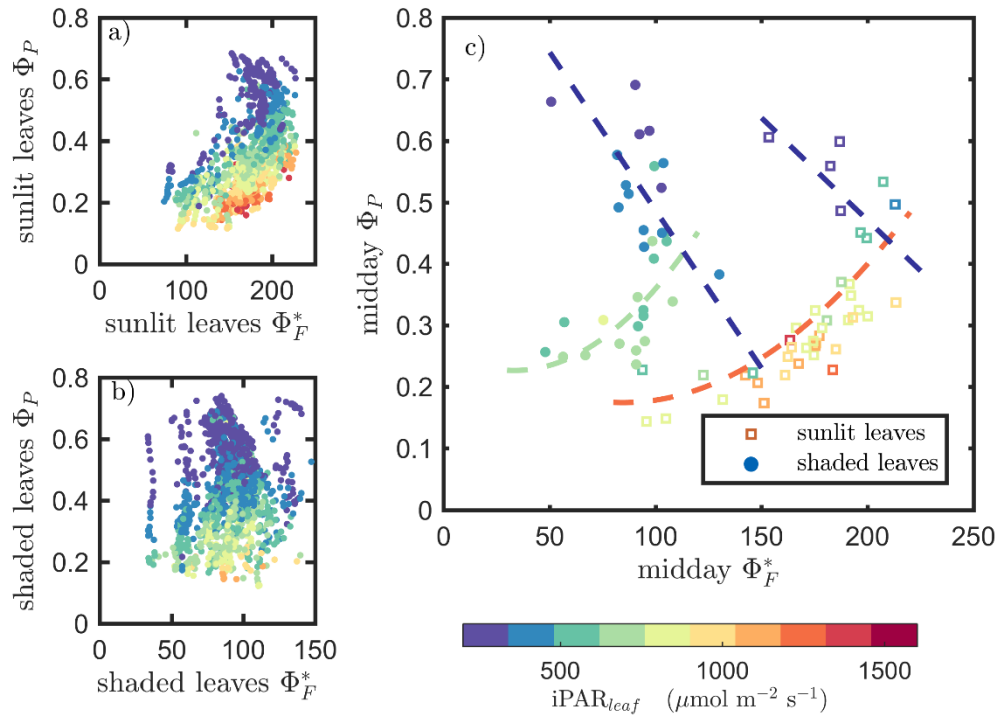
Figure 4: Photosystem energy partitioning obtained from *in situ* active fluorescence measurements made on individual leaves of a corn canopy during the 2017 growing season. Shown are the absolute light use efficiency of photochemistry (Φ_P), the reversible heat dissipation (Φ_N), the relative light use efficiency of sustained heat dissipation (Φ_D^*), the relative light use efficiency of fluorescence (Φ_F^*) and the photosynthetically active radiation absorbed by individually leaves ($APAR_{leaf}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$) for sunlit leaves (red solid lines) and shaded leaves (blue dashed lines). The nighttime periods from sunset to sunrise of the next day are marked with grey rectangles and the daylight measurements from 9:00 to 17:00 are indicated with red tracks.

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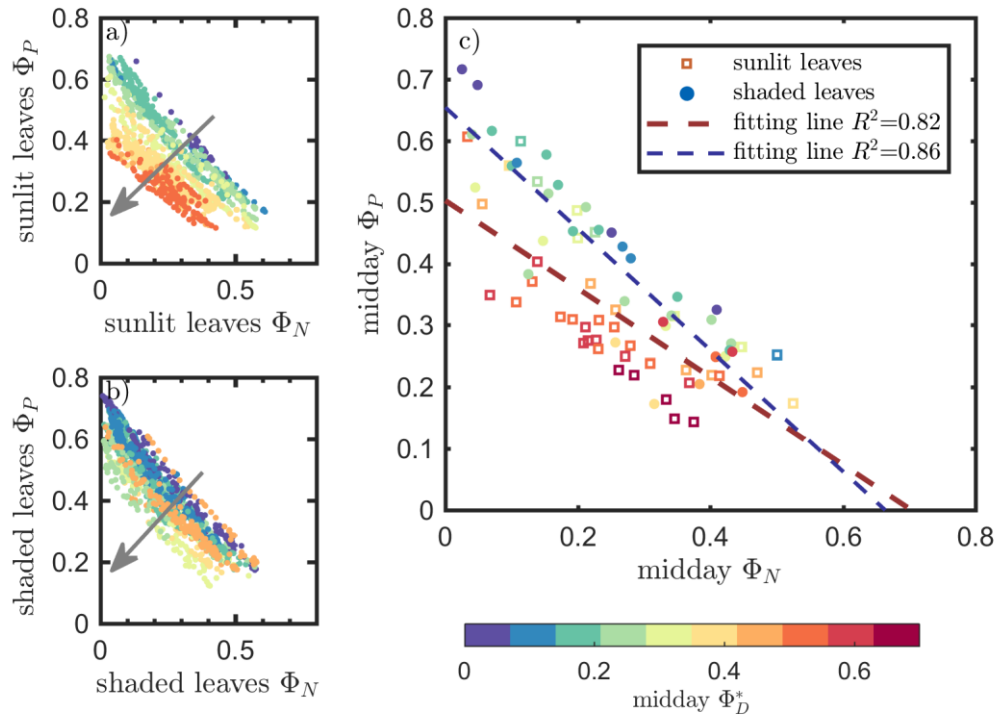


985 **Figure 5: Summary chart of the efficiency responses presented in Fig. 4 for sunlit leaves.** The energy partitioning in both nighttime (sunset - sunrise) and midday (11:00 - 14:00) measurements for one representative date per growth stage (Y, DOY 196; M, DOY 232; and S, DOY 254) is diagrammed in the pie charts. Clearly, the photosynthetic efficiencies (P, green) are constrained, especially during daytime, by the combined action of reversible thermal dissipation efficiency (N, yellow) and the F + D (fluorescence and sustained thermal dissipation, red) efficiency.

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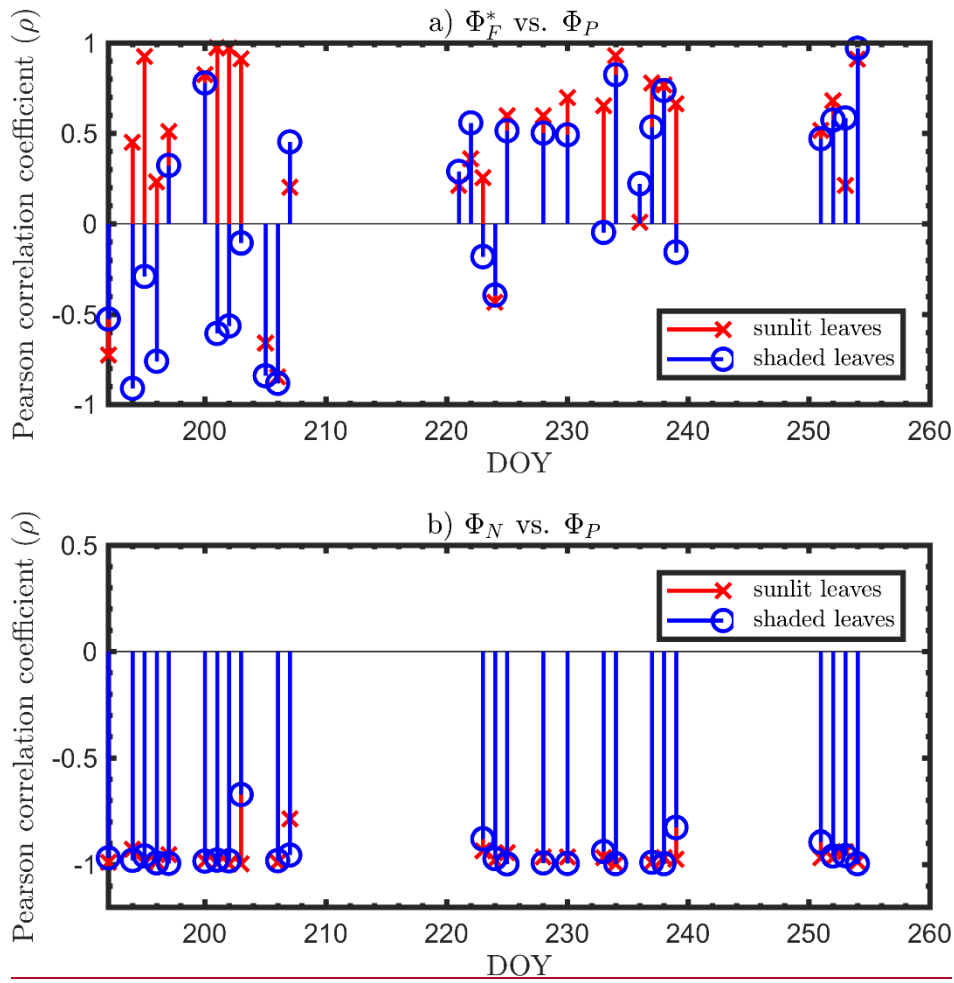
995 **Figure 6: Relationships between the light use efficiency of photochemistry (Φ_p) and the relative fluorescence light emission efficiency (Φ_F^*) for sunlit leaves and shaded leaves across the 2017 growing season in a corn canopy are shown: all daytime measurements (9:00 - 17:00, a and b); and midday (11:00 - 14:00) seasonally-averaged measurements (c). Colors refer to the $iPAR_{leaf}$ values shown in the legend bar, daylight measurements (9:00 - 17:00, a and b), and seasonally midday-averaged (11:00 - 14:00, c) of light use efficiency of photochemistry (Φ_p) and relative fluorescence light emission efficiency (Φ_F^*) for sunlit leaves and shaded leaves across the 2017 growing season in a corn canopy. The data in (c) were classified into two groups by $iPAR_{leaf}$ with a threshold value of $500 \mu\text{mol m}^{-2} \text{s}^{-1}$.**



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Figure 7: Relationships between the light use efficiency of photochemistry (Φ_P) and the reversible heat dissipation (Φ_N) for sunlit leaves and shaded leaves across the 2017 growing season in a corn canopy are shown: all daytime measurements (9:00 - 17:00, a and b); and midday (11:00 - 14:00) seasonally-averaged measurements (c). Colors refer to the midday Φ^*_D values shown in the legend bar. daylight measurements (9:00 - 17:00, a and b), and seasonally midday-averaged (11:00 - 14:00, c) of light use efficiencies of photochemistry (Φ_P) and reversible heat dissipation (Φ_N) showing the change in the relative light use efficiency of sustained heat dissipation (Φ^*_D) for sunlit leaves (a) and shaded leaves (b). The arrows indicate the shift in linear response between Φ_P and Φ_N as Φ^*_D becomes the dominant energy pathway, thus lowering the photosynthetic potential.



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Figure 8: Diurnal correlations between Φ_F^* and Φ_P , and between Φ_N and Φ_P for sunlit and shaded leaves. The Pearson correlation coefficients for the days with more than five available observations are presented.

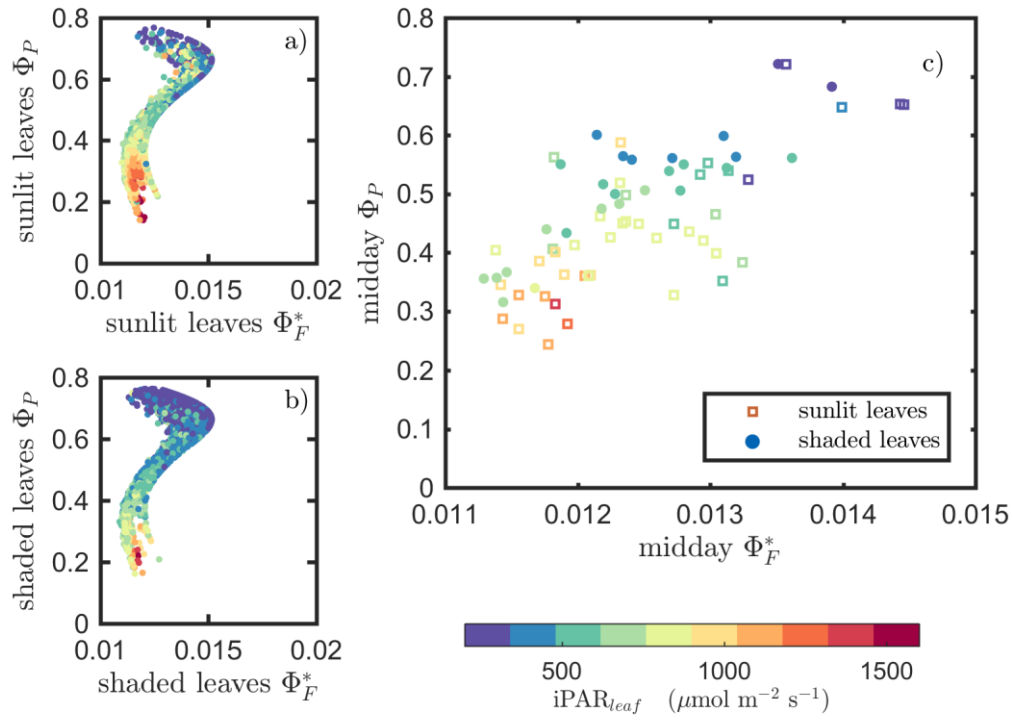


Figure 98: Reproduction of Fig. 6 with simulated variables from the biochemical model of Van der Tol et al. (2014).

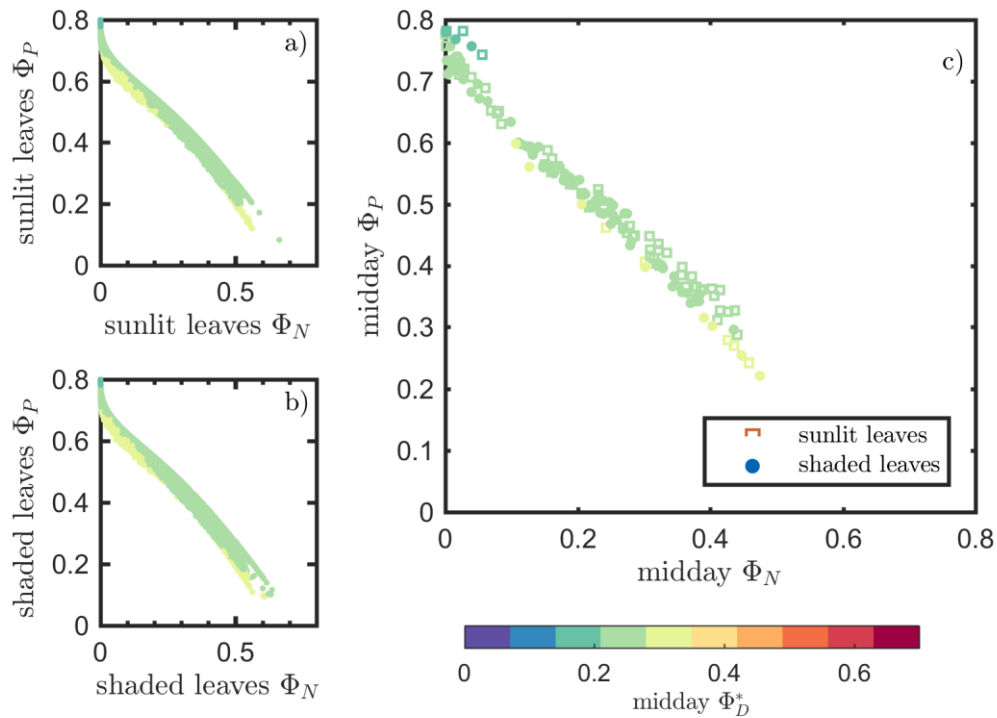
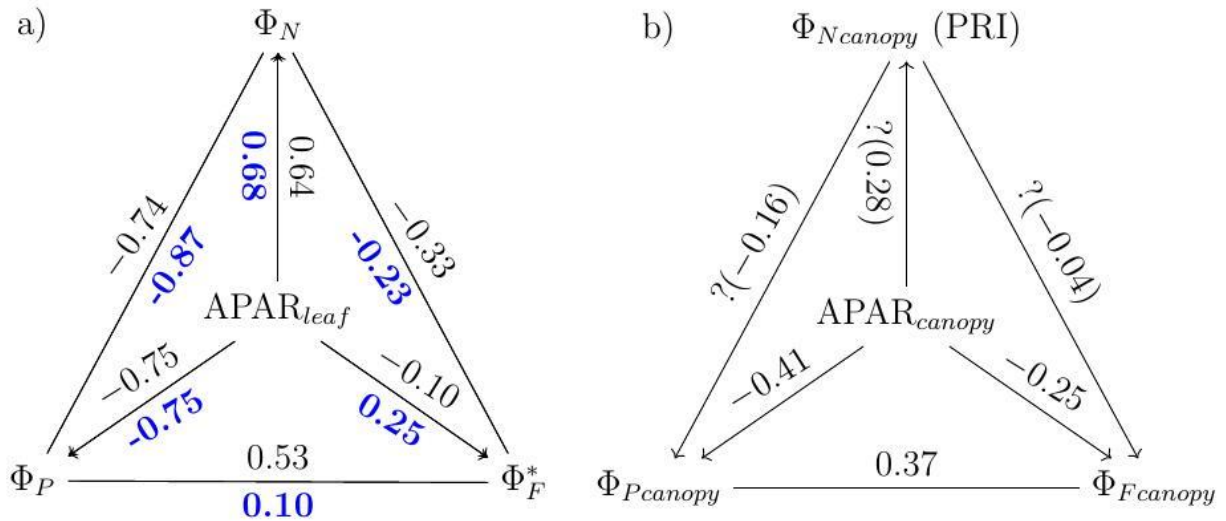
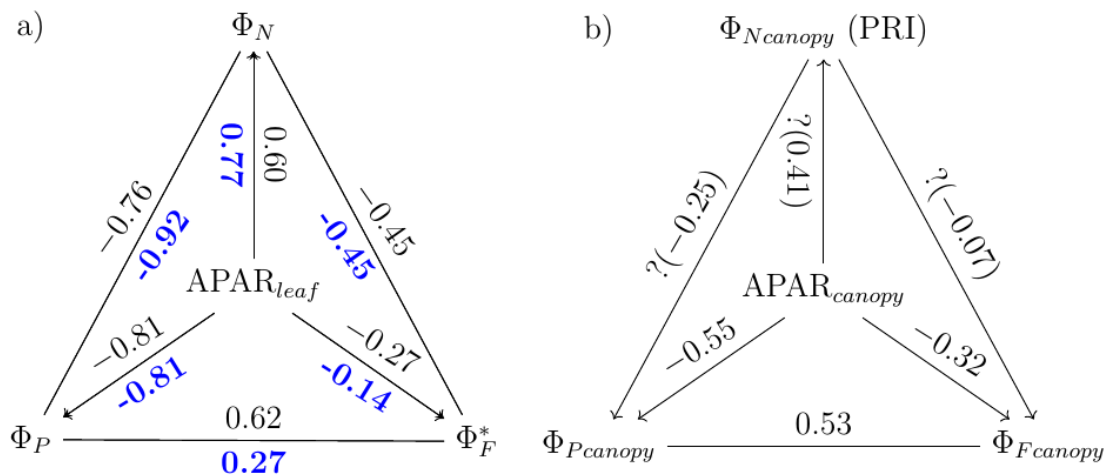


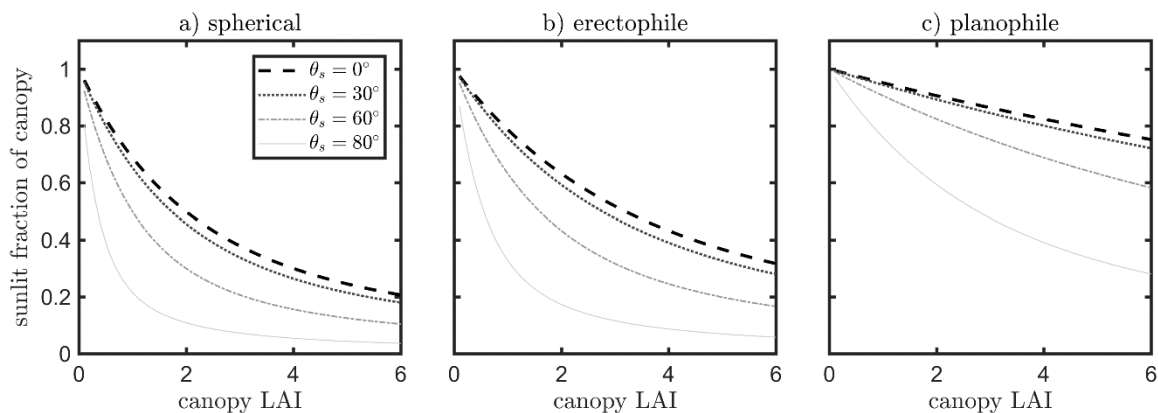
Figure 109: Reproduction of Fig. 7 with simulated variables from the biochemical model of Van der Tol et al. (2014).



1020 **Figure 10**: Pearson correlation coefficients between absorbed PAR ($APAR_{leaf}$ and $APAR_{canopy}$), and light use efficiencies for **all data**
obtained for a corn canopy across the 2017 growing season at both leaf (a) and canopy levels (b). Light use efficiency of
photochemistry (Φ_P), relative fluorescence emission efficiency (Φ_F^*), and efficiency of variable heat dissipation (Φ_N) of sunlit leaves
and shaded leaves (indicated in bold, blue text) during daytime (9:00 to 17:00) are obtained from *in situ* active fluorescence
measurements made on individual leaves. Canopy light use efficiency of photochemistry ($\Phi_{Pcanopy}$) and of fluorescence ($\Phi_{Fcanopy}$)
1025 are approximated by $GPP/APAR_{canopy}$ and $F_{760}/APAR_{canopy}$ respectively. PRI is used as an indicator of canopy light use efficiency
of variable heat dissipation ($\Phi_{Ncanopy}$), but the exact values of $\Phi_{NFcanopy}$ are unknown (noted with “?” markers). The leaf-level and
canopy-level variables had 10-minute and half-hour resolutions, respectively.



1030 **Figure 12. Reproduction of Fig. 11 with only midday measurements (11:00-14:00). Data correspond to subsamples previously shown**
in Figs. 3e, 6c, and 7c.



1035 **Figure 14:** Fraction of sunlit canopy changing with canopy LAI and solar zenith angle (θ_s) for canopy with spherical (a), erectophile (b) and planophile (c).

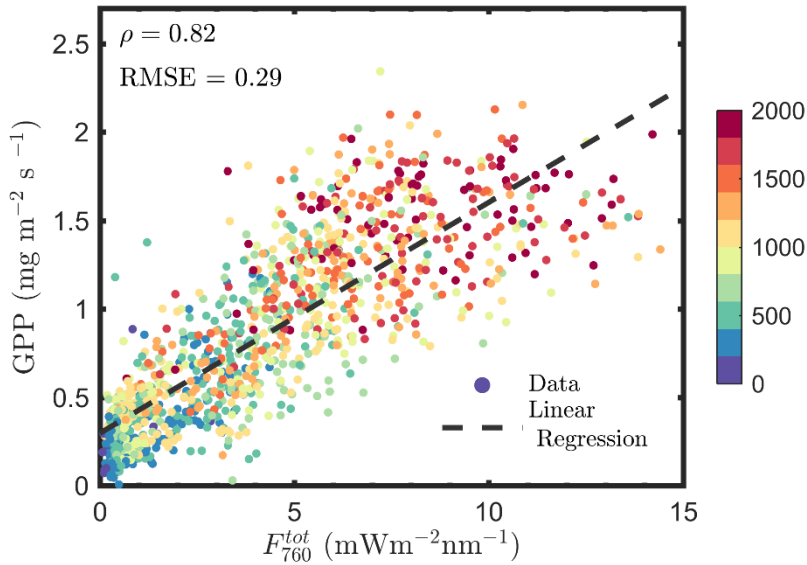


Figure 14: Relationships between far-red total emitted SIF by the canopy (F_{760}^{tot}) and GPP. F_{760}^{tot} was estimated by using the fluorescence correction vegetation index (FCVI).

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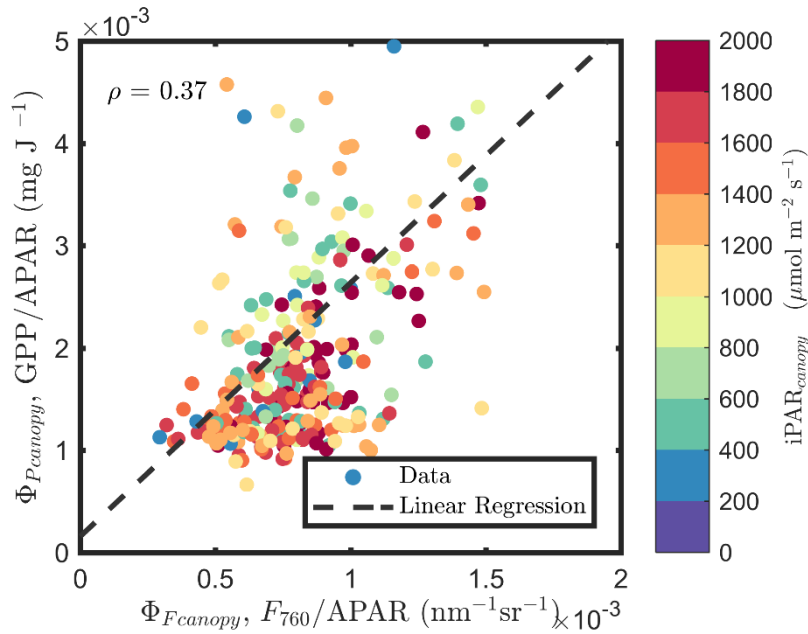


Figure A1: Relationships between $\Phi_{Fcanopy}$ and $\Phi_{Pcanopy}$, estimated as $F_{760}/APAR$ and $GPP/APAR$, respectively, of a corn canopy in the 2017 growing season with half-hour temporal resolution during daylight hours.

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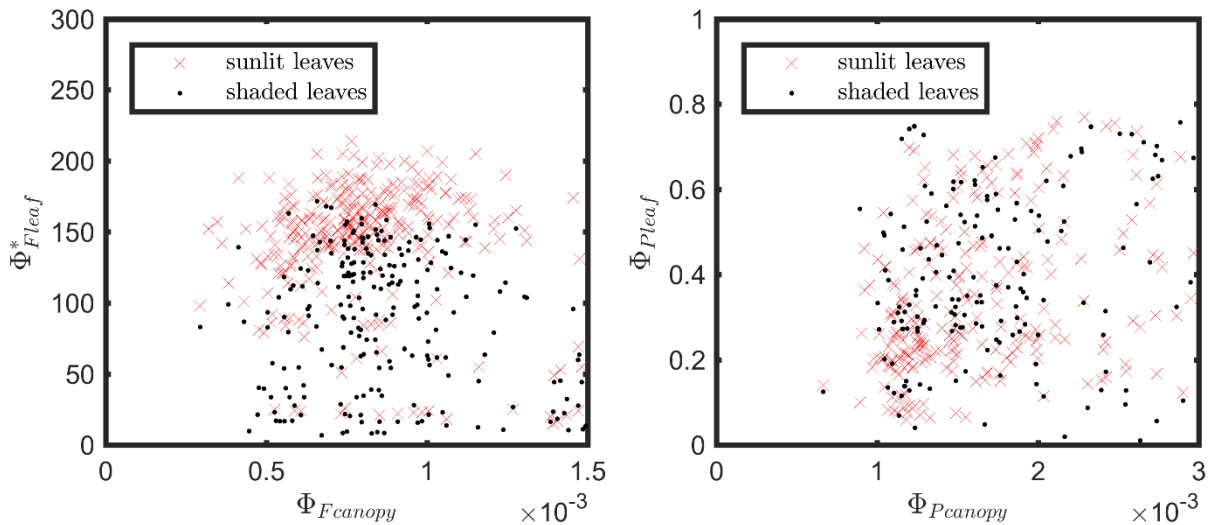


Figure A2: Relationships between leaf and canopy Φ_F (a), and leaf and canopy Φ_P (b). $\Phi_{Fcanopy}$ and $\Phi_{Pcanopy}$ were estimated as $F_{760}/APAR$ and $GPP/APAR$, respectively. Φ_{Fleaf} and Φ_{Pleaf} were derived from MoniPAM active fluorescence measurements.