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 reviewers' comments

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Anonymous Referee #1

General comments

In this study Peiqi Yang and co-authors analyze observations from 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 canopy has been removed from the relationship. At the leaf level they found that the role of thermal dissipation was 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.

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 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.

Minor comments

5. l. 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.

6. l. 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.

7. l. 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. l. 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.

9. l. 116: Should it be 'carbon fluxes' instead of 'crop fluxes'?

Response: Yes. We have corrected the mistake.

10. l. 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. l. 144: Sometimes 'MoniPAM', few times 'MONIPAM'. The writing could be uniform throughout the text.

Response: We have revised accordingly by consistently using MoniPAM.

12. l. 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. l. 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.

14. l. 224: Would you have a reference for the crops Vcmo value? Which temperature response are you using for it?

Response: The value of Vcmo varies with temperature. In Zhang et al (2014), the estimated Vcmo values of corn range from 11 to 75 with an average of 37 u mol m-2 s-1. In Houborg et al. (2013), the reported Vcmax at 25 °C (i.e., Vcmo) of 11 to 48 umol m-2 s-1 for corn during the growing season.

Vcmo refers to the Vcmax at 25°C. For the temperature response of Vcmax, we use 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).

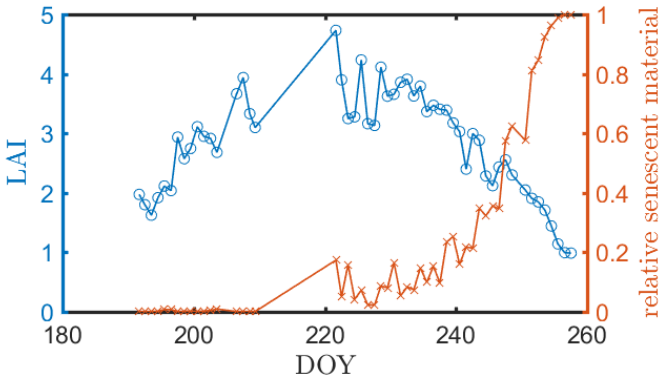

Fig. retrieved values of LAI and relative senescent material from TOC reflectance by inverting a radiative transfer model.

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 accordingly.

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.

20. l. 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. l. 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. l. 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. l. 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. l. 341: Sorry, what does your 'seasonally averaged' means?

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

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

Response: Yes. We have revised the text accordingly.

28. l. 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. l. 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.

30. l. 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. l. 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. l. 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.

33. l. 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. l. 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.

35. l. 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. l. 456: So are you now only referring to the study be 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 PhiN is responsible for regulating the correlation between PhiP and PhiF. The reviewer is right that the positive relationship exists for sunlit leaves. We have addressed this in the revision.

37. l. 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. l. 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. l. 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. l. 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.

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.

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.

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