

Interactive comment on “Remote sensing of ecosystem light use efficiency with MODIS-based PRI – the DOs and DON’Ts” by A. Goerner et al.

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We appreciate the comments made by the two anonymous referees and John Gamon. They raised some interesting points and helped to make the manuscript more clear.

Below is our point-by-point response.

Reviewer comments: **[RC]**

Author comments: **[AC]**

C4661

Response to comments of anonymous referee 1

[RC] My main concern about this paper is that this paper tries to evaluate PRI, but it uses satellite derived FAPAR, which may play a significant role in this.

[AC] This is a valid concern, therefore we have analyzed the relationship between MODIS PRI and the satellite derived FAPAR. As shown in Figure 5 and stated in section 3.6, it turned out that there is a significant relationship between PRI and faPAR for deciduous sites, but not for evergreen sites. So we do consider the relation between faPAR and PRI in our study. The conclusion in the revised version of the paper is more clear on this.

[RC] Also, it is well known that the MOD17 product does a reasonable job in some cases but by far not in all cases. I don't really think it is valid comparing MODIS PRI to MOD17 and then drawing conclusions about the usefulness of one or the other. Many studies have shown (and this study discusses) that -at least conventional- PRI measurements are dependent on a lot of things, so we would expect the authors to have expected there to be a reasonable relationship in the first place? It is quite well established that MOD17 does not work everywhere (see for instance Heinsch et al., 2002) and it is also known that just doing a MODIS PRI has its problems as well.

[AC] We agree that evaluating LUE based on PRI by direct comparison to LUE derived from the MOD17 model would not be very meaningful since we would not know which LUE (if any) is correct. However, we did not do this. The study presented here deals with the question 'Can light use efficiency be modeled from MODIS PRI with a universally applicable relationship or a relationship that is valid for certain ecosystem types?'. We did this evaluation by comparison with in-situ LUE, independent of the MOD17-approach. The comparison between MOD17-LUE and in-situ LUE is an additional exercise to see if the estimation of LUE (and subsequently GPP) at water-stressed sites would benefit from using PRI instead of a conventional method, i.e. the MOD17 model.

C4662

[RC] Title ['Remote sensing of ecosystem LUE with MODIS-based PRI - the Dos and Don'ts'] does not match content, content is more a comparison between MOD17 and MODIS derived PRI

[AC] The second part of the title has been dropped. The title reads now 'Remote sensing of ecosystem LUE with MODIS-based PRI'.

[RC] p 6936 line 25: "Numerous approaches to model GPP have been taken (Beer et al., 2010), among which light use efficiency based models are very popular." Awkward wording, please adjust

[AC] In the revised version the sentence has been changed to 'Many diagnostic models of primary productivity are based on a light use efficiency approach (e.g. Running 2000, Yuan et al 2007, Beer et al., 2010).'

[RC] line 27: "Light use efficiency models are based on the assumption that photosynthetic assimilation of vegetation is a function of the amount of photosynthetically active radiation absorbed by plants" This is not really an assumption, is it..The monteith definition of GPP is very generic

[AC] True. In the revised manuscript, this sentence has been changed to 'All light use efficiency models represent photosynthetic assimilation of vegetation as a linear function of the amount of photosynthetically active radiation absorbed by plants.'

[RC] p6937 line 7: Wasn't that the goal of this study to find out whether this model can be applied globally? You should probably add something like "in theory"

[AC] To make the sentence more clear, it has been rephrased as follows: 'The simplicity of this approach, with little need for ancillary data, makes it possible to base these models on remote sensing products and meteorological fields (Hilker et al., 2008a; McCallum et al., 2009). Thus, an important prerequisite for application on the global scale is fulfilled.'

C4663

[RC] line 13: "Eq. (2) is generally agreed upon" You can delete this, eq 2 is the definition of fapar, nothing to agree upon here

[AC] This is a good point. The sentence has been changed to 'It should be noted, although the definition of aPAR is clear, faPAR and incident PAR derived from different sources and can differ substantially (e.g. McCallum et al., 2010).'

[RC] line 15: you should probably add a few sentences here explaining what Lue is. Say that it is driven by the most limiting of may factors, and changes in space and time

[AC] To improve clarity, the text beginning on line 12 page 6937 has been changed to: 'LUE is influenced by many factors and thus varies in space and time. Factors limiting LUE include plant water availability and atmospheric water demand as well as temperature and plant nutrition. LUE is usually modelled by constraining a certain maximum LUE according to a set of environmental conditions. The determinants of LUE and on which time-scales they act are only partially resolved.'

[RC] line 23: While studies using airborne fluorescence measurements had promising results, there is no space-borne sensor yet. WEll the reason for that is that fluorescence faces similar, if not even more difficult issues than PRI. For instance the signal is incredibly small compared to all the background effects.

[AC] We agree that pointing out the difficulties of space-borne fluorescence measurements might help novice in the field. We thus changed the sentence to 'While studies using airborne fluorescence measurements had promising results, the signal-to-noise ratio needs to be improved to be useful for satellite-based observations; efforts are ongoing (Meroni et al, 2009).'

[RC] p6938: "However, the PRI has some well known limitations (Grace et al., 2007). Multiple studies showed that the PRI signal is affected by the viewing and illumination geometry, including the fraction of sunlit and shaded leaves seen by the sensor, canopy structure, and background reflectance (Barton and North, 2001; Nichol et al.,

C4664

2002; Suarez et al., 2008; Sims and Gamon, 2002; Louis et al., 2005; Drolet et al., 2008; Hilker et al., 2009; Middleton et al., 2009)."

Not so sure about this. First of all I would argue that the limitations are not generally well known. In fact, I have the impression that many people just use PRI without really considering the extraneous effects and then find or don't find some relationships, which of course can never be applied on a larger area, because the extraneous conditions will change. Also, I would disagree that the influence of canopy structure and geometry (shading) on PRI is a limitation. Quite the opposite is true. I would think that this is a valid signal we are seeing, because obviously PRI is driven by the amount of excess light, which is higher in a sunlit crown than in a shaded part of the canopy.

[AC] No doubt the fraction of shaded/sunlit parts of the canopy has an important influence on the light use efficiency of vegetation and not just the PRI signal. However, which fraction of sunlit leaves is seen by a satellite depends on the position of the sensor relative to the canopy and the sun as well as the canopy structure. If the vegetation structure is not well known, uncertainty remains whether changes in PRI are due to a different position of the sensor or due to actual changes in LUE. Synchronous multi-angular observations would allow to determine the shadow fraction and thus reduce uncertainty.

This explanation has been included in the discussion.

[RC] p6942: "Albeit, from a previous study (Goerner et al., 2009) and preliminary experiments we know that correcting MODIS reflectances with readymade bidirectional reflectance distribution function (BRDF) parameters either has no effect on the PRI signal (when using POLDER/PARASOL based parameters (Bacour and Bréon, 2005), see Fig. 2 in supplementary material) or only seems to increase noise in the PRI signal (when using the MODIS MOD43 product, see Fig. 3 in supplementary material)." Hilker et al., 2009 (cited in this paper) gives an explanation for this. PRI changes as a function of the sun observer geometry. Hall et al., 2008 showed that this effect is a result of the photosynthetic downregulation in leaves, which is due to different proportions

C4665

of shadow fractions. Conventional atmospheric corrections are not designed for multi-angular acquisitions, hence they would destroy this directional observation of downregulation. As a result it is wrong to state that "readymade bidirectional reflectance distribution function (BRDF) parameters either has no effect on the PRI signal (when using POLDER/PARASOL based parameters (Bacour and Bréon, 2005), see Fig. 2 in supplementary material) or only seems to increase noise in the PRI signal". It depends on how this is applied (see for instance Hilker et al., 2009 and Hilker et al., 2008 RSE)

[AC] We think the above statement is true for the case specified, but maybe the term "readymade" is misleading. The out-of-the-box atmospheric corrections that have been an option for this study did rather corrupt the PRI signal as opposed to remove noise caused by atmospheric effects. We agree that it would be beneficial to take into account the effects of vegetation structure on the shadow fraction and thus changes in LUE due to changes in illumination intensity (as described in Hall et al. 2008). However, the multi-angular reflectance measurements needed for this were not available for this study. We exchanged "we know that correcting MODIS reflectances with readymade bidirectional reflectance distribution function (BRDF) parameters" for "we know that correcting MODIS reflectances with bidirectional reflectance distribution function (BRDF) parameters from existing data bases"

[RC] 6947: "On a site level, LUEMOD17 has in every setting much less agreement with observations than LUEPRI. LUEMOD17, opt. performs much better. However, only for one setting, the pooled FR-Pue observations, it is slightly superior to LUEPRI. The agreement between LUEMOD17.opt and the reference LUE increases slightly (without changing any of the statements above) when using faPAR from MODIS collection 4 instead of 5 to calculate LUEMOD17 because the MOD17 parameters have been optimised based on collection 4 data (not shown)."

Well that is not surprising though, because if at that site VPD and temperature are the limiting factors, of course the model would perform well. The point is, that this is not the case everywhere. You cannot really pick these few sites and then conclude that on

C4666

a site level the MOD17 product is superior to MODIS PRI

[AC] We do not conclude that MOD17-LUE is superior to PRI-based LUE, it is the other way around (for the study sites, a global statement is indeed not possible). To make this more clear, we have rewritten these lines as follows:

'For the sites we have studied, LUEMOD17 has in every setting much less agreement with observations than LUEPRI. LUEMOD17, opt. performs much better, though not superior to LUEPRI except at FR-Pue with MODIS viewing angles ranging from 0-40°.'

[RC] 6948: "The the fraction of PAR absorbed by the vegetation is rather stable throughout the year for the evergreen sites" What does that mean? Again I find it very problematic to use a satellite derived fapar to derive PRI and then compare it to MOD17

[AC] The evergreen sites in the study (FR-Pue, IT-Cpz, US-Me2) have little seasonal variation in the faPAR signal, but considerable variation in the PRI signal (C.f. Fig. 5). Thus for evergreen sites the PRI-signal is not confused by changes in leaf area/faPAR. We have changed the sentence to 'The fraction of PAR absorbed by the vegetation at the evergreen sites shows little seasonal variation compared to the changes in PRI'. Concerning the other comment: satellite faPAR is not used to derive PRI, but it is used to calculate the amount of absorbed photosynthetically active radiation, and thus LUE (via the empirical models discussed in section 2.3.3). This PRI-based LUE is then compared to in-situ LUE. The revised version of the manuscript makes clear that the benchmarking with MOD17-LUE is not the main evaluation of LUE_{PRI} , but only an additional point of reference (section 3.4).

[RC] 6950: "Unsurprisingly, the gain in accuracy through using PRI is highest for evergreen sites where changes in LUE are largely independent from greenness and changes in leaf area (see also Running and Nemani, 1988; Gamon et al., 1992)." Why would LUE (not PRI) be dependent on leaf area and greenness in the first place.

C4667

It is per definition the efficiency with which absorbed PAR can be used to produce biomass

[AC] The link between LUE and greenness/LAI is indirect. For example in temperate deciduous forests LUE and the amount of leaves and pigments follow similar seasonal patterns. We agree that 'dependent' does not express this precisely, so the sentence has been changed to 'Unsurprisingly, the gain in accuracy through using PRI is highest for evergreen sites where changes in LUE are largely unrelated to greenness and changes in leaf area (see also Running and Nemani, 1988; Gamon et al., 1992)."

Response to comments of anonymous referee 2

[RC] The PRI and fPAR observations may be expected to be consistent across sites, since all sites are observed by the same instrument and processed in the same way. However, the flux data were collected at multiple sites by different investigators. Has the variability in the flux data been examined in the LaThuile dataset? How much variation in the grouped PRI-LUE relationships is due to biases in the flux data between sites and years?

[AC] We are confident that the patterns we have observed are real. Many studies have addressed the robustness of eddy flux measurements, also with regard to differences between sites. Papale et al. (2006) provide an extensive summary of the uncertainties related to eddy flux data and present a standardized processing method that has been applied to all net ecosystem exchange data within the Fluxnet database. Given a homogeneous site, the largest uncertainty results from the so-called u^* -correction. The eddy covariance data used in this study have been processed using the same spike detection, storage correction, u^* filtering, gap-filling and partitioning methods applied in the LaThuile data collection processing.

Another source of uncertainty, the partitioning of net ecosystem flux into ecosystem respiration and gross primary productivity, has been addressed by Lasslop et al. (2010). Their comparison of two partitioning methods shows a strong correlation

C4668

and no significant biases for gross primary productivity and ecosystem respiration. Although the overall agreement of the two partitioning methods is good, there can be large deviations for specific sites or years. We therefore checked the influence of the partitioning method on the relationship between LUE and PRI for the study sites (c.f. Fig. 1 in this document) and found no change in the patterns. In fact, since GPP is a gross flux, the relative error is quite small, while for NEE (not considered here) the error can be relatively larger.

The high frequency site data are aggregated to half-hourly data by the principal investigators of the individual sites with different software, which presents another source of uncertainty. A comparison of different techniques performed by Mauder et al. (2008) indicates a good agreement among the software within 5–10% difference for 30-min CO₂ flux values. Considering this uncertainty does not change the results presented in this manuscript. The quality evaluation by Goeckede et al. (2008) for the CarboEurope-IP network demonstrated a high average data quality, and good representativeness of the measurement data for the specified target land cover types.

Göckede, Mathias, Thomas Foken, Marc Aubinet, Mika Aurela, J Banza, Christian Bernhofer, J M Bonnefond, et al. 2008. Quality control of CarboEurope flux data – Part 1: Coupling footprint analyses with flux data quality assessment to evaluate sites in forest ecosystems. Biogeosciences 5: 433-450.

Lasslop, Gitta, Markus Reichstein, Dario Papale, Andrew D Richardson, Almut Arneth, Alan G Barr, Paul Stoy, and Georg Wohlfahrt. 2010. Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. Global Change Biology 16: 187-208. doi:10.1111/j.1365-2486.2009.02041.x.

Mauder, M., T. Foken, R. Clement, J.A. Elbers, W. Eugster, T. Grünwald, B Heusinkveld, C4669

and O. Kolle. 2008. Quality control of CarboEurope flux data? Part II: Inter-comparison of eddy-covariance software. Biogeosciences 5: 451-462. <http://hal.archives-ouvertes.fr/hal-00297936/>.

Papale, Dario, Markus Reichstein, Marc Aubinet, E Canfora, Christian Bernhofer, Werner L Kutsch, B Longdoz, et al. 2006. Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. Biogeosciences 3: 571-583.

[RC] The title does not really describe the content and should be changed.

[AC] The second part of the title has been dropped. The title reads now 'Remote sensing of ecosystem LUE with MODIS-based PRI'.

[RC] Some of the sentences in the paper are awkward, a pass by an editor would make the paper easier to read.

[AC] Thanks to the reviewer comments we believe the paper is more readable now.

Response to comments of referee John Gamon

[RC] A few findings appear to contradict other published studies, for example, publications showing the 550 nm region to be a good reference band at the whole-stand scale (Gamon 1992, Middleton et al. 2010), and other studies showing the value of off-nadir view angles for optimal PRI retrieval (many studies, including those by Hall, Hilker, Drolet cited in the manuscript). Since there is no clear consensus on these issues yet, this study adds valuable insights to these topics, and a bit further discussion of these topics may be warranted.

[AC] The discussion of these aspects has been expanded (see below).

[RC] Other findings are consistent with previous publications that show a strong confounding effect of seasonally changing greenness, canopy or stand structure on PRI,

indicating that the component of PRI related to PSII LUE (the xanthophylls cycle) is often heavily confounded by seasonal shifts in pigments pool sizes (see Stylinski et al. 2002). When sampling complex landscapes, PRI can be heavily confounded by spatial or temporal variation in green vegetation cover or structure as shown in figure 5. All of these effects appear may well be present to varying degrees for the ecosystems sampled in this study, and further discussion of these confounding effects seems in order, given the strong link with FAPAR found for several sites (figure 5). Not surprisingly, these effects appear particularly strong for MODIS band 1 (the red band); previous studies (e.g. Gamon et al. 1992) indicate the green reference band (550 nm, close to MODIS Bands 4-12) best corrects for these confounding effects, and that other reference bands are often more confounded by varying green canopy structure. Clearly, this is a complex issue, but one that deserves further discussion and links to previous work on the topic of the “best” MODIS band. Regarding the link between PRI and FAPAR for seasonally greening ecosystems (ZA-Kru and US-MMS), the recent review paper by Garbulsky et al. 2010 may be instructive. Note that the original PRI formulation in the paper cited (Gamon et al. 1992) used 550 nm as the primary reference band for these reasons. Later studies noted that for leaf-level reflectance, 570 nm appeared to be the best reference band. For this reason, 570 nm has been picked up as the “standard” reference band, but there is little compelling evidence that this is a suitable band for MODIS PRI. In fact other more recent studies (Middleton et al. 2009 cited in this manuscript) also noted that 550 nm appeared to be a good reference band, as found at some of the sites in this study. This manuscript adds additional insight into the topic of “best” PRI formulations, and further discussion is warranted.

[AC] We included further discussion of these issues both in the introduction and the discussion section. The relevant section of the introduction now reads like this: ‘The original PRI formulation by Gamon et al. (1992) used 550 nm as the primary reference band since, according to a study on sunflowers, it seemed least affected by changes in green canopy structure. It also had 531 nm and reference wavelength swapped compared to recent use (c.f. eq. 3). Later studies noted that for leaf-level reflectance, 570

C4671

nm appears to normalise best for confounding effects like pigment content and chloroplast movement (Gamon et al. 1993, 1995). Thus, 570 nm became the most widely used PRI reference band. Recently, Middleton et al. (2009) showed for a Douglas fir forest that reference bands in the ranges 540-574 nm, 480-515 nm and 670-680 nm have a high correlation with foliage LUE. An overview on protocols used for PRI studies can be found in a review by Garbulsky et al. (2010). PRI can be a useful proxy for LUE because changes in reflectance at 531 nm are a side effect of mechanisms that protect the photosynthetic system in the leaves from excess light by down-regulating carbon assimilation (for an extensive summary, see Middleton et al., 2009; Coops et al., 2010). PRI also correlates with the total content of carotenoid pigments (Stylinski et al., 2002), this needs to be considered when looking at seasonal changes in PRI.’

See also below.

[RC] The last part of the title (“-the DOs and DON'Ts”) doesn't clearly fit the contents or presentation, and could probably be dropped.

[AC] Done

[RC] Abstract, line 7 (and p. 6939 – the use of the term “efficiency” is confusing. Perhaps “effectiveness” would be a clearer term here.

[AC] Thanks for the hint. We have exchanged “efficiency” for “effectiveness” in the indicated places.

[RC] Abstract, line 10 - “dependance” (with an a) should be spelled “dependence” (with an e).

[AC] Done.

[RC] Introduction, p6937 - From remote sensing, several other LUE formulation options exist, including those based on indices of surface temperature or moisture. A brief

C4672

men- tion of these other possibilities seems in order.

[AC] Some references to other ways of deriving LUE were added after 'Factors limiting LUE include plant water availability and atmospheric water demand as well as temperature and plant nutrition. LUE is usually modelled by constraining a certain maximum LUE according to a set of environmental conditions'

We have revised the discussion to include some examples of remotely sensed constraints of a maximum light use efficiency.

[RC] Introduction, p. 6938 – “aircrafts” should be replaced by “aircraft sensors” since it is really the sensors doing the sensing (not the plane).

[AC] 'Aircrafts' has been replaced by 'airborne sensors'.

[RC] Introduction , p. 6938 – “hesitation” to evaluate a LUE model based on MODIS PRI is probably more an issue of “difficulty” (getting the data and doing the work). Many people have considered this kind of study, but have fallen short due to difficulties with data access.

[AC] The wording has been changed to "These difficulties, along with data access problems, might have hindered the evaluation of an LUE model based on MODIS PRI across space and time."

[RC] Introduction , p. 6938 – in addition to being “widely apart,” coverage of multiple sites represent varying structure and view angle, all of which add considerable complexity to the problem.

[AC] It is true that focusing on the distance between sites distracts from the real difficulties (that have been mentioned in the sentences before). Thus 'that are widely apart' has been removed.

[RC] Introduction (last sentence) – The statement “. . .we try to comprehensively evaluate the aspects of a PRI-based LUE estimation” is vague – which aspects exactly?

C4673

- Please list or explain.

[AC] This sentence was meant to summarize the paragraph. As the paragraph is rather short, a summary is not really necessary, especially since it is redundant with the introductory sentence of that paragraph. 'Hence, we try to comprehensively...' has been removed in the current manuscript.

[RC] Page 6939 – isn't Kruger a subtropical (not a tropical) location?

[AC] It is true that the location is sub-tropical. However, the vegetation is typical of a tropical savanna. The description is now clearer on that issue.

[RC] Page 6940 – “Ready-made faPAR products are known to differ” – from what? From each other? (Please clarify).

[AC] Thanks for pointing out this lack of clarity. Indeed it should read 'differ from each other.' This has been changed.

[RC] Page 6941 6944 (and elsewhere)- The issue of sensor angle remains unclear because it is not defined relative to sun position. Without this information, it is difficult to judge the significance of the angle binning results.

[AC] Since the study cannot be repeated within a reasonable time replacing the sensor angle with a different metric, the following remark has been added to the discussion: 'The impact of the sun's position on the PRI-LUE relationships in this study should be limited by the similar data acquisition times (c.f. Fig. 1 in manuscript). Nevertheless, a follow on-study should consider the sensor angle relative to the position of the sun to obtain certainty on the influence of the image acquisition geometry on the PRI-LUE relationship.'

[RC] Page 6945 – The explanation for why ZA-Kru has the strongest deviation from the 1:1 (LUE-LUE) LUE line is not entirely clear.

C4674

[AC] To improve clarity, the revised manuscript contains the following explanation: 'The slope of the regression line between half-hourly and daily LUE for ZA-Kru has the strongest deviation from the 1:1 line. Midday LUE at ZA-Kru is lower compared to other sites, while LUE in the late afternoon and evening is on average higher than at the other sites. This might be due to differences in moisture limitation. The atmospheric moisture demand increases during middays stronger than at the other study sites (see Fig. 5+6 in supplementary material).'

[RC] Page 6946 – the fact that different sites have different optimal PRI reference bands probably reflects the different canopy structures (see above).

[AC] The discussion has been amended in this respect (see also below).

[RC] Page 6948 – A similar comment can be applied to the discussion of structure on PRI (the review of Garbulsky et al. 2010 might be helpful here).

[AC] The part of the discussion that deals with the relationship between LUE/PRI and vegetations greenness has been expanded and should be clearer now. Thank you for making us aware of the review of Garbulsky et al.. It has been added as a reference.

[RC] Page 6950 – indices of surface temperature or vegetation water content, available from certain sensors, might provide useful alternatives to PRI for LUE.

[AC] A remark on vegetation water content and surface temperature along with references has been added to the discussion.

[RC] Page 6951 – The statement that “It is unclear whether a satellite-derived PRI with a reference band at 570 nm , as favored for hand-held and air-borne sensors,” neglects the history of the evolution of the PRI formulation summarized above, which actually began with a green reference band close to MODIS band 12. 570 nm was subsequently derived with leaf-level measurements in mind. Consequently, the choice

C4675

of “best” reference band for MODIS remains an open issue, and this study clearly adds to the story!

[AC] The misleading sentence has been deleted and the respective passage has been extended: 'The optimal reference bands we determined (MODIS bands 1, 4, 10, 12) fall within the spectral regions identified by Middleton et al. (2009) and Cheng et al. (2009a) as useful PRI reference wavelengths in a study on foliar LUE in a Douglas fir stand. Middleton et al. (2009) also showed that a PRI based on the relatively broad spectral bands of MODIS (10 nm) correlates well with PRI values derived from 3 nm wide bands. The results of our analysis suggest that the usability of different reference wavelength might depend on species composition and stand structure. The first study on PRI by Gamon (1992) pointed out that no single reference wavelength suited all purposes equally well (e.g. tracking LUE in unstressed and water stressed sunflowers). The present study adds to the body of knowledge showing that 570 nm is not the only reference bands suitable for PRI. A data base encompassing more sites with a diversity of functional and structural traits would be desirable to arrive at a final conclusion in this regard. The review by Garbulsky et al. (2010) points out that the optical properties of the canopy are influenced - apart from species and environmental conditions - by the fraction of dead and woody biomass, vegetation density and spectral properties of the soil, all of which can affect the suitability of reference bands.'

[RC] Page 6952 – “Dependant” (with an “a”) should be dependent (with an “e”).

[AC] Done

[RC] Page 6952 – The ending of the paper might benefit from some suggestions on next directions.

[AC] Suggestions for future work are now mentioned throughout the discussion, many of them were added in response to helpful review comments. The suggestions fall into the categories 'improving knowledge on PRI' and 'exploring alternatives for estimating LUE'.

C4676

C4677

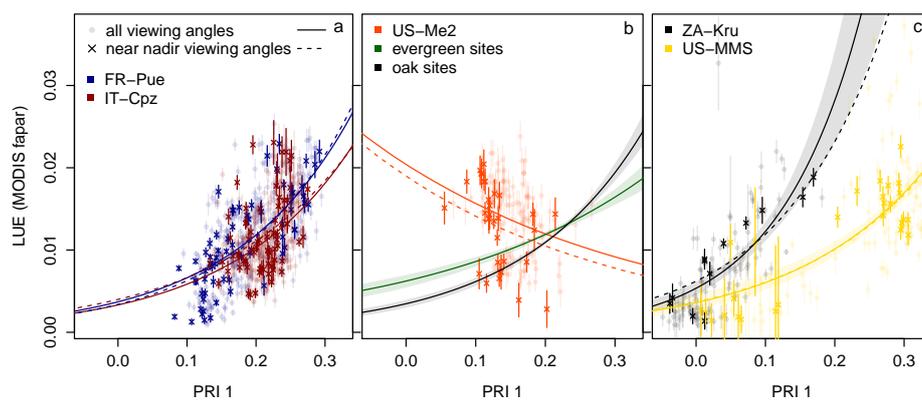


Fig. 1. Corresponds to Fig. 2 in the manuscript. The error bars represent twice the mean difference in LUE between partitioning based on nighttime or daytime data.

C4678