

Interactive comment on “Plant communities as drivers of soil respiration: pathways, mechanisms, and significance for global change” by D. B. Metcalfe et al.

D. B. Metcalfe et al.

daniel.metcalfe@slu.se

Received and published: 28 June 2011

Reviewer 2)

Comment: I have only few comments that may help to improve the readability of the paper. In general, I think the focus of the paper needs to be made more clear. Furthermore, the text could be sharpened, since some information is scattered throughout the manuscript and, finally, some parts need more detailed explanation (see specific comments below). Especially, from the abstract it was not entirely clear for me what follows, also because some statements seemed rather disconnected from the rest.
Response: Please see our detailed responses to each comment, with line numbers,

C1702

below. We have revised the manuscript text and inserted a new figure, to link together different sections better and more clearly illustrate the relevance of the different discussion topics specifically for R. We have modified the structure of the Abstract and added some text to make its focus much more clearly targeted at R. For example, we now specifically state why belowground carbon partitioning is important for understanding R (Lines 59-60) and mention the different components of R (Lines 51-54).

Comment: p 2146, l 4-7: I would move this sentence more to the end of the abstract. Before, it may be helpful to motivate the need for such a review, for example by showing the discrepancy between state of knowledge about the diversity of pathways plant communities can affect R and how this knowledge is represented in vegetation models. After this, I would shorten, but better connect your findings. Response: We have modified the structure of the abstract and added some text to make the different sentences in the abstract better connected together, and to make the focus much more clearly targeted at R. We acknowledge the point about putting the review overview text only after the need for such a review has been explained, however by the end of the abstract we have already presented not only the motivation for the review but also all of the key findings. We feel that it is important to place this sentence before the findings because it provides an overview of our focus, and hence helps to structure and connect together our different findings. So we have decided to place this sentence after the initial general motivation but before the presentation of the key findings (Lines 54-58).

Comment: p 2146, l 9-11: This sentence does not logically connect to the previous one and it remains unclear why a shift towards fast growing plants with nutrient rich litter could provide a positive feedback mechanism, which I think is also not the case (see below). Response: We agree that this statement is rather uncertain, and at least deserves more explanatory text. So we have modified the sentence accordingly (Lines 69-73)

Comment: p 2146, l 21-22: For me it remains unclear and vague how experimental

C1703

and field studies would improve model accuracy. This sentence calls for a very concrete outline of experiments and field studies in your paper, which I think is not given (or scattered throughout the text). Either remove this sentence, or, more interestingly outline how such experiments shall be designed. Response: We have removed this sentence from the abstract because we feel that the subsequent text, highlighting priority areas for research, makes a similar point but in a more useful way (Lines 74-79). We feel that the discussion of the priority areas for research in the conclusions section, which includes some methodological details, should fulfill the purpose of outlining the kinds of experimental approaches which would make the greatest advances in our understanding of this topic (Lines 638-683). In addition, we also cite some synthesis papers which have specifically focused on experimental and field R measurements (Lines 120-121, 641-642, 1137).

Comment: p 2150, l 15-17: I cannot follow the point that shifts in plant community composition towards greater dominance of faster growing species or those with rapid turnover would provide a positive feedback. This can only be the case if C_{efflux} from the soil is greater than the C_{influx} into the soil. The only process I could imagine would be a priming effect and the release of old carbon stored in the soil, however I cannot find priming mentioned in your text. Response: Our intention with this sentence was to make the point that changes in R with climate change may be greater than anticipated when including plant community shifts in addition to abiotic effects on microbial activity. We have now modified the sentence to clarify this (Lines 181-184). The basic mechanism for operation of the feedback is possible (greater R = great atmospheric CO₂ and climate change = greater community dominance by fast turnover species = greater R), but we agree that it is debatable as to whether faster growing plants would necessarily drive an increase in whole ecosystem CO₂ emissions (even if they increased R) because photosynthetic uptake could also increase, so we have removed any reference to this feedback.

Comment: p 2151, l 7-18: What about warm and infertile sites such as tropical low-

C1704

lands, where soil nutrient status and herbivory favor plants maximizing resource retention? E.g. Fine et al. (2004) Herbivores Promote Habitat Specialization by Trees in Amazonian Forests, *Science* 305, 663-665. In this case R may not be amplified, but dampened by the plant community. Response: We have now removed the last part of the last sentence in this section, in recognition of the fact that herbivory may both promote and suppress R. We have now included some references to justify the text in this section (Lines 210-212). We have also slightly changed the first sentence to remove the implication that warmth and fertility are always positively correlated (Lines 210-211). Thus, we acknowledge there is substantial variation in soil fertility within similar climatic zones, and there are contrasting climates across sites with similar levels of soil nutrients. We now more explicitly acknowledge that R may be both positively and negatively affected by herbivory (Lines 212-213), and cite the Fine et al. (2004) paper where appropriate (Line 236). We note that the findings of the Fine et al. (2004) study are not necessarily contradictory to our claims. The evolutionary selective pressure imposed by herbivores need not be clearly related to their abundance or diversity. We could not find this data in the Fine et al. (2004) paper, but we suspect that the absolute amount of herbivores and rates of herbivory were lower at the infertile white sand site, but that the selective pressure imposed on the plants to develop defenses was nevertheless greater because the paucity of soil resources meant that the costs of losing leaf material was much higher than the more fertile site.

Comment: p 2151, l 23-28: You make the point here that plant strategies that maximize resource retention are those which also allocate a greater portion of their assimilates to belowground organs. I wonder if this relationship really exists. You refer to Figure 1 here, but I think a reference would be important. For example, in nutrient poor tropical lowlands plant strategies invest a lot of resources into fine root growth, but at the same time may have high root turnover rates through increased rates of herbivory or not if they invest in protective traits. Since both may happen under similar environmental conditions, I think this needs further explanation. E.g. Fine et al. (2004) Herbivores Promote Habitat Specialization by Trees in Amazonian Forests, *Science*

C1705

305, 663-665. Response: According to the functional balance theory (Cannell and Dewar, 1994), plants should allocate C to organs to maximize uptake of the most limiting resource. So, we reason that under infertile or dry conditions, where resource conserving species tend to dominate, these plants may allocate more C belowground. We have revised this section to clarify that this is a hypothesis still awaiting extensive field testing, and specifically mention that other factors such as herbivory can confound this pattern, using the Fine et al (2004) reference as an example (Lines 233-236). We also now include a range of relevant references to studies showing shifts in root : shoot ratios with soil fertility and moisture, but recognize that this pattern may not hold when considering global patterns within a single vegetation type (Lines 233-245). In comparison to above and belowground biomass stocks, simultaneous measurements of both TBCF and GPP fluxes from the same site are very rare. But from the synthesis of data from forest sites in Litton et al., (2007), which we think represents the most comprehensive view of currently available data, there is a tendency for arid sites (< 500 mm per year) to have a relatively high portion of GPP dedicated to TBCF (> 50

Comment: p 2154, l 4-8: Please explain how you derive your hypothesis that TBCF dedicated to mycorrhizae originates from the geographic variation of TBCF across forests. I wonder if this hypothesis might be biased because of a geographic bias in studies towards high and mid latitudes. What about mycorrhiza in tropical nutrient poor soils (e.g. in the Amazon Basin where P seems to be a limiting nutrient). I wonder if there is some literature from the tropics to include here (e.g. Hättenschwiler et al. 2011: Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis, *New Phytologist*, 189: 950–965), in case there are no studies on mycorrhiza in the tropics, it might be worth pointing out this research need. Response: We have now modified this section to clarify our reasoning and provide more background information (Lines 302-311).

Comment: p 2157, l 1: Please explain further why invaded ecosystems would have higher R, this seems very speculative to me and may be context dependent. Again,

C1706

only what has been assimilated can be respired, otherwise there must be a depletion of the soil carbon stock through a shift in community composition. However, you do not mention this and it remains unclear for me, what the underlying mechanisms would be. Please clarify. Response: This statement was derived from a large-scale meta-analysis of comparative studies of invasive plant species, which provides evidence for a large increase in production and decomposition in invaded ecosystems compared with native ecosystems (Lines 380-382). While we acknowledge that there is little direct evidence for shifts in R following invasion, we reason that if more organic material is produced and if this material decomposes faster after invasion, then this should translate into increased R (Lines 383-385). However, we strongly agree that this pattern is very context-dependant (Lines 410-413) and discuss, at length, different mechanisms which might explain whether an invading plant will cause shifts in R (Lines 385-410)

Comment: p 2158, l 20-27: I think from natural gradients it is impossible to say that diversity doesn't matter, since diversity effects can only be tested within similar vegetation types, because of confounding effects across vegetation types, which may result from different environmental constraints (e.g. differences in climate, soil nutrient status, disturbance regime). Moreover, I think the latitudinal diversity gradient is not a good example here, since it is subject to ongoing debate and multiple hypothesis for its origin exist. In most cases productivity is only used as an explanatory variable, however experiments in grasslands show a clear relationship between diversity and productivity (within one vegetation type). See e.g. Marquard et al. (2009) Positive biodiversity–productivity relationship due to increased plant density. *Journal of Ecology* 97, 696–704. You may also consider that Fig. 2 shows mainly data for above ground production, while data on below ground production hardly exist. Also the loss of above ground carbon through insect herbivory in the tropics is probably not considered in Figure 2, which can be quite large in the tropics. Response: This is a topic about which there has been considerable debate. Although a detailed discussion about this debate is outside the scope of this review, we emphasize that there has been considerable disagreement among researchers about the relevance of the grassland studies to which the reviewer

C1707

refers for understanding the role of diversity on ecosystem functioning in real communities. While the reviewer raises problems with confounding issues in studies in natural gradients, we think if diversity was an important driver in nature relative to other ecological drivers then we would expect to see ecosystem process rates in nature to increase with increasing diversity. The fact that this is not usually observed (or indeed that the reverse is more commonly observed) is taken by us to mean that whatever effects diversity per se may have on ecosystem functioning are of insufficient strength for its signal to be detectable against the background of other drivers of ecosystem processes. Regarding the latitudinal diversity gradient, while we recognize that the underlying mechanisms for the gradient are still not resolved, the existence of the gradient itself is very well established (Gaston 2000, Hillebrand 2004). We use this example to point out simply that the lack of any strong change in R over a very large and spatially consistent increase in plant diversity towards the tropics indicates that large-scale patterns of R in natural systems are probably overwhelmingly dominated by other factors than diversity (Lines 436-439). We now acknowledge that our picture of patterns in plant production is principally shaped by observations of aboveground growth, and that further measurements of overlooked components such as belowground production and herbivory are required to provide a more complete view. (Lines 174-177).

Comment: p 2161 Section 5: I believe this section would benefit from a table summarizing which plant traits in general have an effect on R, via which process, in which DGVM (land surface model) this process is represented and how, and maybe the potential for a positive or negative feedback. The white areas of such a table would immediately show needs for future research. Response: We agree that such a table would be very useful but feel that our current state of knowledge is, unfortunately, at too early a stage to so confidently designate mechanisms linking plant traits to R, and the potential for feedbacks. Presentation of data in such a format risks conveying an artificial sense of certainty about the direction and magnitude of plant-R feedbacks. Nevertheless, there is some information available, and so our approach is to present this in the text where we can allot ample space to describing the type and amount of

C1708

evidence for different links and patterns, together with a critical assessment of potential gaps. With regards to the model representations of plant traits, this would involve a very exhaustive, detailed meta-analysis beyond the scope of the current review which is primarily focused on the biological mechanisms linking plants to R. Such a review would also overlap substantially with the very detailed synthesis by Ostle et al. (2009) which focused entirely on representation of plant-soil interactions within global climate models. Instead, we summarize what we think are some of the most important characteristics of current models in terms of their treatment of plants and R, and highlight major areas for further work to integrate ecological mechanisms into current models.

Comment: p 2165, l 5-7: Again, I cannot follow this point, because increased assimilation and respiration balance each out, which is not a positive feedback, please clarify. Response: Our intention with this sentence was to make the point that changes in R with climate change may be greater than anticipated when including plant community shifts in addition to abiotic effects on microbial activity, but we agree that it is debatable whether faster growing plants would necessarily drive an increase in whole ecosystem CO₂ emissions (even if they increased R) because photosynthetic uptake could also increase, so we have removed any reference to this. We have now modified the sentence to clarify (Lines 603-606).

Comment: p 2165, l 19-22: I have difficulties to follow this point, maybe you can explain a bit further. What about this relationship across vegetation types? In general, I think the distinction between within and across vegetation types is important to make, since it may cause some confusion. You do this in the paper in some cases but not in others, I would recommend to be more consistent, especially in the abstract and the conclusion. This is particularly important when referring to plant traits, which are usually measured at the individual plant level and also for discussing the effect of trait diversity. As mentioned before, diversity effects can only be identified within similar vegetation types. Response: Since this is the conclusion we have tried to summarize patterns without too much complicating detail. We discuss this pattern in more detail in the

C1709

main text, but have tried to rephrase this sentence to clarify (Lines 616-620). We agree that it is important to emphasize within and between-vegetation differences. We have tried to raise this distinction wherever appropriate throughout the manuscript. (Lines 60-63, 193-194, 256-265, 616-623). Our response to the point regarding the effects of diversity is detailed above.

Comment: p 2147, l 2: "feedbacks", please explain between which components feedbacks occur, and how R impacts and feed backs. Or do you mean "impacts" on R? Response: We meant "impacts" so we have revised this sentence to clarify (Lines 79-82). We leave more detailed discussion of the precise nature of the feedbacks/controls/impacts on R for the main text of the manuscript.

Comment: p 2147, l 2: here it might be worth mentioning that there are feedbacks of terrestrial ecosystem to the climate system, and that not only climate change impacts terrestrial ecosystems. Response: Following your comment above, we have removed reference to "feedbacks" in the abstract. We strongly agree with this point and hope that the reference to the role of R in the "earth-climate system" conveys some of this message: that R is a component within an interconnected system, and as such may interact with other components (such as the climate) in a bidirectional way (Lines 81-82).

Comment: p 2148, l 1: "conflicting results" in terms of what? please explain, which are the "conflicting results" that you are referring to. Response: We have modified this sentence to clarify (Lines 114-117).

Comment: p 2149, l 21: Do you mean "Effects of aboveground litter quantity and quality" on R Response: We mean the effects of plant communities on aboveground litter quantity and quality, and hence on R (Lines 159-163)

Comment: p 2151, l 19: Do you mean "Effects of plant allocation below-ground" on R or the effects of plant communities on plant allocation below-ground? Response: See response above.

C1710

Comment: p 2152, l 14: "towards" more photosynthetically active ... Response: We have modified this sentence following your suggestion (Lines 256-259).

Comment: p 2153, l 23: Which aboveground plant properties do you mean? Response: This sentence has been modified to provide more detailed information (Lines 289-293).

Comment: p 2155, l 16: "Effects OF microclimate ..."? Response: See our response above. We mean the effects of plant species on microclimate, and hence on R.

Comment: p 2161, l 14: You forgot to mention the SEIB-DGVM here, to which you are referring later. Response: Thank you for pointing out this error, we have now included the key reference to the SEIB-DGM model (Lines 507-508).

Comment: p 2163, l 4: you mention land surface models here. Do you mean DGVMs or land surface models that run as part of climate models (e.g. CLM or JSBACH). Please clarify and/or give a reference. Response: We acknowledge that the DGVM term may not apply for all of the examples we cite, so we have replaced this term throughout the manuscript with the more general term "carbon cycle models" or "CCM's".

Comment: p 2164, l 18: It may be more appropriate to cite here: Reu et al. (2010) The role of climate and plant functional trade-offs in shaping global biome and biodiversity patterns. *Global Ecology and Biogeography*. DOI: 10.1111/j.1466-8238.2010.00621.x. Response: We have substituted this reference according to your suggestion (Lines 590).

Comment: In general there is a large body of literature on plant functional trade-offs (more than acquisitive vs conservative plant growth strategies) and allocation patterns, especially relevant for section 2.2 where you address below-ground allocation. Here I also miss some theoretical considerations, this may be relevant since below-ground allocation is hard to measure. You may find some of the pioneering work in: Bazzaz, F., Grace, J., and Raven, J.: Plant resource allocation, Academic Press, San Diego, California, USA, 1997 Grime, J.: Plant strategies, vegetation processes, and

C1711

ecosystem properties, John Wiley Sons Inc, Chichester New York, 2001 Response: Thank you for pointing out this highly relevant reference. We have looked through this book and now cite two key chapters in section 2.2: Heilmeyer et al., 1997 and Lerdau and Gershenson, 1997 (Lines 233-242).

Please also note the supplement to this comment:

<http://www.biogeosciences-discuss.net/8/C1702/2011/bgd-8-C1702-2011-supplement.pdf>

Interactive comment on Biogeosciences Discuss., 8, 2145, 2011.

C1712