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Discussions

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Interactive comment on "Altered phenology and temperature sensitivity of invasive annual grasses and forbs changes autotrophic and heterotrophic respiration rates in a semi-arid shrub community" *by* M. Mauritz and D. L. Lipson

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We would like to thank both reviewers for their time and their comments which will certainly improve the manuscript. Since the major concerns of both reviewers were quite similar they will be addressed together. The responses to each reviewer's specific, more minor concerns are below.

Overall the reviewers felt that the manuscript was interesting and relevant but the analyses perhaps too simplistic and that the presentation could be improved. We believe

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that the criticisms of the analyses are largely because our methods were unclear. We will improve this aspect of the manuscript and in doing so address several of the major concerns.

Response to major concerns:

More concise statement of goals:

The reviewers suggest a more concise statement of goals, better use and citation of the literature. The goal of this paper was to gain a better understanding of autotrophic (Ra) and heterotrophic (Rh) partitioning of soil respiration and to compare soil respiration between native shrubs and invasive annuals. We evaluated seasonal changes in Ra and Rh and temperature and moisture sensitivity of all soil respiration components. We found that the temperature response function of all soil respiration components is highly dependent on soil moisture and varied between vegetation types. In invaded areas respiration rates were substantially higher than under shrubs, primarily due to greater invasive Ra contributions. Soil respiration in invaded areas responded more rapidly to temperature increases and both Ra and Rh are able to tolerate higher temperatures compared to shrub areas. We discuss several possible explanations: altered soil microclimate, changes in belowground carbon quality and supply, altered microbial community and differences in invasive and shrub phenology. We attempted to cite applicable literature widely and broadly; in the revised manuscript we will ensure that literature is cited correctly. Restructuring the methods and analyses, and addressing some of the other reviewer concerns, will help to clearly reflect appropriate citation of the literature.

Simplistic analyses:

Both reviewers expressed concern that the analyses are too simplistic. The reviewers point out that the temperature and moisture functions are inappropriate and the selection of soil moisture categories is subjective. We believe that the criticism of simplistic analyses stems from the fact that our methods poorly convey our data analysis. All

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analyses were done on natural log transformed data, therefore our linear temperature responses are equivalent to an exponential temperature response on untransformed data which corresponds to a Q10 analysis. The polynomial temperature response curve, ln flux = B0 + B1*VWC + B2*VWC2 was fit purely to illustrate how respiration changes with moisture, and would not be an appropriate model for predicting soil respiration. The same is true of the polynomial temperature response curve. In the revised manuscript we will clarify the methods and include the following points (summarized in a table):

1. A Q10 function, Rs = B0*exp(B1*T) does not fit the seasonal data set and cannot predict the declines in soil respiration when soil moisture becomes limiting

2. Rs = B0 * exp(B1*T) * exp(B2*VWC + B3*VWCˆ2) is a common model eg: (Vargas and Allen, 2008;Tang and Baldocchi, 2005) and is OK. . .

3. But a much better fit is found if an interaction term is included for temperature and moisture such that Rs = B0 * exp(B1*T) * exp(B2*VWC) * exp(B3*T*VWC)

4. The ability of temperature to predict respiration becomes worse as soil moisture declines and respiration becomes increasingly dependent on soil moisture. This is currently shown in a partial correlation analysis, on ln transformed data, in the supplemental materials. It is nice to show this, but not central to the manuscript and will remain in the supplemental material.

5. To further explore the interaction between temperature and moisture we arbitrarily binned the data into 5% soil moisture categories, found that moisture and temperature were no longer correlated, and fit Q10 responses. This illustrates very nicely the interaction between temperature and moisture.

6. We will change our data presentation in order to illustrate how Q10 changes with soil moisture (similar to the modeled Q10 changes shown by (Lellei-Kovacs et al., 2011)) for total, autotrophic and heterotrophic respiration

7. On a seasonal basis temperature is a better predictor of invasive Ra than shrub Ra. In months at the beginning and end of the growing season, Ra falls below the temperature response function. We argue this is primarily because early in the season the shrubs are not yet phenologically active and later in the season the shrubs prepare for summer dormancy resulting in low Ra, decoupled from temperature. This is supported by diurnal Ra patterns.

7i. We will include an analysis to show changes in diurnal temperature sensitivity of Ra. In winter, spring and early summer invasive Ra responds positively to temperature. In winter and spring shrub Ra responds positively to temperature but in early summer shrub Ra has no diurnal pattern and does not change with temperature.

Causality:

Both reviewers expressed concern that causality is being inferred without appropriate experimental design. It is true that we did not manipulate invasion nor were we able to test pre- and post- invasion. However, for two reasons, we believe that altered respiration patterns in the invaded areas are due to the presence of invasives rather than to pre-existing differences. First, we show that higher respiration rates are largely due to autotrophic respiration. Exclusion of roots causes a greater decline in respiration rates in the invaded areas than in the shrub areas. In contrast heterotrophic respiration rates in invaded and shrub areas are quite similar in magnitude. This suggests that higher respiration is due to the presence of invasives. Second, we have data that show the edaphic soil conditions in invaded and shrub areas are almost identical. Again, this suggests that differences in respiration rate, temperature or moisture sensitivity are indeed biological in origin. In the revised manuscript we will provide a table which shows the edaphic factors under the two vegetation types. We will also adjust our language throughout to clarify that we did not directly test causation.

VWC binning by eye:

The reviewers expressed concern that the data was inappropriately binned into soil

moisture categories and are presumably concerned that this could bias our conclusions. Our main purpose for splitting the data into soil moisture categories was to explore the interaction between soil moisture and temperature and show that the respiration response to temperature depends on soil moisture conditions. The way the methods are currently worded it sounds like the data was split visually based on the polynomial moisture curve, this was not the case. The data was arbitrarily binned into 5% soil moisture categories; data <10% was combined into one category to increase the number of data points and because a <5% category did not provide much additional information. After binning the data we verified that temperature and moisture were no longer correlated in each soil moisture categories which also allowed us to independently compare the predictive power of moisture and temperature (partial correlation analysis shown in supplemental material). Splitting the data using regression tree analysis gives a moisture threshold at 6.8% for total respiration and 7.8% for heterotrophic respiration. Qualitatively the result is the same, positive temperature responses when the soil is wet and negative when the soil is dry. Splitting the data by quartiles, based on soil moisture, creates cut-offs similar to our 5% bins and does not influence our conclusions. We think it is informative to use the 5% categories because they capture different parts of the growing season and allow differences between vegetation types, under similar moisture conditions, to be discussed in terms of altered abiotic and phenological responses.

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Response to specific points: Referee 1

Pseudo-replication:

The reviewer is concerned that the study was conducted within a small area and that the replicates are pseudo-replicated and that we therefore cannot infer causality between invasion and higher respiration rates (also addressed above). While the site is quite small, the chambers in invaded and shrub patches are at least 2m apart and the distance between any two shrub or invaded patches is close to 4m. Previous work in

Coastal Sage Scrub has found that shrub patches are auto-correlated up to a distance of approximately 5m (Strahm, 2005). Neighboring pairs of chambers in shrub and invaded areas area likely to occupy an auto-correlated patch, but the distance between two shrub or invaded area replicates should be sufficient to be true replicates within our study area. We will mention this in the methods.

Itemized suggestions:

1. Page 6336, line 10: "increased" – careful about causality This will be changed so that causality is not inferred

2. P. 6336, l. 10: specify time period of "cumulative" numbers This change will be made in the revised manuscript

3. P. 6337, l. 14: "Rt" is an unusual term to use for soil respiration; consider something more standard (Rs, Fs, etc) True. It makes more sense to use Rs, thanks. Rt will be changed to Rs in the revised manuscript.

4. P. 6337, l. 17: "Högberg" (umlaut over o) Thanks. This was an error from the citation manager, the change will be made in the revised manuscript.

5. P. 6337, l. 17-18: reword. It's not the relative contribution per se affects soil C storage, it's that all these reflect balance of heterotrophs and autotrophs This section will be reworded for more clarity.

6. P. 6339, l. 13: specify USA This change will be made in the revised manuscript.

7. P. 6340, l. 28 (Eq. 1): not Ra=Rt-Rh? Thanks. It should indeed read 'Ra = Rt-Rh', the correction will be made.

8. P. 6342, l. 12: why the conversion to K here? This correction was recommended by Licor. Converting the temperatures to K keeps the correction consistent with the units used when the fluxes were initially calculated.

9. P. 6343, l. 20-21: these polynomials are crude, completely abiotic ways to charac-

terize respiration response to T and VWC; why not at least use a standard Q10-style model? See above

10. P. 6344, l. 1-5: how were these breakpoints determined? Doing so algorithmically (i.e., using a reproducible process) would be good See above

11. P. 6345, l. 22: "μmol"

This change will be addressed in the revised manuscript

12. P. 6348, l. 2: "altered" – see comment #1 above; also applies to beginning of discussion and other places This will be addressed throughout the manuscript to make sure that causality is not inferred where it is not certain.

13. P. 6351, l. 5-: move to discussion

This section will be moved to the discussion.

14. P. 6351, l. 23: "well outside of" ? This sentence will be rephrased to clarify that we expected respiration to tolerate and respond positively to temperatures in a higher range than 15-20 °C.

15. P. 6352, l. 1-5: you can't just assert with no evidence that Tang & Baldocchi got the wrong answer because of low sampling frequency (especially since we're talking about season and annual numbers) This statement was not intended to imply that the estimates byTang and Baldocchi (2005) are incorrect, merely to offer a comparison with other soil respiration estimates obtained by two different methods. We believe it to be interesting that our estimates are in a range similar to those based on continuous eddy flux measurements (Xu and Baldocchi, 2004), but higher than those based on direct soil respiration measurements which are not continuous and do not capture rain events (Tang and Baldocchi, 2005). There is only one other published estimate of annual soil respiration in Coastal Sage Scrub (Wolkovich et al., 2010) so it is difficult to offer comparisons from the same ecosystem. The estimates from Wolkovich et al are based on lab incubations of a labile and potentially mineralizable C pool; they

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are closer to the range of Tang and Baldocchi (2005). As stated this highlights the discrepancy between soil respiration estimates obtained by different methods. This is not to say that, given the data presented in any study, the estimates are incorrect. However it does emphasize the importance of continuous data sets and particularly the contribution of dynamic periods, such as precipitation events, which will be poorly represented in weekly or monthly soil respiration measurements and lab incubations. We will rephrase this sentence so as not to imply that any other study is incorrect.

16. P. 6354, l. 20: start new paragraph This change will be made in the revised manuscript.

17. Table 3: seems like this should just be summarized in text We agree that this information does not warrant a separate table; it will be removed in the revised manuscript.

18. Figure 7: connect points for clarity? Points will be connected in the revised manuscript.

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Referee 2

1. P6336 L10 – add time units - g C m-2 per year?

Yes, per year. This change will be made in the revised manuscript.

L14 – "invasion increase temperature sensitivity in Rt and Rh when wet and decreased when dry" What timeframe are you referring too, daily, seasonal temperature sensitivity? L15 – How can the altered temperature sensitivity be due to phenology of invasives if Ra temperature sensitivity is not altered as well?

These sentences will be revised for greater clarity.

There were seasonal and diurnal changes in temperature sensitivity of Rt, Rh and Ra in invaded areas. When soils were wet Rt, Rh and Ra in invaded areas all increased more rapidly with temperature compared to shrub areas. When soils were dry Rt and

Rh declined more rapidly under shrubs (figure 5). Invasive Ra was always more tightly coupled to temperature than in shrubs. Particularly at high temperatures and low soil moisture, shrub Ra did not respond to temperature. In contrast invasive Ra declined rapidly and predictably as temperatures increased (figure 6). Shrub Ra changed independently of temperature at the end of the growing season presumably because of phenology but possibly also because shrub Ra is decoupled from surface temperatures. The diurnal Ra patterns from the winter into the summer show more rapid decline in shrub than in invasive Ra. This suggests that altered temperature sensitivity of shrub Ra is not just a decoupling from soil surface temperatures but has a largely phenological component.

2. P6337 L3 – on an annual basis L15 – Ra is often younger C than Rh, but not always. This statement should be reworded.

The statement will be revised.

3. P6338 L10 – Rh and Ra partitioning when dry is system dependent, check your references are incorrect. In annual plant ecosystem, this is true because all annuals are dead. But in a perennial plant ecosystem, often the Rh is more sensitive to moisture than Ra. . . thus Rt is usually dominated by Ra when dry because plants have roots that can get water from depth, where as the majority of microbes are in the upper soil layers, and cannot access water at depth. L13 – This study was done on perennial grasses, not annual – it is in the title of the paper. Increase Ra with respect to what?

Thanks. Changes will be made to this section to ensure correct citations and to clarify that the seasonal response of Rh and Ra is vegetation specific and can be difficult to predict.

4. P6340 Equation 1 should be: Ra = Rt-Rh

Thanks. This change will be made in the revised manuscript.

5. P6341 âĂć Unnecessary text on data quality control.

This section will be made more concise in the revised manuscript.

6. P6344 L8 – "invaded areas became hotter than shrubs" this is a problem throughout the manuscript, shrub areas, plots, or chambers should be used.

This will be revised for consistency; we will refer either to 'invaded areas' and 'shrub areas' or 'invasives' and 'shrubs'.

Subsection headers, for example "3.2 Invasion increased respiration rates" should be less causal for example "Greater respiration rates in invaded areas"

This change will be addressed in the revised manuscript.

Figures – One multipanel figure with Rt,Rh,Ra – soil temp – and soil moisture would be informative instead of two separate figures and no time series of temperature.

In the revised manuscript the temperature and moisture data will be presented in one figure; figure 3 with weekly average moisture and temperatures will be removed.

Fig 1,3 – what do the grey and white areas represent?

Grey and white areas distinguish different parts of the season as indicated in the top graph of each figure.

Fig 5 – why not do the temperature and moisture analyses with Ra and Rh, instead of Rt and Rh.

This is the only continuous soil respiration data set that exists for Coastal Sage Scrub and the San Diego region. We think it is important that all analyses are done on Rt rather than only on the derived Ra rates.

We used the temperature and moisture analyses of Rt and Rh to inform the Ra analysis. The Ra temperature sensitivity analysis was done similarly to the Rt and Rh analyses to understand the autotrophic response and highlight the role of phenology.

Fig 7 – connect symbols with lines

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This change will be made in the revised manuscript.

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