

Response to reviewer #1:

We would like to thank the reviewer for the time to provide a thorough review. We have provided our response for each of the comments (shown in bold) below, to improve the paper.

The manuscript tries to provide a new parameter set for the representation of shrubs in the ED2 – DGVM. The implementation aims to improve GPP estimation in shrublands. Yes, shrublands are under-represent in DGVMs and need more consideration, but I think the present manuscript need an extensive revision to show that shrublands work well within the ED2 model. For two sites a simple methods is used to optimise the parameter values, but the study provide no cross-validation and no further application is given.

This initial study had 2 years of data available from the flux towers (2015-2016), and thus we maximized this available data. Since submittal of the paper, an additional year of flux tower data became available (2017) and we have now included this for subsequent validation in our revision. Additional revisions (please see below) have also been made.

As I have general caveats about the methods used in this study I will list them here and will not go into much detail.

- 1. Most importantly, the method used here to optimise parameters is not state of the art. There are a lot of methods usually applied to solve the problem of parameter optimization as the Monte Carlo Analysis or genetic optimisation algorithms. Then it would be possible to include all important parameter for the optimisation procedure.**

We agree that additional optimizations (and sensitivity) should be performed; for this analysis we used the exhaustive (brute force) method due to computational and study limitations. We spent extensive time on developing the shrub (representing sagebrush) PFT for the EDv2.2 model (e.g. establishing allometric relationships) and several preliminary model run-ups to match with the ecosystem conditions. We've modified the paper to highlight this intent and the conclusions we may draw from the existing work. Again, this research is intended to introduce the sagebrush PFT and its implementation in EDv2.2. Additional robust optimization and sensitivity analyses, and broad spatial scale analysis are the next steps. And we have suggested these in the Discussion and Conclusion sections.

2. **Secondly, the same as for the parameter optimisation, the parameter sensitivity measure should be performed with a more comprehensive method (e.g. using partial rank correlation coefficient (PRCC) or Fourier Amplitude Sensitivity Test (FAST)). A freely available paper (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2570191/>) gives an overview of the methods, which can be used to conduct parameter optimisation and sensitivity tests.**

We used the Sensitivity Index (SI) which is a straightforward linear (and thus efficient) approach. Again, our intent here was to perform preliminary analyses to demonstrate the sagebrush PFT and more robust analyses will need to take place to demonstrate the value of using ED within sagebrush-steppe. Please also see above responses.

3. **Another point is that the authors should use both sites to optimise the parameter set, if they want to apply the model on a broader scale. Furthermore, I didn't understand why the study provides the 10 best ensemble means, these can't be better than the best estimate. But anyhow the authors don't provide a cross-validation. Hence it is impossible to evaluate the performance of the optimised parameters as these are used for the optimisation already.**

We agree, and we have optimized the second site (WBS, see section 2.6 and Figure 4) similar to LS and modified the relevant text accordingly. In addition, we calibrated the model using two years of flux tower observation (2015 and 2016) and used 2017 observation for validation, which we did not have at the time of submittal. We agree that we need to perform validation with additional observation sites, in order to evaluate the model performance at the regional scale. However, the two additional observation sites in the region are very different from our calibration sites in terms of vegetation composition and morphology. Our intent here is to present the 10 best simulations for each site to document our results, about the range of parameter combinations and potential reference to further studies on sagebrush PFT.

Some other important points are striking:

Metrological data are used for a different time period as the GPP data to which parameters are optimised. If you perform a parameter optimisation specifically for a site, you should use the metrological data of this site, which are normally provided by the EC tower data. But at least the same time period needs to be used.

During submittal, we used random years of the meteorological forcing data (WRF) (from 2005-2015) because the data were not available beyond 2015 for the domain we used (at 3 km). We agree with your comments and, in the revision, used meteorological forcing data (WRF) for the same years as the model simulation years which ranged from 2001 to 2017, using 1 km resolution data.

The authors state that the equilibrium is reached after 15 years, which seems to be very short. Figure 2 gives a hint that equilibrium is maybe not reached.

For the previous version of the manuscript, we used eight years for sensitivity analysis which was shown in Figure 2. In this version, we have revised the sensitivity analysis with a 15 year run. A strength of this study is that we are able to initialize the EDv2.2 model using the current state of the ecosystem. In our study we initialized the model with the mean cohort figures based on inventory data (section 2.3. main manuscript) from each of the study sites following approaches similar to other studies (Medvigy and Moorcroft, 2012; Antonarakis et al., 2014). To clarify, we modified the manuscript accordingly (P.8.l.13).

It is not clear to me if the ED2 model used here includes the nitrogen cycle or if the fire dynamics is turned off for the optimisation procedure.

We ran the optimization by turning off the fire dynamics in the model. But, it includes the nitrogen and other biogeochemical processes in a DGVM. Please note that in recent years the two sites have not been disturbed by fire.

It is strongly stated in the introduction that fire dynamics plays an important role in the global carbon balance, but isn't treated in the study!

Correct, but again this study is focused on developing the shrub PFT and initial ED modeling runs for sagebrush ecosystems. Our study lays the foundation for future studies that can incorporate fire dynamics and other disturbance effects. We have emphasized this in the introduction and conclusions in the revised manuscript.

Authors mentioned that they have changed the allometric equations, but it is never written how, please add that to your manuscript as it is an important information. But also how the used parameter are applied in the model would be a nice additional information. This would help the reader to understand why parameters are sensitive or maybe not.

Thank you for the comment - we provided the shrub allometric equations in P.7.1.7 and additional information here P.6.1.13 to P.7.1.3. We used these coefficients as some of the sagebrush PFT parameters as shown in supplement Table S1.

Why do you use a different parameter range for optimisation and sensitivity test, or did I get it wrong?

We used a broader range (based on literature and other land models) in our sensitivity analysis in order to cover the entire range of possible values of the sagebrush parameters. We used these findings to be more efficient and realistic in our optimization. We clarified this in the manuscript section 3.2.

And how did you define the parameter range? I missed some references here. The TRY database is an extensive source to determine the parameter range.

We used existing literature for defining sagebrush (or common shrub) parameters, and also a range of parameters for shrub PFTs adopted by other land models (like CLM) to define the parameter ranges (Please see reference column in Table 4). We reviewed the TRY database and they have limited information (eg. sla, shrub height and leaf width) for sagebrush.

You have not shown any measures in the figures.

The Bias, RMSE, NSE are in the tables and we have now added the measures (NSE, RMSE) for the best case to the figures, as well.

And I do not agree that it is a good match for a site-specific optimisation as stated in the manuscript.

In this revision, we optimized both sites with meteorological data and using representative vegetation conditions from the respective locations trying to match the site conditions (P.8.1.5). Given the complexity of these sites, we feel that the representation of the optimization is sufficient for an initial demonstration.

Lastly, there are a lot of statements in the abstract and in the introduction about the global importance of shrublands for the global carbon cycle, but authors don't show an application.

We have revised the manuscript to focus more on the sagebrush PFT development and preliminary performance evaluation of the ED model runs. We have also discussed that with this first step in sagebrush parameterization we could scale up the model performance to regional scales with further refinement in parameterizations (see Conclusions).

Response to reviewer #2

We would like to thank the reviewer for the time in doing a thorough review of the manuscript. Our response to each of the comments (shown in bold) is as given below.

General comments This article is about the optimization of sagebrush parameters based on GPP in the EDv2.2 model and in Great Basin.

The development and optimization of specific vegetation - here a specific shrub – are currently a key research area to increase model adequacy with observations and enable the simulation of the future development of our ecosystems. However, contrary to that suggested by the actual title, in this article there is no presentation of GPP results estimation but rather only some “optimization and validation” of parameters. Moreover, the article does not present some general case but more a specific situation: a very small zone (200m² simulated, 2 years of observation in 2 points). I suggest to change the title to make it more explicit. The model used here is EDv2.2, which seems interesting for medium scale simulation. But the methods used limit the scope (and so the interest) of this study. The two different sites of observation are located close to each other but differ in the type of sagebrush present (a small specie and a big specie). However, only one allometry parameterization is proposed. Your choice to have a dynamic vegetation is curious considering you work on two very specific and well documented sites for one unique year (one for optimization and one for validation). Some of the methods used (as the use of sensitivity index) rely on strong hypotheses, that have been presented only in the discussion. Some deeper bibliography could have made it possible to anticipate errors. The purpose of the article to estimate GPP is thus more a local application of the optimization of parameters in order to simulate (not here) the GPP. Due to the small data set and the validation performed without any statistical test (and one of the two cases that seems not so adequate), there is no insurance that the method could be applied for other years (to predict) or in other sites. As no specific development was presented here, except an adaptation of parameters for sagebrush allometry, the relevance of this article for publication in GMD can be questioned.

We have revised the title of the manuscript to better match the content. The study is primarily focused on the development of shrub (sagebrush) PFT parameters to use in EDv2.2, and to

observe the performance of the model for the newly developed sagebrush PFT (and wherein we used GPP as variable to conduct these comparisons). We agree that allometric relationships for different sites could not properly capture the fine scale heterogeneity in the ecosystem. For this study, we limited our objective in developing general sagebrush parameters, without trying to separate uniqueness of different sagebrush species. We used simple sensitivity and optimization analysis methods, to constrain the selected parameters. In further studies, we intend to capture the non-linear dependencies among these parameters to better constrain them for model estimates; however this is outside the scope of the present study.

Globally, considering the 14 detailed comments presented below, the editorial and figure quality of the present manuscript, I consider that in this state this article lacks of consistency and does not reach the standard quality expected for GMD.

Please see our responses below.

Specific comments

- 1) Not only simulations or field observations can be used to quantify GPP (p.1 l.6). A third essential data set comes from satellites and remote sensing, providing continuous values (spatially and over time). There is for example the GPP from the FLUXCOM project Tramontada et al., 2016 <https://doi.org/10.5194/bg-13-4291-2016> and Jung et al, 2017 <https://doi.org/10.1038/nature20780>) or from a linear relationship with the Sun-Induced Fluorescence (Su et al., 2017 <http://resolver.caltech.edu/CaltechAUTHORS:20171016-145548969>). Of course the problem of isolating the GPP for a PFT remains ... as is the case for the observations used in this study. Moreover, this GPP data can be used (if you know the vegetation distribution) to do more efficiency optimization and/or validation (largest temporal and/or spatial scale).**

Thank you for the suggestions - we agree that additional data are ideal to quantify GPP. Given the context of this paper (please see comments above), we are limiting our analysis to the flux towers and future work will incorporate the remotely sensed data products and should be useful to assess GPP in broader spatial terms.

- 2) **As indicated in the article (p.2 l.19), it could be difficult in models to represent and parameterize specific ecosystems and they are historically not well simulated. But this is currently a major point of development in land surface models, as for tundra (mosses, shrubs,...) which are now more and more represented. The sentence “Semi-arid, nonforest ecosystems provide an excellent example of this limitation” (p.2 l.20) has to be more documented. More generally, a short review of the current state of what is done in different models would be necessary in this article. Nevertheless, it is probable that these models are not yet sufficient to reproduce specifically the sagebrush.**

Thank you, we agree and have additional references cited P.4.l.1.

- 3) **Globally all the references of the article have to be checked. There are wrong dates in the reference list (e.g. for Bradley and Chambers), some references are missing (e.g. Skamarock et al, 2008 and Wright et al., 2004), others are never used in the text (e.g. Brabec et al,2001 and NPS, 2018) and one seems wrong (Davidson et al., 2011 about amazon forest to illustrate tundra). You also have two undifferentiated “USDA, 2018”.**

Thank you for pointing this out and we have updated the references throughout the manuscript.

- 4) **In the introduction (as suggested in the title) you say that you are going to predict the GPP (p.3 l.4). This seems a little ambitious compared to what is actually done in the result section: an optimisation and validation. In my sense, prediction consists in running the model in the future and simulating the future evolution of GPP.**

We have changed the title and agree that we are not predicting GPP but estimating GPP to evaluate the model performance with a sagebrush PFT.

- 5) **At the beginning of the methods (p.3 l.16 to 23), you are doing a distinction between two types of model: “gap” or “big leaf”. If the general differentiation between both is clearly understandable, some inaccuracies have to be checked and the references have to be improved / updated. (a) p.3 l.20 and l.22 you indicate that in individual based models you can have competition, coexistence and disturbance, and that it is a limit for the big leaf model. But you have also big leaf models (DGVM) with competition,**

disturbance,... (b) p.3 l.23 you indicate that individual-based models have problems due to computing cost, but this is becoming less and less of a problem and currently many large-scale models (initially big leaf) have developed individual based version. Moreover, in this article the small spatial and temporal scale clearly does not seem to be a limit, and following your distinction would seem in this case most appropriate?

Thank you for pointing this out. We agree with the reviewer that there are some “big leaf” models with competition. The challenge with these models, however, is they do not capture the demographic processes such as vertical light competition, competitive exclusion, and successional recovery from disturbance. To make it more clear, we changed the word “competition” in the manuscript to “demographic processes”. Considering comments on the IBMs, we agree with the reviewer that computation time is becoming less important in these models. However ED2 is not purely an IBM, as we mentioned in the manuscript (P.3.l.18) its a cohort based model which incorporate different processes.

6) In the parameter description and associated equations (p.4 l.13 to p.5 l.11), you need to be clearer: it is difficult to follow. Directly when you list the eleven parameters I suggest that you use the same order that you use after and that you indicate directly the name of the variables used in the equations (1) and (2). For clarity, these abbreviations have to be everywhere in italics (p. 4 l.22, l.27, 28,...) and called back each time that they are used (e.g. p.5 l.4 for “CO₂ concentration within the leaf boundary (*D_s*)”). Moreover, it is not indicated what the *C_s* parameter is (equation 2). I suggest also that you indicate how the “stomatal control is affected by soil moisture” (p. 5 l.3).

Thank you for pointing this out. We have added a table (P.4.l.10) to describe parameters we have used for the analysis and put it in a sequential order to match the writing in the text. We also added text to clarify how ‘stomatal control is affected by soil moisture’ in P.5.l.10. Additionally, we have provided reference (mainly Moorcroft et al., 2001; and Medvigy et al., 2009) for detailed information on equations and processes.

6) You have to take care about the quality of the figures and tables, and the associated legends (even in the supplementary). The figures have to be clearly understandable. (a)

in Figure 1, the WRF grid does not make it possible to see the vegetation around the simulated polygon. I suggest that you indicate in the legend the general location (at least “USA”) and the signification of “LS” and “WBS”. (b) in table 1 you indicate for the “DBH to Height” an equation with negative “b” value with a negative term “-b x DBH”, so the Ht is negative. Moreover you have to give the units of variables (in cm?). (c) in table 3 you use “*” for optimized parameters and for value ranges from EDv2.2. (d) in Figure 3 and 4 you give the number of “days” in “2016”. However, it seems not to correspond exactly to a year and it is never explicit: in the text “spring” is for the days “200 to 250” and in the figure 4 “2016” starts from October (2015?). Please revise the x-axis labelling. (e) in Table S1 you have to indicate clearly the dimensions for each parameter and in a consistent manner (eg “[m]”). (f) in table S2 I suggest that you indicate how the rank is done (by NSE) and that you give the dimension of the parameters. (g) in figure S1 it is not possible to see clearly the differences between simulations. Maybe you could use monthly means?

Thank you for pointing this out. We have updated these figures / tables. (a) we updated figure 1 related to study area which now shows location of LS and WBS sites in Reynold Creek Experimental Watershed (RCEW) area, (b) We removed -ve in the coefficient and provided unit for DBH, (c) in table 4 (earlier 3) we adjusted the confusion with regards to the use of “*” symbol, (d) we have updated the figures to make it more readable (e) we provided information about NSE score equation used in the ranking (Supplement P.6.l.9). (f) we have provide unit for applicable parameters (Supplement Table S1), (g) we updated the figure (Supplement Fig S2) to show average monthly GPPs to make different simulations more discernible.

7) The 2.3 section is called “Inventory and EC tower data” but is mainly about allometric equations. Moreover the approach method to describe shrub allometry can be improved. You suggest that the problem comes from the fact that the model is “originally developed for tropical forest” (p.6 l.9), when it seems to be more precisely due to allometric equations developed for trees and not for shrubs. Then, it could be appropriate to explicitly indicate that from the allometric data available, you transformed them (if I understand well) to a theoretical height considering that the shrub is a cube (?). But more importantly, it could be beneficial if you evaluate the impact of this hypothesis, for example by showing the adequacy between “DBH to

Height” results or the height simulated compared to observed height. There is also another solution: to change the allometric equation for shrubs, as is used in other models (e.g. Druel et al., 2017 <https://doi.org/10.5194/gmd-10-4693-2017>).

This is a good idea and we compared the predicted height from the cube root volume with observed sagebrush height using a new set of data from the Great Basin (see Supplement FigS1). We observed a good match between observed and predicted heights for sagebrush.

- 8) There is no overlapping between the period of station data (2015-2016) and the years used for the forecast, 2006 to 2014 (p.7 l.12). If it can be understandable to use random years for long term “spinup”, using “random years” for all simulations and optimization/validation can introduce a new bias superimposed on the parameter set. Even more important, if you use a random forecast year to simulate specifically 2015 and 2016 (validation and simulation), that means the difference between both simulations is a random year?**

We used corresponding years of meteorological data for simulation in the revised manuscript. We used 1 km WRF data from 2001 to 2017 for both the sites studied. This will help reduce the interannual uncertainty that may arise from using meteorological data from a random year.

- 9) For the initial parameterisation of the 11 parameters, you choose a sensitivity index. But there are two fundamental hypotheses to use such index: you expect that the responses to the parameters are linear and that there is no interaction between parameters. Unfortunately, you never indicate those hypotheses! It is true that at the next step (for optimization) you use a more adapted method (not requiring such hypotheses) and that in the discussion you put two related sentences, but the method is not consistent with the optimization and the hypotheses are required from the beginning. The test of the mean of the best sets of 10 parameters shows that the hypotheses were not well considered.**

We agree that the chosen method assumes linear dependencies of selected parameters with the target variable. We spent extensive time on developing the shrub (representing sagebrush) PFT for the EDv2.2 model (e.g. establishing allometric relationships) and several

preliminary model run-ups to match with the ecosystem conditions. We used the exhaustive (brute force) method due to computational limitations. This study was mainly intended to introduce the sagebrush PFT and its implementation in EDv2.2.

We agree that additional robust optimizations (and sensitivity) should be performed. We've modified the paper to highlight this intent and the conclusions we may draw from the existing work. We have added lines to state the limitation of the applied SI method and our assumption on parameters under methods section (P.8.l.18).

10) You indicate that your “simulations were configured to allow” that other plants than shrubs can grow in the model (p.9 l.1). That means that you specifically activated the competition between species and so other plants can grow? If this is the case, you introduce new uncertainties and so probably directly biases to the optimization and comparison with GPP observations! I really do not understand why you do not use the observed fraction of vegetation in your two (well documented) stations. On the one side you work on very few observations and simulated points (in time and space), but you do not limit the variability induced by the model configuration. Why?

The study site is heterogeneous and thus we need to allow additional PFTs to grow to capture total GPP. We do not understand the question here but to clarify we used density information for initialization that has been collected at the sites.

12) The results section suffers from the limitation of the method: only one polygon is simulated, two observation sites considered, with heterogeneous vegetation inside each site (grasses and shrubs) but also between sites (Low Sagebrush /W. Big Sagebrush), and only two years of data (with one not complete for one site), one for simulation and one for validation. Thus, it is not possible to represent inter-annual or spatial variability. Likewise, no statistical tools are used to validate the optimization. We can just observe that one is coherent (WBS) and the other is bad (LS) (the value of the differences are also missing, e.g. p.14 l.5 to 8). In conclusion it is not obvious that the values obtained for the parameters can be used for other years or sites.

As stated above, we have simulated both sites with respective ecosystem and atmospheric conditions to address variation between the sites. In our revised analysis, we could use two years of data for calibration and another year for validation. We agree that these are not sufficient to capture inter annual variability but we were mostly limited with the available observation data from the sites. We agree that the values cannot be used for other years and sites until further optimization is performed. We have stated this in the Conclusion (P.17.l.18).

13) Not being a specialist of optimization, I cannot say something precisely on this part. But, the choice of the optimization method is not justified or discussed. There exists currently other methods less computationally costly (such as genetic algorithms) and it is possible to extract statistic values to evaluate the efficiency (such as the variability fraction explained before and after the optimization).

We agree there additional optimization tools could improve the results and provide robust information on sagebrush PFT parameters (Please refer to answers to Q.9 for more).

14) The discussion allows to go further, but showing mostly the limits of the methods used for the study, which should have been stated earlier in the methods (e.g. the nonlinear dependence among parameters). This shows also the gap between the objective indicated (to predict the GPP of sagebrush) and the results (not really validated, even in very restrictive conditions).

Good point, we have tried to clarify the objectives and the results and how our study has contributed to the overall modeling of shrub-steppe (P.2.l.30). We have stated limitation of our tools (P.8.l.18) and potential improvements we would achieve with different methods (P.17.l.2)

Specific comments

p.1 l.10. Suggested change: “one of the most critical” to “one critical”

The text has been changed.

p.1 l.28-31. Suggested change. Remove from “we expect that. . .” (to put in the conclusion?)

As suggested, the lines were removed.

p.2 l.3. Need for a reference for “anthropogenic CO2 emissions”

The text has been removed.

p.2 l.4. Suggested change: Add a small definition for “photosynthesis”

We have updated the text.

p.2 l.10. Suggested change: “distinct ecosystems” to “distinct ecosystems at large scale”

We changed the texts

p.2 l.20. There are currently two spaces after “ecosystems”.

We corrected.

p.2 l.27. How do they suppress fire?

Removed the text ‘suppress fire’

p.2 l. 34. After “Great Basin”, indicate the density of station (or indicate if there are only two stations. . .)

The text is revised.

p.3 l.13. This section (2.1) could gain in clarity if you distinguish (a) the general model presentation (p.3.14 to p.4 l.8) and (b) the presentation of parameters used in this study and their related equation(s).

We tried to differentiate the information in the section through different paragraphs . We added a table showing parameters used in the study followed by brief descriptions and controls of the parameters.

p.3. l.18 “plant function type” abbreviation is already defined just above (p. 3 l.6).

We updated the text accordingly.

p.3 l.23. You use acronym “IBMs” which is not defined. Please define it l.21.

We corrected as per your suggestion.

p.4 l.13. Suggested change: parameters. These included” to “parameters:”

The text has been revised.

p.4. l.18-19. Suggested change: “here we are trying to describe the ones related to the parameters we have use in this study” to “here describe the ones related to the parameters used in this study”

We made suggested change.

p.5 l.8. It could be important to state from where the “allometric allocation” comes from, and maybe indicate that they are in Table 1 ?

We referred Table 1 for the allometric equation referred in the text P.5.l.18

p.5 l.16. Please clearly indicate where it is (country, state).

We updated with region and Country.

p.5 l.16 to 18. If I understood well, you have to indicate that the “200 m x 200 m polygon” is the simulated area in this study (using the 3km resolution WRF forecast). Likewise, in the legend of Figure 1 (p.6 l.2) change “study polygon” to “simulated polygon”.

We updated the Figure 1 showing study area.

p.6 l.16. Suggested change: Add a line break before the “GPP data. .”

We updated with a line break to separate two types of data sources.

p.8 l.4. If the sagebrush parameters come only from bibliography, put the citation l.2.

We updated the text to appropriately represent the procedure P.8.l.3. We also updated supplement Table S1 with all PFT parameters to clearly state the source/reference of different parameters.

p.8 l.10. Indicate why “370 ppm” or to which year that corresponds (2000?).

we updated the text as suggested (P.8.l.11)

p.9 l.29. Change “Fig. 2b and d” by “Fig. 2b, c and d”.

We made necessary edits as suggested.

p.12 l.21. Change “Table 5” to “Table 6”.

We made necessary corrections.

p.15 l.4. Suggested change: “was observed” to “was obtained”

Changed the text P.16.l.10.

p.16 l.16. Suggested change: Add a line break after the “GPP.”

We made the edits as suggested.

p.16 l.20. I am not sure that you can say “quite well”.

Text has been updated.

Developing and optimizing~~Optimizing~~ shrub parameters representing~~to~~ ~~estimate gross primary production of the~~ sagebrush (Artemisia spp.) ecosystems in the Northern Great Basin~~ecosystem~~ using the Ecosystem Demography (EDv2.2) model

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Abstract. Ecosystem dynamic models are useful for understanding ecosystem characteristics~~Gross primary production (GPP)~~
~~is one of the most critical processes in the global carbon cycle, but is difficult to quantify in part because of its high~~
~~spatiotemporal variability. Direct techniques to quantify GPP are lacking, thus, researchers rely on data inferred from eddy~~
~~covariance (EC) towers and/or ecosystem dynamic models. The latter are useful to quantify GPP~~ over time and space because
of their efficiency over direct field measurements and applicability to broad spatial extents. Their application, however, is
challenging due to ~~However, such models have also been associated with~~ internal model uncertainties and complexities arising
from distinct qualities of the ecosystems~~ecosystem~~ being analyzed. The~~Widely distributed~~ sagebrush-steppe ecosystems in
western North America, for example, has substantial spatial and temporal heterogeneity as well as variability due to~~are~~
~~threatened by~~ anthropogenic disturbance, invasive species, climate change, and altered fire regimes, which collectively make
modelling dynamic ecosystem processes difficult. Ecosystem Demography (EDv2.2) is a robust ecosystem dynamic model,
initially developed for tropical forests, that simulates energy, water, and carbon fluxes at fine scales. Although EDv2.2 has
since been tested~~land managers have focused~~ on different ecosystems via development of different Plant Function Types
(PFT), it still lacks a shrub PFT. In this study, we developed and parameterized a shrub PFT representative of sagebrush
(Artemisia spp.) ecosystems in order to initialize and test it within EDv2.2, and to promote future broad-scale analysis of
restoration ~~techniques, the effects of these activities and their interactions with fire~~, climate change, and fire regimes in the
invasive species on ecosystem dynamics are poorly understood. In this study, we applied an ecosystem dynamic model,
Ecosystem Demography (EDv2.2), to parameterize and predict GPP for sagebrush-steppe. Specifically, we parameterized
ecosystems in the sagebrush PFT within EDv2.2 to estimate gross primary production (GPP), using data from two sagebrush
study sites Reynolds Creek Experimental Watershed (RCEW), located in the northern Great Basin. ~~Our primary objective was~~
to develop and parameterize a sagebrush (Artemisia spp.) shrubland Plant Functional Type (PFT) for use in the EDv2.2 model,
~~which will support future studies to model estimates of GPP under different climate and management scenarios.~~ To accomplish

this, we employed a three-tiered approach: 1) To initially parameterize the sagebrush PFT, we fitted allometric relationships for sagebrush using field-collected data, gathered information from existing sagebrush literature, and parameters borrowed values from other land models. 2) To determine influential parameters PFTs in GPP prediction EDv2.2. Second, we used a sensitivity analysis to identify identified the five most sensitive parameters. 3) To improve model performance and validate results out of eleven that were found to be influential in GPP prediction based on previous studies. Third, we optimized these the five parameters using an exhaustive search method to estimate predict GPP, and compared results with performed validation using observations from two Eddy Covariance (EC) sites in the study area. Our modeled results were encouraging, with reasonable fidelity to observed values, although some negative biases (i.e., seasonal underestimates of GPP) were apparent. We expect that, with further refinement, the resulting sagebrush PFT will permit explicit scenario testing of potential anthropogenic modifications of GPP in sagebrush ecosystems, and will contribute to a better understanding of the role of sagebrush ecosystems in shaping global carbon cycles.

1 Introduction

Ecosystem dynamic models have been widely used to estimate terrestrial carbon flux and to project ecosystem characteristics. Terrestrial gross primary production (GPP) is a major driver of the global carbon cycle as it plays an important role in regulation of atmospheric CO₂ by offsetting anthropogenic CO₂ emissions. GPP quantifies the rate of carbon uptake from the atmosphere through photosynthesis and is often presented as one of the most critical elements in global carbon research because of its high spatiotemporal variability (Chen, 2012; Zhao and Running, 2010). Since direct techniques to quantify GPP are lacking, researchers derive estimates using observations from eddy covariance (EC) towers or using ecosystem dynamic models (Dong et al., 2017; Turner et al., 2006; Zhao et al., 2005). Ecosystem models have been widely used to estimate terrestrial carbon flux and to project ecosystem dynamics over time and space (Dietze et al., 2014; Fisher et al., 2017), largely due to their efficiency over direct field measurements and their applicability to broad broader spatial scales. However, these models have also been associated with high levels of internal uncertainty and questions regarding complexity associated with their applicability to distinct and often complex ecosystems. Mainly, three different types of errors have been associated with these models: (1) process error arising from formulations in the model and associated parameters, (2) forcing error related to the quality of meteorological data, and (3) the initial ecosystem state at large scale. Sagebrush the start of the simulation (Antonarakis et al., 2014; Huntzinger et al., 2012). Initialization error is generally not an issue for long term simulations, and researchers can minimize both forcing and initialization errors by using observational data rather than reanalysis data (Antonarakis et al., 2014; Medvigy et al., 2009). Indeed, process error is the most problematic, as it can mask uncertainties caused by forcing errors and can create potential bias in predictions. Fortunately, process error can be quantified and minimized by systematically comparing model predictions with observable ecosystem metrics (Braswell et al., 2005; Dietze et al., 2014; Medvigy et al., 2009).

Another critical limitation to widely applying ecosystem dynamic models is their suitability for a unique ecosystem for which they have not been parametrized. Semi-arid, non-forest ecosystems provide an excellent example of this limitation, including sagebrush (*Artemisia* spp.) ecosystems, one of the most widespread community types in Western North America provide a good example of these types of modelling challenges, as these ecosystems are spatially heterogeneous and shaped by complex dynamics over time. Sagebrush ecosystems hold both high ecological and socio-economic value, but they have been reduced to nearly half of their historical range and are declining at an alarming rate (Knick et al., 2003; Schroeder et al., 2004). Various factors have contributed to this decline, including land clearing, invasion of nonnative species such as cheatgrass (*Bromus tectorum*), and climate change, that have collectively altered vegetation composition, hydrological function, and wildfire frequency (Bradley, 2010; Connelly et al., 2004; McArthur and Plummer, 1978; Schlaepfer et al., 2014). In an attempt to restore portions of the sagebrush ecosystem, land managers have focused on suppressing fire, reducing flammable vegetation, controlling invasive species, and seeding native species (Chambers et al., 2014; McIver and Brunson, 2014). There are relatively few studies that have evaluated carbon flux in sagebrush ecosystems in response to prescribed fire or restoration activities, and most of them used observational data from Eddy Covariance (EC) stations. However, given Previous studies identified temporal variation in net carbon exchange rates after restoration treatments, including documenting increases in carbon uptake in the large spatial extent of the sagebrush biome (>500,000 km²; Miller early years after prescribed fire (caused by re-sprouting shrubs and fast growing grasses), followed by an eventual levelling off to pre-fire conditions (Cleary et al., 2010; Fellows et al., 2018). However, because of the paucity of EC station sites in sagebrush landscapes, the function of this ecosystem remains poorly understood, especially when coupled with the large spatial extent of the sagebrush ecosystems in the Great Basin, the collective effects of restoration activities, fire, climate change, and invasive species on ecosystem the spatiotemporal dynamics of structure, composition, and spatiotemporal dynamics function of ecosystem are poorly understood.

In this study, we applied an ecosystem dynamic model, Ecosystem Demography (EDv2.2), is a process-based ecosystem dynamic model that approximates the behaviour of ensembles of size and age-structured individual plants to capture sub-grid level ecosystem heterogeneity using partial differential equations (Medvigy et al., 2009; Moorcroft et al., 2001). This, to parameterize and predict GPP for sagebrush ecosystems in an experimental watershed located in the northern Great Basin. The Great Basin is a ~500,000 km² cold desert region dominated by expansive, shrub steppe ecosystems. Our primary objective was to develop preliminary sagebrush Plant Functional Type (PFT) parameters in the EDv2.2 model, based on sensitivity analysis and optimization, with respect to GPP prediction. EDv2.2 was originally developed to study for tropical forest ecosystems with trees as a primary component, but (Moorcroft et al., 2001), and it has since been modified and applied to several different ecosystems, including tested in boreal forests (Trugman et al., 2016), and temperate forests (Antonarakis et al., 2014; Medvigy et al., 2009; Medvigy et al., 2013). However, and tundra (Davidson et al., 2011), however, its application to semi-arid shrubland ecosystems has not been explored and it lacks a shrub Plant Function Type (PFT) to study these ecosystems. Thus, we developed and parameterized a sagebrush PFT for EDv2.2, and used it to estimate gross primary

production (GPP) for the sagebrush ecosystems in the Reynolds Creek Experimental Watershed (RCEW) located in the Northern Great Basin, a cold-desert region dominated by expansive, shrub-steppe ecosystems.

In this study, our primary objective was to develop preliminary sagebrush PFT parameters in EDv2.2 and to constrain uncertainties through optimization of selected PFT parameters. To accomplish this, we employed a three-tiered approach. First, we parameterized the sagebrush PFT, by fitting allometric relationships for sagebrush using field-collected data, information from existing sagebrush literature, and borrowing parameters from other land models. Second, to identify the most influential parameters in GPP prediction, we used a sensitivity analysis and identified the five most-sensitive parameters affecting changes in GPP estimates. Third, to improve upon and assess model performance, we optimized the five most sensitive parameters using an exhaustive search method to estimate GPP, and then compared the results with observations from two Eddy Covariance (EC) sites in the study areas. Our preliminary ~~Preliminary~~ parameterization of the sagebrush shrub PFT is an important, ~~from this study, will be a~~ first step towards further study of studies on shrubland ecosystem function using EDv2.2 or similar process-based ecosystem ~~any other terrestrial~~ models.

2 ~~Material~~Materials and methods

2.1 Ecosystem Demography (EDv2.2) model

~~The Ecosystem Demography~~ (EDv2.2) is a process-based terrestrial biosphere model ~~that, which~~ occupies a mid-point on the continuum of ~~models from~~ individual-based (or gap) ~~models to~~ area-based (or big-leaf) models (Fisher, 2010; Smith et al., 2001). Area-based models like LPJ-DGVM (Lund-Potsman-Jena Dynamic Vegetation Model) (Sitch et al., 2003), and BIOME BGC (Running and Hunt, 1993 as cited in Bond-Lamberty et al., 2014) represent plant communities with area-averaged representation of a ~~plant function type (PFT)~~ for each grid cell. The simplification and computational efficiency of these models make them widely applicable for regional ecosystem analysis, however, this advantage often comes in trade-off with their ~~limitation to properly failure~~ to capture light competition ~~and~~, competitive exclusion, ~~and disturbances~~ (Fisher, 2010; Bond-Lamberty et al., 2014; Smith et al, 2001). On the other hand, individual-based models (IBMs) such as JABOWA (Botkin et al., 1972), and SORTIE (Pacala et al., 1993) represent vegetation at the individual plant level thus making it possible to incorporate community processes like growth, mortality, recruitment ~~competition, coexistence~~, and disturbances. ~~Lately, there have been drastic improvements in computation efficiency, traditionally IBMs would~~ ~~The disadvantage of IBMs is that they are~~ often be confined to limited spatial and temporal scales due to ~~their added~~ computational burden. EDv2.2 is a cohort based model where individual plants with similar properties, in terms of size, age, and function, are grouped together to reduce the computational cost while retaining most of the dynamics of IBMs. Each cohort is defined by a PFT, number of plants per unit area, and dimensions of a single representative plant like diameter, height, structural biomass, and live biomass (Fisher et al., 2010).

~~The In EDv2.2~~, land surface in EDv2.2 is composed of a series of gridded cells, which experience meteorological forcing from ~~a~~ corresponding gridded data or from a coupled atmospheric model (Medvigy, 2006). The mechanistic scaling from

individual to the region is achieved through size and age structured partial differential equations that closely approximate mean behaviour of [a](#) stochastic gap model (Medvigy et al., 2009; Moorcroft et al., 2001). Each grid cell is subdivided into a series of dynamic horizontal tiles, which represent locations that [experience](#)~~had experienced~~ similar disturbance history and [have](#)~~has~~ an explicit vertical canopy structure. This mechanism helps capture both vertical and horizontal [distributions](#)~~distribution~~ of vegetation structure and compositional heterogeneity compared to area-based models (Kim et al., 2012; Moorcroft et al., 2001; Moorcroft et al., 2003; Sellers et al., 1992). EDv2.2 consists of multiple sub-models for plant growth and mortality, phenology, disturbance, biodiversity, hydrology, land surface biophysics, and soil biogeochemistry, to predict short-term and long-term ecosystem flux and to represent natural and anthropogenic disturbances (Kim et al., 2012; Medvigy et al., 2009; Zhang et al., 2015). Sub-models in EDv2.2 rely mostly on many PFT-specific parameters, representing unique attributes of that particular group of species, to resolve the stated biological processes (Knox et al., 2015). [Studies on shrub parameterization has been done in LPJ-GUESS for tundra region \(Miller and Smith, 2012; Wolf, 2008\), however, it is clearly limited for semi-arid shrubland ecosystems.](#) EDv2.2 has parameters defined for 17 different PFTs including grasses (C3 & C4), conifers,~~and~~ deciduous trees (temperate & tropical), and agricultural crops. In this study, we identified parameters for [the](#) sagebrush (shrub) ecosystem to simulate it in the model as a new PFT. Furthermore, since we [tried to explore model performance based](#)~~focussed~~ on GPP [estimates](#)~~prediction~~, we selected eleven different parameters related to plant ecophysiology and biomass allocation ~~from overall~~ to conduct sensitivity and optimization ([Table 1](#)).~~study~~. We [mainly relied on](#)~~used~~ similar studies (Dietze et al., 2014; Fisher et al., 2010; LeBauer et al., 2013; Medvigy et al., 2009; Mo et al., 2008; Pereira et al., 2017), [our](#) preliminary sensitivity analyses, and consultation with other developers and users of the EDv2.2 model to select [the parameters](#)~~these parameters. These included maximum photosynthetic capacity at 15°C (V_{m0}), specific leaf area (SLA), fine root turnover rate, leaf turnover rate, storage turnover rate, slope of stomatal conductance-photosynthesis relationship (stomatal slope), ratio of fine roots to leaves (Q), water conductance, cuticular conductance, growth respiration factor (GRF), and leaf width.~~

Table 1. Parameters used to explore model performance for sagebrush PFT.

Parameter	Description	Unit
V_{m0}	Maximum carboxylation rate at 15°C	(μmolm-2s-1)
Stomatal slope	Slope of stomatal conductance-photosynthesis relationship	-
Cuticular conductance	Intercept of stomatal conductance-photosynthesis relationship	(μmolm-2s-1)
Water conductance	Supply coefficient for plant water uptake	(ms-1kgCroot-1)
Leaf width	Controls leaf boundary layer conductance (m)	(m)
SLA	Specific leaf area	(m2kg-1)
GRF	Growth respiration factor	-
Q-ratio	Ratio of fine roots to leaves	-

Leaf turnover rate	Inverse of leaf life span	(a-1)
Fine root turnover rate	Inverse of fine root life span	(a-1)
Storage turnover rate	Turnover rate of plant storage pools	(a-1)

[Detailed](#)

~~As we can find detailed~~ descriptions of sub-models of EDv2.2 [are available](#) in ~~the~~ existing literature (Medvigy et al., 2009; Moorcroft et al., 2001); ~~thus,~~ here we ~~are trying to~~ describe the ones related to the parameters ~~we have~~ used in this study. The ecophysiological sub-model has a coupled photosynthesis and stomatal conductance scheme developed by Farquhar and Sharkey (1982) and Leuning (1995), ~~respectively,~~ [and which estimates](#) ~~takes care of~~ leaf-level carbon and water fluxes. Leaf-level carbon demand of C₃ plants is determined by the minimum of light-limited rate (J_e) and Rubisco-limited rate (J_c), and V_{m0} controls the later as given by Eq.(1) after being scaled to a given temperature.

$$J_c = \frac{V_m(T_v)(C_{inter} - \Gamma)}{C_{inter} + K_1(1 + K_2)} \quad (1)$$

where, $V_m(T_v)$ is the maximum capacity of Rubisco to perform carboxylase function at a given temperature T_v scaled from V_{m0} ([Medvigy et al., 2009](#)); C_{inter} is the intercellular CO₂ concentration, Γ is the compensation point for gross photosynthesis, K_1 is the Michaelis-Menten coefficient for CO₂, and K_2 is proportional to the Michaelis-Menten coefficient for O₂. Stomatal conductance which is modeled using Leuning (1995), a variant of Ball Berry model (Eq. 2), is influenced by *stomatal slope* and *cuticular conductance*.

$$g_{sw} = \frac{MA_o}{(C_s - \Gamma)(1 + \frac{D_s}{D_o})} + b \quad (2)$$

where, ~~A_o is photosynthetic rate,~~ g_{sw} is stomatal conductance for water, [A_o is photosynthetic rate,](#) M is *stomatal slope*, b is *cuticular conductance*, D_o is empirical constant, D_s is water vapour deficit and CO₂ concentration within leaf boundary, and Γ is as described above. Stomatal control is also affected by soil moisture supply term, which is a function of soil moisture, fine root biomass, and *water conductance*. [When the available water supply is less than the demand predicted by photosynthesis-conductance model, then photosynthesis, transpiration, and stomatal conductance are all linearly weighted down to match the supply \(Dietze et al., 2014\).](#)

Water and CO₂ concentrations within the leaf boundary layer ~~are~~ influenced by *leaf width* along with other factors like wind speed, leaf area index, and molecular diffusivity of heat. *Specific leaf area* (SLA) has units of leaf ~~area~~ per unit leaf carbon and is used [to](#) scale up leaf-level ~~fluxes~~ to canopy-level fluxes. ~~Relationships~~ [Relationship](#) between growth respiration and net photosynthesis ~~are~~ controlled by the *growth respiration factor*. In EDv2.2, while leaf biomass is determined by [PFT specific](#)

allometric ~~equation (as shown in Table 2 for sagebrush)~~~~equations~~ based on diameter, fine root biomass is defined by a *ratio of leaves to fine roots*. Leaf turnover and fine root turnover rates together influence overall litter turnover rate, even though in deciduous trees dropping of leaves also affects this rate. Turnover rate of stored leaf pool and storage respiration depends on *storage turnover rate*, size of stored leaf pool, and storage biomass.

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2.2 Study area

~~While the PFT was developed broadly~~~~We initialized and performed parameter optimization~~ for sagebrush, ~~we focused~~
~~ecosystems in~~ the EDv2.2 model ~~runs at the RCEW site, using field data and two EC station sites~~ located in the Northern Great
Basin region of Western United States (Fig. 1). ~~This site is Reynolds Creek Experimental Watershed (RCEW) and Critical~~
~~Zone Observatory (CZO)~~, operated by the USDA Agricultural Research Service and is also a Critical Zone Observatory (CZO)
(referred to as RC-CZO) (Fig. 1). We used ~~two~~ a 200 m x 200 m polygons centered at two EC sites within RC-CZO to closely
represent the footprint area of these sites. ~~polygon with center location of 43.15 N and 116.72 W and a mean elevation of 1583~~
~~m~~. The AmeriFlux US-Rls EC station, located at 43.1439 N and 116.7356 W and at an elevation of 1583 m, is within the
Lower Sheep Creek drainage in RCEW. ~~is approximately 0.7 km from the center of our study site~~. The ~~area within the~~ footprint
of this ~~site tower~~ is dominated by low sagebrush (*Artemisia arbuscula*) and Sandberg bluegrass (*Poa secunda*) (Stephenson,
1970; Seyfried et al., 2000) and is characterized as having light cattle grazing (AmeriFlux, 2018). The second ~~Another~~
AmeriFlux tower, US-Rws, is located at 43.1675 N and 116.7132 W in the Nancy Gulch drainage, within about 2-~~5~~ km distance
to the northeast ~~of from~~ the US-Rls site ~~study polygon~~. This area is dominated by Wyoming big sagebrush (*A. tridentata* ssp.
wyomingensis) and bluebunch wheatgrass (*Pseudoroegneria spicata*) (Stephenson, 1970). Hereafter, these two sites are
designated as LS (for low sagebrush) and WBS (for Wyoming big sagebrush), respectively.

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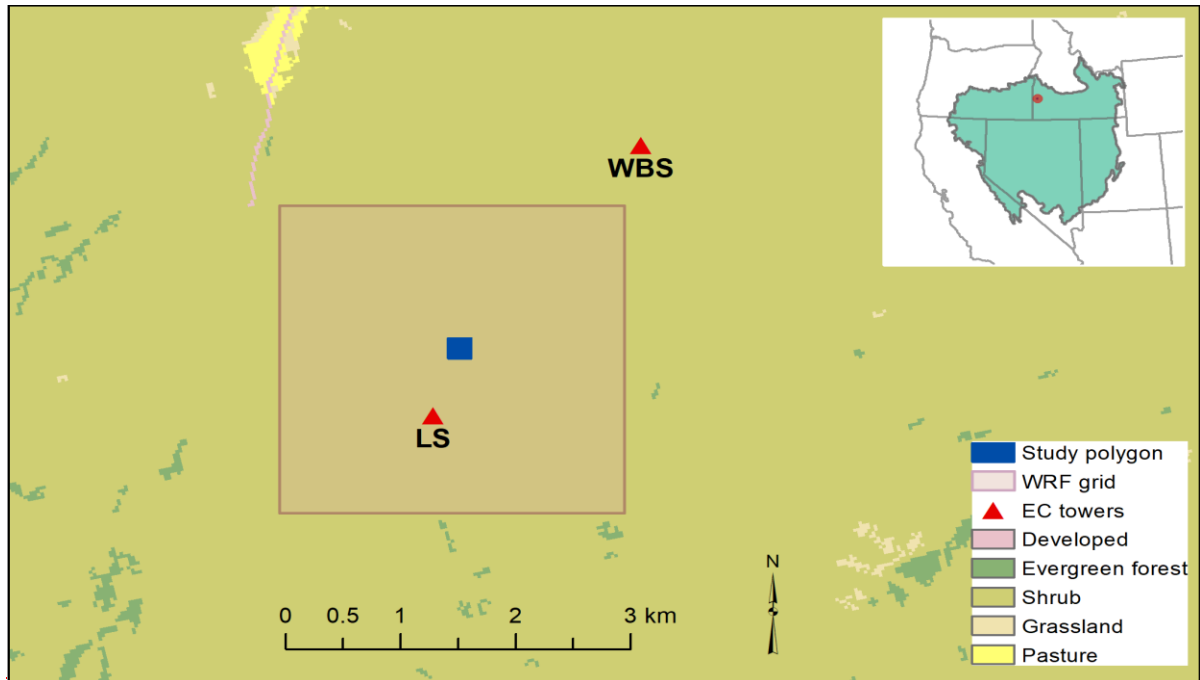
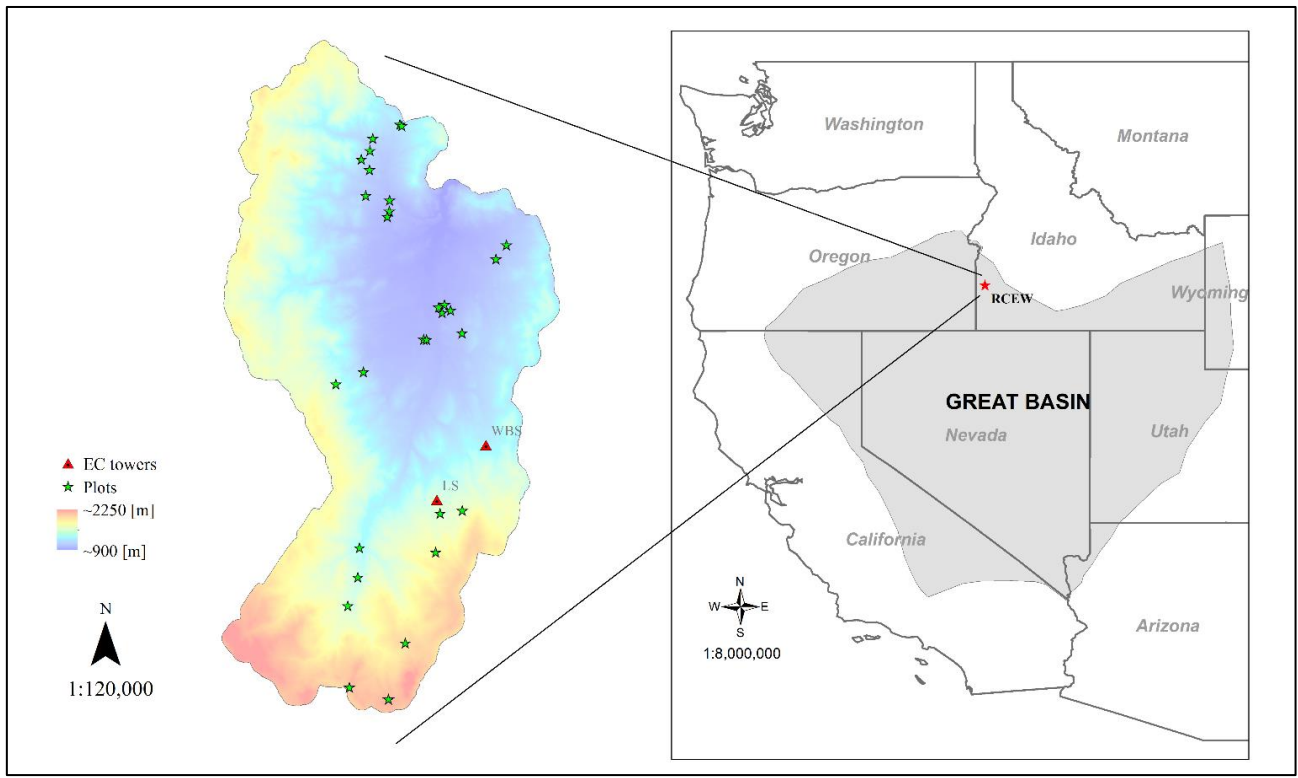


Figure 1. Location of ~~the 200 m x 200 m study polygon used in the EDv2.2 model; the Weather Research and Forecast (WRF) grid (3 km resolution); and the eddy covariance (EC) flux sites where studies were performed. Field plots depicted were used to develop the allometric equations, tower locations; with 2011 land cover (Homer, et al., 2015) in the background.~~ The inset map shows the location of the study area within the Northern Great Basin (LCC, 2018).

2.3 Inventory and EC tower data

A field inventory dataset of sagebrush shrubs from RCEW recorded in 2014 (Glenn et al., 2017) was used to fit the allometric equations (~~in EDv2.2, which were developed for temperate PFTs) in EDv2.2,~~ and to initialize the ecosystem structure for the model ~~simulations~~simulation. Variables used to fit allometric equations for the sagebrush ~~shrub~~ included volume, crown diameter, height, and stem diameter. EDv2.2 was originally developed for tropical forests, and thus typically specifies allometric relationships in terms of diameter at breast height (dbh). However, this length-scale variable has limited application to shrubs of the sagebrush-steppe ecosystem, which rarely exceed 1.5 m in height. Thus, we developed a substitute length-scale variable for dbh that effectively corresponds to shrub volume. To accomplish this, shrub volume was first calculated using crown area (characterized as an ellipse, and approximated with semi-major and semi-minor axis lengths) and height, and the cube root of this volume was then used as the characteristic length-scale variable required to parameterize allometric relationships in EDv2.2. To test this relationship, we compared height predicted from cube root volume with observed sagebrush height using a different set of data from the Great Basin (Qi et al., 2018). We found a good fit for the data (r² = 0.71) with a small negative bias of -1.88 cm, and a random residual distribution (Fig. S1). We identified the coefficients in allometric equations (Table ~~24~~) for shrub height, leaf biomass, structural biomass, canopy area, and wood area index as a function of this cube-root of volume (used as DBH in the equation).

GPP data ~~from for 2015 to 2017 and 2016~~ water years were derived from the LS and WBS EC stations (Fellows et al., 2017) using the REdDyProc software in R (Reichstein et al., 2005) to fill and partition net ecosystem exchange (NEE) into ecosystem respiration and GPP.

Table ~~24~~. Coefficients for sagebrush (shrub) PFT to allometric equations in EDv2.2 (temperate PFTs).~~.)~~

Relationship	Equation	Coefficients
DBH (<u>cm</u>) to Height (<u>m</u>)	$Ht = a(1 - e^{b \times DBH})$ $1 - e^{-b \times DBH}$	a = 4.7562, b = -0.002594
DBH (<u>cm</u>) to Woody Biomass (<u>kg</u>)	$WB = \frac{a}{C2B} \times DBH^b$	a =5.709 x 10 ⁻⁸ , b=4.149
DBH (<u>cm</u>) to Leaf Biomass (<u>kg</u>)	$LB = \frac{a}{C2B} \times DBH^b$	a=2.582 x 10 ⁻⁶ , b=2.746
DBH (<u>cm</u>) to Canopy Area (<u>m</u> ²)	$CA = a \times DBH^b$	a=6.35 x 10 ⁻⁵ , b=2.18
DBH (<u>cm</u>) to Volume (<u>m</u> ³)	$V = a \times Ht \times DBH^b$	a=2.035 x 10 ⁻⁵ , b=2.314
Volume (<u>m</u> ³) to Root Depth (<u>m</u>). 7	$D = a \times V^b$	a = -3.0, b = 0.15

DBH ([cm](#)) to Wood Area Index, $WAI = n_{plant} \times a \times DBH^b$ a= 0.0096, b =2.0947
 DBH = diameter at breast height; Ht = height; WB=woody biomass; C2B=~~carbon~~[Carbon](#) to [biomass](#)~~Biomass~~ ratio; LB=~~leaf~~[biomass](#)~~Leaf Biomass~~; CA=canopy area; V=volume; D=root depth; WAI=wood area index.

2.4 Meteorological forcing data

Outputs from a long-term, high resolution climate reanalysis obtained from the Weather Research and Forecast (WRF) model (Skamarock et al., 2008) were used to provide meteorological forcing data for the EDv2.2 model (Table [32](#)). The WRF outputs correspond to atmospheric temperature and specific humidity at 2 m height, wind speed at 10 m height, downward shortwave radiation and long-wave radiation at ground surface, surface pressure and accumulated precipitation (Flores, et al., 2016). The spatial and temporal resolutions of the data are [13](#) km and [1 hour](#)~~3 hours~~, respectively. The EDv2.2 model then partitions shortwave radiation into direct and diffuse, visible and near-infrared components as summarized by Weiss and Norman (1985). We obtained these forcing data ~~for nine years~~ from ~~2001~~[2006](#) to ~~2017 for two~~[2014](#) at the WRF ~~pixels~~[pixel](#) corresponding ~~to the polygon study area~~ and bounding ~~the~~ LS [and WBS sites \(Fig. 1\)](#).~~EC site location. For each year of EDv2.2 simulation, a random year of meteorological forcing data was chosen from the available range of data.~~

Table [32](#). Meteorological forcing data from WRF model used for simulation.

Variable	WRF name	Unit
Temperature at 2 m	T2	K
Surface pressure	PSFC	Pa
Accumulated precipitation	RAINNC	mm
Terrain height	HGT	m
U wind (zonal) component at 10 m	U10	m/s
V wind (meridional) component at 10 m	V10	m/s
Specific humidity at 2 m	Q2	Kg/kg
Downward longwave flux at ground surface	GLW	w/m2
Downward shortwave flux at ground surface	SWDOWN	w/m2

2.5 Initial parameterization and sensitivity analysis

We identified initial [sagebrush](#) shrub PFT parameters based on field allometric equations, previous research studies on the sagebrush ecosystem ([Ahrends et al., 2009](#); Cleary et al., 2010; Comstock and Ehleringer, 1992; Gill and Jackson, 2000; Li et al., 2009; Olsoy et al., 2016; Qi et al., 2014; [Sturges, 1977](#); [Tabler, 1964](#)), and [information from other general](#)~~existing~~ PFT parameters in ~~the~~-EDv2.2 ~~model for C3 grass, northern pines, and late conifers~~ (Table S1 in the Supplement). The initial ecosystem ~~states~~[state](#) for the model run ~~for the LS and WBS sites were~~[was](#) designated to be a single sagebrush ~~cohort~~ with ~~an average cube root volume (diameter) of 0.6 m, average height of 0.52 m, and density of 1 plant/m² representing~~ [average spacing from the 2014 field inventory data. For the LS site, we used 0.57 m of cube root volume \(diameter\) and 0.56 m for height and](#)

for WBS we used 0.62 m of cube root volume and 0.63 m for height. The soil column was configured to be 2.3 m deep with 9 vertical layers and a free-drainage lower boundary. Corresponding to a gravelly loam soil in the study site (USDA, 2018a2018), we used a soil texture with 55% sand, 25% silt, and 20% clay, for both sites. Initial soil moisture was set to near saturation with no temperature offset, and the initial atmospheric carbon dioxide level matching the year 2001 (370 ppm), when we initialized the simulation. We ran the EDv2.2 model with these initial settings and initial shrub PFT parameters for the sensitivity analysis at the LS site for a fifteen-year simulation period. We selected this simulation period based on our pre-sensitivity trial runs, previous studies (Medvigy and Moorcroft, 2012; Antonarakis, et al., 2014) where authors had initialized model using inventory data, and taking into account that there have been no major disturbances in recent history in these sites. We used only one of our sites (LS site) for the sensitivity analysis because we assumed both the sites are quite similar in terms of meteorological forcing (given their proximity) and ecosystem conditions, and particularly as we used a range of maximum and minimum values of parameters in the analysis. was set at 370 ppm. The EDv2.2 model was then run with these initial settings and initial shrub PFT parameters values for an 8-year simulation period.

Since our study was more focused on preliminary parameterization of sagebrush PFT, we limited the sensitivity analysis to explore linear dependence of selected parameters over target variable, assuming minimum non-linear dependence among these parameters.

We used a sensitivity index (SI) suggested by Hoffman and Gardner (1983) (Eq. 3) to perform a preliminary one at a time sensitivity analysis and rank the parameters. BecauseSince, this index is highly affected by the extreme values of parameters being studied, it is recommended that the parameter range cover the entire range of possible values. SI has been used in different areas of studies including ecology (Waring et al., 2016) and hydrology (Wambura et al., 2015), mostly to assess the effect of parameters on target variables, and sometimes to reduce the number of variables for further analysis.

$$SI = \frac{GPP_{max} - GPP_{min}}{GPP_{max}}, \quad (3)$$

where, SI is sensitivity index, GPP_{max} is the value of GPP corresponding to the simulation with the maximum value of a parameter, and GPP_{min} is the value of GPP corresponding to the simulation with the minimum value of a parameter. We identified minimum and maximum possible values for each of the selected parameters based on previous sensitivity and optimization studies, the range of parameters for other PFTs in EDv2.2, and our preliminary sensitivity analyses (Table 43). EDv2.2 was then run for a fifteen-an-eight-year period with both minimum and maximum values of each parameter while keeping all other parameters constant. The average daily GPP outputs throughout the simulation years for maximum and minimum values of parameters were used to deriveget GPP_{max} and GPP_{min} respectively. WeBased on SI, we limited the optimization and validation to the five most sensitive parameters-from the list of eleven, to keep time and computing performance manageable.

2.6 Optimization and validation

In the third step, an optimization of the five selected parameters was performed for both the LS and WBS sites using an exhaustive search (brute force) method within the specified range of values. This process was performed to identify the best values for the five selected parameters for each EC station in predicting GPP. For each site, we ran 720 simulations with a unique combination of parameter values for fifteen years (2001-2016), at which point it was assumed to reach an equilibrium with climate. EDv2.2 simulations were configured to allow for growth of the C3 grass, northern pines, and late conifers together with the shrub PFT. This was done because although the vegetation assemblage in the flux site footprints are of flux sites is primarily composed of sagebrush and grasses, conifers are present in some parts of the experimental watershed (Seyfried et al., 2000). For each simulation, we calculated a skill score, Nash-Sutcliffe efficiency (NSE) (Nash and Sutcliffe, 1970), to compare the final-year-simulated GPP from 2015 and 2016 with those derived from both the LS and WBS EC stations for respective years 2016. Although, NSE is closely related to root mean square error (RMSE) (or mean square error, MSE), the skill score from it can be interpreted as comparative ability of the model over a baseline model, which is the mean of site observations in this case. While the RMSE value depends on the unit of predicted variables, which can vary from 0 to infinity, the NSE is dimensionless and varies from negative infinity to 1 (Krause et al, 2005; Gupta et al, 2009). NSE is calculated using Eq. (4):

$$NSE = 1 - \frac{\sum_{i=1}^n (O_i - P_i)^2}{\sum_{i=1}^n (O_i - \bar{O})^2} \frac{\sum_{i=1}^n (O_i - \bar{O})^2}{\sum_{i=1}^n (O_i - \bar{O})^2}, \quad (4)$$

where, O_i is observation, P_i is predicted value, $\bar{O}$ is mean of observation, and n is number of observations. For both EC stations, we selected the 10 best simulations based on NSE scores and computed ensemble means of all five parameter values. We then ran the EDv2.2 model using the ensemble mean parameter values and best case (highest NSE) parameter values for both EC sites. The simulated GPP from these runs ensemble mean parameter values and the best case (highest NSE) were then compared against respective EC site data from 2017-2015, which was withheld from the optimization as a means of providing an independent validation.

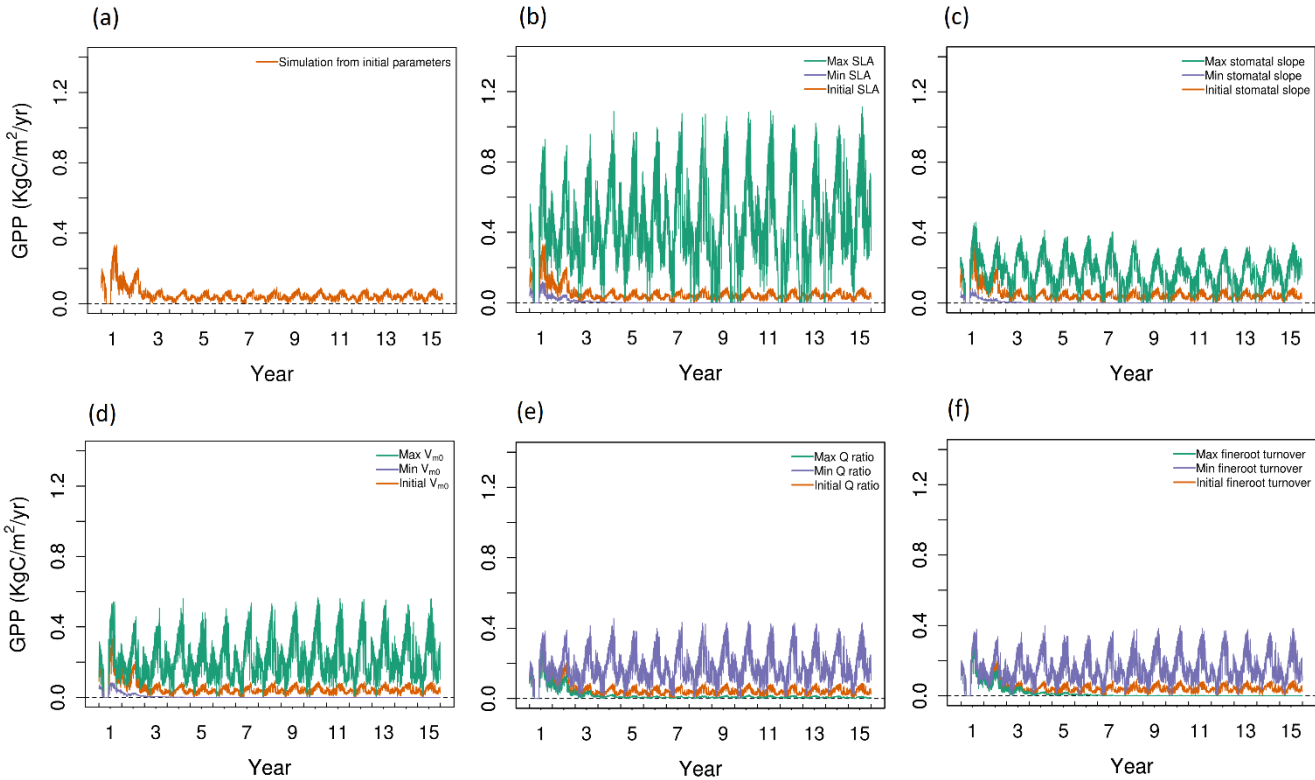
3 Results

3.1 Initial parameterization and sensitivity analysis

For the model run based on the initial values of parameters (Table S1 of Supplement), the fifteen-year simulations produced an annual cycle in GPP that decreases in amplitude during the initial 1-3 years, and remains at a level of approximately 0.07 kgC/m²/yr in the remaining years (Fig. 2a). Observed GPP in 2016 were 0.51 kgC/m²/yr and 0.38 kgC/m²/yr for the LS and WBS sites, respectively. This result was significantly lower than the observed GPP from either of the EC sites, and

thus we followed up with sensitivity and optimization analysis to constrain some of the influential~~warranted changes in initial values for one or more~~ parameters.

Based on the SI ranking, SLA, stomatal slope, V_{m0} , ~~SLA, stomatal slope,~~ fine root turnover rate, and Q-ratio were identified as the top five sensitive parameters compared to the other parameters explored (Fig. 2; Table 43). Related studies (Dietze et al., 2014; Medvigy et al., 2009; Pereira et al., 2017; Zaehle et al., 2005) have also identified similar model parameters being important in estimating GPP. In our study, higher parameter values of SLA, ~~V_{m0} ,~~ and stomatal slope, and V_{m0} , resulted in higher GPP estimates (Fig. 2b, c, and d), whereas for Q-ratio and fine root turnover rate ~~and Q-ratio,~~ higher parameter values produced lower GPP (Fig. 2e and f). The impact of shifts in SLA, V_{m0} , and stomatal slope values are observed from the very beginning of the simulations, while changes in fine root turnover rate and Q-ratio parameters start to show differences from roughly 3-4 years after the initial model run. Although not ranked in the top five, ~~leaf turnover rate,~~ cuticular conductance, leaf turnover rate, and growth respiration factor also had considerable influences over GPP (Table 43).



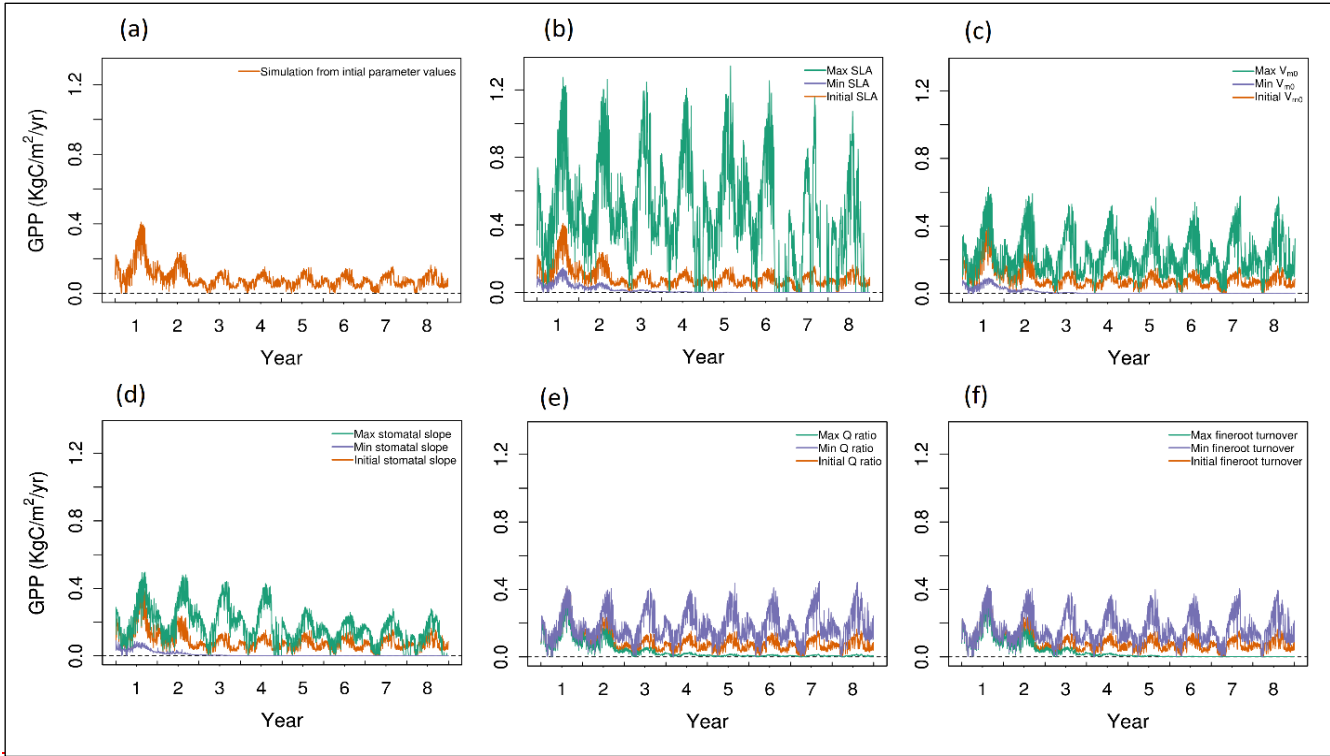


Figure 2. Simulated daily GPP outputs from 1-158 years for the study location with (a) initial values of all five parameters, and (b-f) maximum (green), minimum (blue), and initial (red) parameter values for SLA, V_{m0} , stomatal slope, V_{m0} , Q-ratio, and fine root turnover rate.

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Table 4. Summary of 3. PFT parameters in EDv2.2 used for the sensitivity analysis of studied PFT parameters ranked by according to Sensitivity Index (SI). Top five parameters denoted by * were selected for optimization.

Parameters	Initial	Min	Max	SI	Reference
SLA (m^2kg^{-1})	4.5	2	15	0.988973*	LambrechtsBarbec (2014); Wright et al., (2007); Brabec (2014); Olsoy et al., (2016) 2004)
V_{m0} ($\mu molm^{-2}s^{-1}$)	16.57	24	1530	0.983962*	DietzeComstock & Ehlerenger (1992); Oleson et al., (2014); Bonan et al., (2014)(2013)
Stomatal Slope V_{m0} ($\mu molm^{-2}s^{-1}$)	716.5	42	3015	0.982954*	Comstock & Ehlerenger (1992); OlesonDietze et al., (2013) 2014)
Ratio of fine roots to leaves/Q-ratio	3.2	0.4	12	0.898801*	Dietze et al., (2014)

Fineroot Turnover rate (a ⁻¹)	0.33	0.1	2	0.895787*	Gill and Jackson, (2000)
Cuticular conductance (μmolm ⁻² s ⁻¹)	10³	10²	10⁷	0.813728	Barnard and Bauerle (2013): Duursma et al., (2018)*
Leaf Turnover rate (a⁻¹)					
Leaf Turnover rate (a ⁻¹) Growth respiration factor	0.331	0.111	20.66	0.779718	*Wang et al., (2013)
GRF Cuticular conductance (μmolm ⁻² s ⁻¹)	0.33	0.1110 ²	0.6610 ²	0.694501	WangBarnard and Bauerle (2013): Duursma et al., (20132018)
Water Conductance (ms ⁻¹ kgCroot ⁻¹)	1.9 × 10 ⁻⁵	1.9 × 10 ⁻⁶	1.9 × 10 ⁻⁴	0.168227	*
Storage turnover rate (a ⁻¹)	0.624	0.33	0.95	0.004	*
Leaf width (m)	0.05	0.01	0.10	0.002	*

* Information about the range comes from range of values for other PFTs in EDv2.2, and our preliminary sensitivity analysis

3.2 Optimization and validation

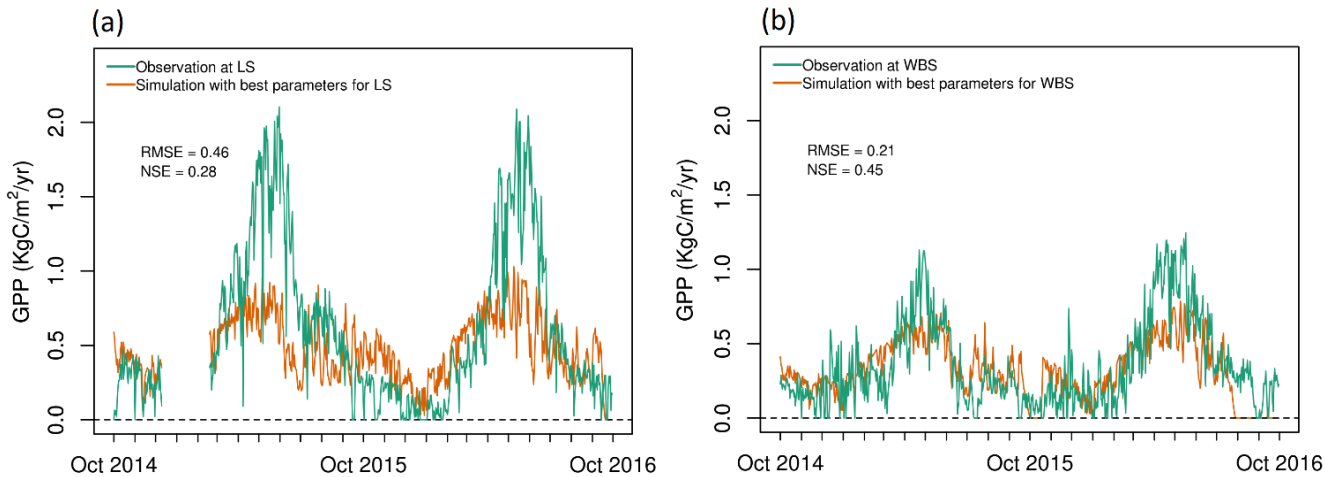
For our exhaustive search of parameter values, we limited search domains for parameters based on previous studies and the result of our sensitivity analysis. SLA search limits were largely based on Olsoy et al. (2016), who suggested a range of 3 to 6 m²/Kg for sagebrush SLA, ~~with but who also hinted at variation due to~~ regional and seasonal ~~variations~~variation. Similarly, limits for V_{m0} were extended slightly beyond Comstock and Ehleringer’s (1992) recommendations for Great Basin shrubs, and the upper limit for stomatal slope was extended slightly beyond that used by Oleson et al. (2013) for a shrub PFT in the Community Land Model (CLMv4.5). We set search domains for Q-ratio based on a leaf and root biomass study of sagebrush by Cleary et al. (2010), and fine root turnover ratio was based on results from a study on *Artemisia ordosica* in a semi-arid region of China (Li et al, 2009). Interval distances (or ‘steps’) were calculated to equally space out the range between the maximum and minimum of each parameter for a given number of intervals (Table 54). Parameters identified as exerting more control on GPP prediction were assigned higher number of steps, resulting in the following: five steps of SLA, ~~and V_{m0}~~ , four steps for V_{m0} , stomatal slope, and three steps for Q-ratio and fine root turnover rate. Among ~~720 possible~~900 simulations for unique parameter value combinations ~~for each site, 92, 180 cases~~ ~~from LS and 116 cases from WBS~~ which did not provide model optimization results because of numerical instabilities (with GPP approaching zero)), were excluded from subsequent analysis.

Table 54. Minimum value, maximum value, interval size, and number of steps for each parameter used in optimization.

Parameter	Min	Max	Interval	Number of steps
SLA (m ² kg ⁻¹)	3.00	9.00	1.50	5
V_{m0} (μmolm ⁻² s ⁻¹)	14.0011.50	21.50	2.50	45
Stomatal slope	7.00	10.00	1.00	4

Fine root turnover (a^{-1})	0.11	0.33	0.11	3
Q-ratio	0.40	3.20	1.40	3

We selected ten simulations with the best NSE scores for both [the](#) LS and WBS sites (Table S2 and Fig. S1 in the Supplement) and determined ensemble means of parameter values for these sites (Table [6](#)[5](#)). We then ran EDv2.2 [from 2001 to 2017](#)~~predict GPP~~ using [parameters with the highest NSE score \(hereafter, the ‘best case’\)](#) and ensemble mean [parameters](#)~~parameter values for each of the EC stations~~ (hereafter, the ‘ensemble case’) [for each of the EC stations.](#) Among the ten best simulations selected for each EC [site](#), ~~four sites, two~~ of them were [common to](#) ~~commonly selected in~~ both sites ([Table S2 in the Supplement](#)). We observed that the variation in parameter values ~~One of them~~ was [more pronounced](#)~~ranked top with highest NSE score (hereafter, the ‘best case’)~~ and the other one was ranked as top fifth for [the](#) LS site, especially with regard to V_{m0} and stomatal slope. Likewise, we observed more variation in GPP estimates among ten best simulations for LS site than ~~top second~~ for WBS site, especially during the peak and trough periods in the plots (Fig. ~~Both of these common simulations, S2 in the Supplement~~). The best case for WBS site showed ~~traces~~~~gradual growth~~ of C3 grass [growth](#) through ~~some intermediate~~ the simulation years even though we initialized [the](#) model with only [the](#) shrub PFT. ~~In the final year of simulation, the ‘best case’ had about 51% of total GPP coming from C3 grass and the other one had about 43% from it (Table S2 and Fig. S2 in the Supplement).~~ (Fig. S3 in the Supplement). Optimized parameter values were ~~only slightly~~[considerably](#) different between the best case and ensemble cases for both ~~sites~~[stations](#), possibly suggesting [little](#) interaction effects among the parameters (Table [6](#)). ~~In the best case,~~ [5](#)). When parameters ~~from ensemble means between two stations were compared, mean V_{m0} for LS was higher by $3 \mu\text{mol m}^{-2} \text{s}^{-1}$ than that for WBS. Mean parameter values for V_{m0} , SLA and stomatal slope were the same~~ was lower by 1 for [both the sites, whereas](#) LS than for WBS site. Another clear difference was with ensemble mean for Q-ratio [and which was higher by 0.70 for LS than for WBS. But, we did not find such differences for SLA and fine root turnover rate](#) [were different.](#)



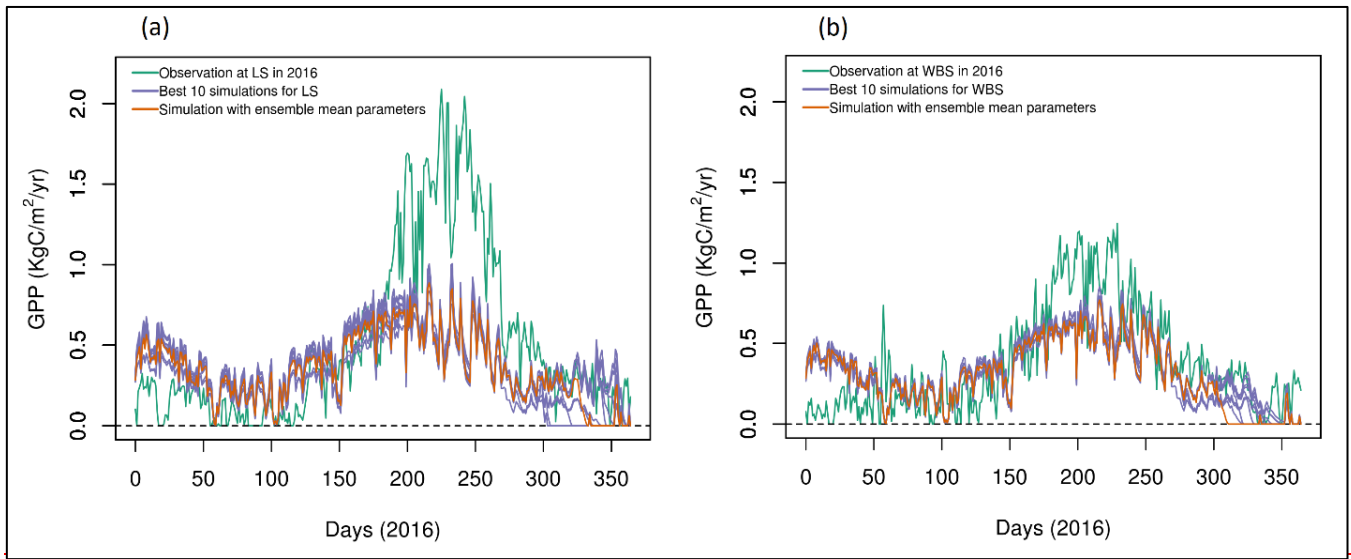


Figure 3. ~~Simulated~~~~Optimization of~~ daily GPP (~~kgC~~~~kgC~~/m²/yr) ~~with best case (highest NSE) compared with~~~~for water year~~ ~~2016 based on~~ EC station observation data from ~~water years 2015 and 2016 for~~ a) LS and b) WBS EC towers. ~~Note that~~ ~~observation data from December 11, 2014 to February 17, 2015 was missing for LS site~~ ~~Spring is shown as roughly 170-255~~ ~~DOY.~~

Figure 3 compares simulated daily GPP from best simulation in the final two model years (October 2014 to September 2016) ~~with modeled year (from the daily ten best simulations and the ensemble case) with the observed GPP from the same period in 2016~~ from each EC station. Optimization results for the LS site in Fig. 3a show that simulated GPP matches well with observed data for most days, except during the spring season, during which strong peaks~~a clear peak~~ in observed GPP ~~were~~~~was~~ not captured by the simulation results. ~~In contrast, the~~ ~~A lower GPP spring peaks for peak in GPP was observed at the~~ WBS site (Fig. 3b) ~~were~~~~and was~~ far more comparable to ~~simulation results. The impact of the simulation results. This~~ spring mismatch in the LS site, ~~resulted in higher Bias and lower NSE when compared to the WBS site (Table 7). Moreover~~ ~~was such that,~~ despite negative biases~~some over-prediction~~ during spring, positive NSE scores~~the fall season for WBS simulations, Bias and NSE were better for WBS than for LS data (Table 5). However,~~ for both sites suggest that ~~EC site comparisons, most simulations resulted in a negative bias, and optimization NSEs for the parameters ensemble cases were generally functioning to allow~~ ~~not as good as for the model to track observed daily GPP over time. best cases.~~

Table 6. Optimized parameter values from best cases (highest NSEs) and ensemble means (mean of top 10 simulations) for LS and WBS EC stations.

Parameters	LS EC station		WBS EC station	
	Best case	Ensemble mean	Best case	Ensemble mean

V_{m0} ($\mu\text{molm}^{-2}\text{s}^{-1}$)	19 14.00	19.00 18.50	19 14.00	18.25 15.80
SLA (m^2kg^{-1})	7.50 6.00	8.10 7.95	6.00 7.50	7.50 8.10
Stomatal slope	9 10.00	8.70 7.60	9 10.00	9.10 8.60
Fine root turnover (a^{-1})	0. 22 33	0. 19 22	0.33	0. 23 24
Q-ratio	3.20	2. 08 64	1.80 3.20	1. 80 94

For validation of the parameter estimates, we ran the model with (i) the best case parameters, and (ii) the ensemble case parameters, for both the LS and WBS sites for a total of 16 years (2001-2017), and compared the simulated GPPs ~~produced from the final year (i.e., 2017 water year); (i) the best case, and (ii) the ensemble case, for both LS and WBS sites,~~ with observed GPP from the respective locations in the same year. Results~~2015. When comparing Bias and NSE derived from the model validation showed higher Biases and lower NSEs for both sites compared to the with that from optimization results (Table 7). We had substantial difference in mean GPP observation for both LS and , we found that simulations for the WBS sites, between optimization (LS = 0.61 kgC/m²/yr, WBS = 0.39 kgC/m²/yr) and validation (LS = 0.55 kgC/m²/yr, WBS = 0.35 kgC/m²/yr) years. Validation results were slightly better for the WBS than the LS site, however, it was not as distinct as site data performed well and with the optimization results. Overall, positive~~relative parity, while those for the LS site performed poorly, especially given the negative NSE values for both ~~best case (-0.193) and ensemble mean case (-0.183) for validation (Table 6). In contrast, validation results for the WBS site showed the model performed well for both cases for both sites suggest the simulated estimates provided better GPP predictions than the observed means., although the NSE from the best case (0.408) was higher than that from ensemble case (0.260).~~ Poor validation results ~~for the LS site could be attributed due to missing data (69 days) from the 2015 observations (i.e., the validation dataset), or possibly due to inter the higher difference in observed mean annual variability in observed GPPs GPP values between 2015 and to 2016 for the inability of LS site than for the model to adequately capture peak spring growth. WBS site.~~

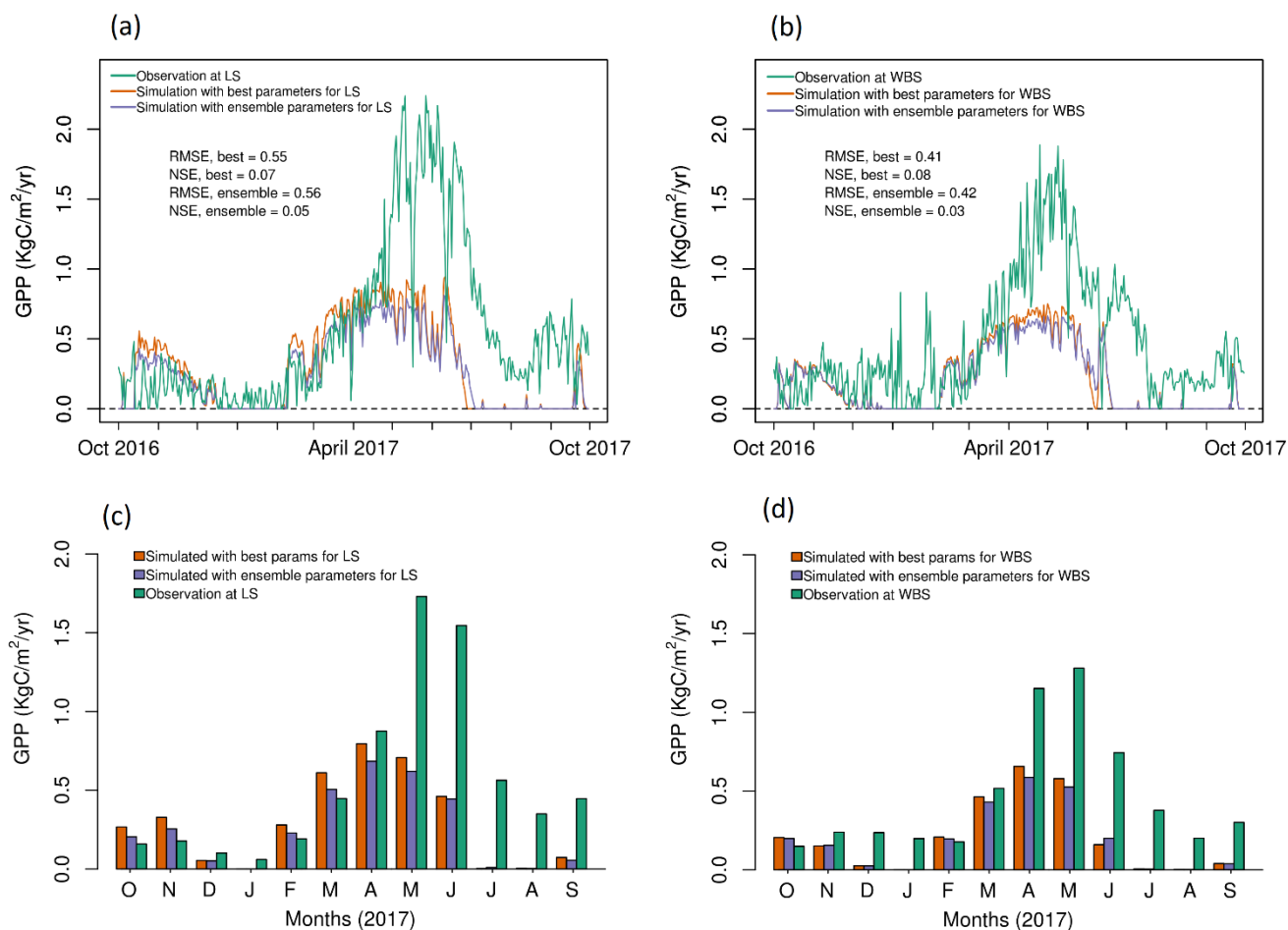
Table 76. Bias, NSE, and RMSE~~NSE~~ for optimization and validation of GPP using parameter values from the best case and the ensemble case for both EC stations.

Simulations	Optimization			Validation		
	Bias ($\text{kgC/m}^2/\text{yr}$) $\text{KgCm}^{2^{-1}}\text{yr}^{-1}$	NSE	<u>RMSE</u> ($\text{kgC/m}^2/\text{yr}$)	Bias ($\text{kgC/m}^2/\text{yr}$) $\text{KgCm}^{2^{-1}}\text{yr}^{-1}$	NSE	<u>RMSE</u> ($\text{kgC/m}^2/\text{yr}$)
<u>LS</u>	-	-	-	-	-	-
Best case	-0. 137 203	0. 277 251	<u>0.456</u>	-0. 257 394	-0. 069 193	<u>0.554</u>
Ensemble case	-0. 185 161	0. 265 203	<u>0.460</u>	-0. 301 354	-0. 046 183	<u>0.562</u>
<u>WBS</u>						
Best case	-0. 028 066	0. 452 417	<u>0.213</u>	-0. 257 004	0. 079 408	<u>0.411</u>

				-			
				0			
Ensemble case	-0.038	0.440	0.216	0	-0.268	0.034	0.421
	076	306		0	260		
				±			
				4			

5 Results shown in Fig. 4 also indicate that the simulated daily GPPs for both sites matched well in late fall until early spring months (October to April) but did not do well in the late spring and summer months (May to September), when compared with observed data in 2017. Daily pattern of simulated GPP were almost identical for both sites with GPP falling down sharply through late summer months and remaining close to zero. We observed similar patterns of decline in the 2017 GPP data during late summer months (July and August) at both sites, though not as sharply as the simulated results (Fig. 4). The observed increase in GPP at the beginning of fall (September) was also not well captured by the simulated outputs. Monthly averages clearly show differences between simulated and observed GPP for May through September (Fig. 4 c & d). Ensemble case simulations for both sites exhibited almost identical patterns as the best case simulation, however at slightly lower levels for most of the months.

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Results shown in Fig. 4 also indicate that the simulated daily GPP matched well with the validation data for the WBS site, but was a relatively poor match for the LS site. In particular, for the LS site, predicted GPP was significantly lower than observed for most of the spring and summer months (Fig. 4c). The validation data (from 2015) for the LS site had clearly higher GPP values for late summer days (Fig. 4a and c), thus resulting in higher negative Bias and negative NSE compared to the optimization results. Predicted daily GPP for this site during the remaining months, however, is comparable with observed values. In contrast, predicted daily GPP for the WBS site matched well with the validation GPP data through most of the year (Fig. 4b and d), with slight inconsistencies during September (under estimation) and October (over estimation). Compared to the best case, the ensemble case simulation for the LS site performed slightly better for most months, much better for July and August, but worse for October and November (Fig. 4c). For the WBS site (Fig. 4d), the clearest differences between the two cases were for April, May, July, and August, during which the best case simulation strongly outperformed the ensemble case.

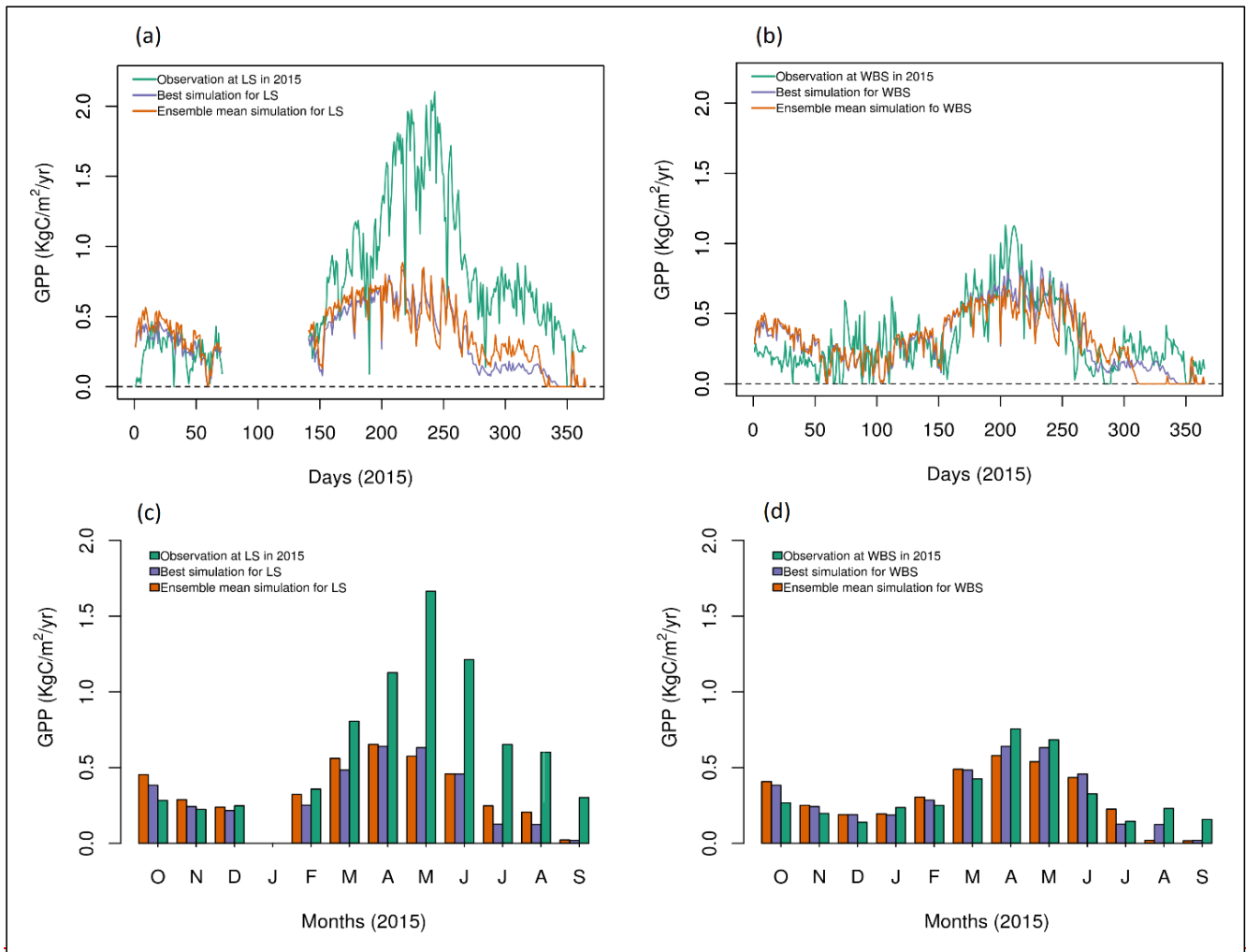


Figure 4. Validation of GPP ($\text{kgC}/\text{m}^2/\text{yr}$) using best case and ensemble case against respective EC station observation data from water year 2015. a) daily GPP for LS, b) daily GPP for WBS, c) monthly GPP for LS, and d) monthly GPP for WBS.

4 Discussion

Using our newly developed sagebrush shrub PFT, we were able to effectively simulate sagebrush ecosystem productivity in EDv2.2 as represented by the two study sites. Simulated results, after about four modeled years, clearly maintained annual shrub GPP over time, although at a lower level than the observed data from these sites. To improve GPP estimates and reduce uncertainty, we assessed our sensitivity of eleven different parameters closely associated with biomass growth. Results from this preliminary analysis were similar to previous studies (Dietze et al., 2014; LeBauer et al., 2013; Medvigy et al., 2009), wherein parameters $-V_{m0}$, SLA, fine root turnover rate, and stomatal slope were found to be the most influential

in determining carbon flux or primary productivity. ~~Variation~~A high variation in parameter values was ~~obtained~~observed among the simulations that resulted in the ~~ten~~ best NSE values (Table S2 in the Supplement). The effects of some parameters (~~stomatal slope, fine root turnover rate, and Q-ratio~~) on GPP prediction ~~differed~~were not the same when ~~they were~~ altered individually ~~versus~~or simultaneously with other parameters. For instance, ~~the~~sensitivity analysis ~~suggested GPP increases~~ when fine root turnover ratio and Q-ratio are lowered individually, yet the best results for each site did not improve (i.e., still under-predicted GPP) with the lowest values of these parameters. Indeed,~~showed an increase in GPP with an increase in addition to first order effects of the studied parameters, the~~ V_{m0} (Fig. 2) and, ~~since our initial GPP prediction was very low, we would expect higher V_{m0} for better prediction. However, when all five parameters were optimized simultaneously, a generally lower value of V_{m0} produced the best NSE (Table 5). Likewise, despite the sensitivity analysis suggesting higher GPP with lower fine root turnover ratio and Q-ratio, the best results were obtained with the same initial values (maximum values in the search domain) for these parameters. Nonetheless,~~ top ten best parameter combinations exhibited variation in parameter values for both EC sites, suggesting interacting effects and ~~potential greater variation of these parameters for either EC site, and resulted in slightly lower mean values than the initial ones. This suggests interaction effects are dominant over first order effects of the studied parameters, and there is likely~~ nonlinear dependence among parameters. Regardless, the negative bias in estimated GPP for the best~~them.~~

GPP simulations resulted from an inability of the model to correctly produce daily GPPs for late spring and summer months. Although~~from this study demonstrated~~ a higher annual GPP could be obtained to compensate for negative bias by changing parameters values, the highest GPP was not necessarily the one with the best NSE, since NSE was calculated based on daily GPP values. Limiting optimization to five of the eleven parameters initially identified may have also contributed to the error and bias observed in our modelled estimates.

GPP simulations for~~closer similarity with observations from~~ the WBS site had better optimization scores than for ~~compared to~~ the LS site, and also a slight edge over the latter for validation results.~~even though the WBS EC station is outside of the WRF pixel used in this analysis.~~ This could be due to ~~slight~~ differences in soils and hydraulic conditions ~~between~~in the sites as we~~field compared to those conditions~~ used similar setups for our simulation~~initialization~~. Moreover, variation between morphological characteristics of the vegetation at the LS and WBS EC towers (characterized by low sagebrush and Wyoming big sagebrush, respectively), including growing seasons~~such as differences in common plant heights~~ and flowering seasons, may also have resulted in the observed differences in GPP (Howard, 1999; USDA, ~~2018b~~2018). Since Wyoming big sagebrush is the dominant species in the Reynold Creek Watershed area (Seyfried et al., ~~2000~~,2000), ~~meteorological forcing data used in this simulation, as well as~~ the allometric equations fitted for sagebrush (representing most areas of RCEW), could favor~~be favoring~~ the more realistic growth pattern of this species in the model (e.g., Fig. ~~43~~ and ~~54~~).

Additionally, differences in the phenology of the associated grass species between the two sites could result in differences in seasonal and annual productivity (Cleary et al., 2015). For instance, the perennial grass at the LS site is Sandberg bluegrass, which is photosynthetically active in early spring and senesces by early summer (USDA, 2016), and thus may have contributed

to the observed higher spring GPP peak at the LS site. Although, we observed small amounts of simulated GPP growth for C3 grasses for certain intermediate years, these levels were ~~In contrast, the associated grass at the WBS site, bluebunch wheatgrass, does not sustained.~~ However, current parameters for C3 grasses were unlikely to adequately produce co-existence of grasses typically senesce by early summer. Indeed, the best optimization result from this study showed a gradual increase in the area, and we C3 grass through the years along with the shrubs, with about 51% of GPP coming from the former by the final year. We could not validate ~~results how close this result was~~ in terms of the actual species composition and ecosystem dynamics of the EC sites, as we did not have GPP observations for unique PFTs. We also observed high inter-annual variation in observed GPP for both sites, leading to poor results in validation of simulation outputs. In summary, site-specific variability, model complexity, and optimizing for only five parameters likely contributed to, or were responsible for. However, the differences between modeled and observed GPP estimates.

While the emphasis of this study was to develop and optimize the shrub PFT parameters, ~~rather than C3 grass PFT parameters for the study area. Although we would~~ expect that simultaneous optimization of both grass and shrub PFTs would result in improved representation of the vegetation composition in the study area. Such an effort, it would also increase increases the number of parameters required, potentially complicating the process of optimization and validation unique to each PFT. Moreover, several studies suggest that the parameters V_{m0} and SLA vary considerably across seasons (Groenendijk et al., 2011; Kwon et al., 2016; Olsoy et al., 2016; Zhang et al., 2014). The mismatch in daily GPP patterns ~~pattern~~ between simulated and flux tower data for specific seasons could be partly attributed to the lack of the model's ability to address these seasonal deviations correctly. Like most other terrestrial biosphere models, EDv2.2 does not incorporate seasonal variation in V_{m0} , SLA, or other model parameters (Medvigy et al., 2009). Finally, we ~~may can~~ achieve better results in parameter optimization and GPP ~~estimates prediction of sagebrush ecosystem,~~ by making some advances in our methods in future studies. For example we can utilize additional. ~~We can adopt some robust~~ sensitivity (including variance decomposition, first order and second order analysis) (Zhang et al., 2017) and optimization (including cost function, gradient descent, and uncertainty analysis) (Richardson et al., 2010) methods to fine tune the sagebrush PFT parameters. Similarly, if we include additional years of ~~instead of relying on a single year of~~ observation data, we may better capture ~~for optimization and/or validation, we can use multiple years of data that would take into account the~~ inter annual variability normally observed in ecosystem fluxes, and potentially improve validation outcomes.

5 Conclusions

This study demonstrates that despite the complexity of the sagebrush-steppe ecosystem, estimating GPP using the newly developed sagebrush PFT is comparable, although with seasonal-bias, to observations obtained from EC station sites. Since our primary focus here was to develop initial parameters (including allometric relationships) for the shrub (sagebrush) PFT in EDv2.2, we focused our efforts on utilizing simple sensitivity and optimization tools to constrain errors associated with simulated GPP. Our identification of coefficients for allometric equations coupled with the other parameters for the ~~In this~~

study, the Ecosystem Demography (EDv2.2) model was used to parameterize shrub PFT parameters and predict GPP for a sagebrush ecosystem in the Great Basin. Initial shrub PFT parameters were identified based on allometric equations fitted with field data, previous studies on sagebrush and shrubs in the sagebrush steppe, and other PFTs (C3 grass, northern pines, and late conifers) in EDv2.2. The WRF model was used to acquire and force simulation with meteorological inputs to predict GPP. The simulation with initial shrub PFT parameters showed annual decline in GPP for 1–3 years and remained at a low level (compared to observed GPP data) for the remaining simulation period. Sensitivity analysis suggested V_{m0} , SLA, stomatal slope, fine root turnover rate, and Q ratio ranked top five in influencing GPP prediction, which agrees with previous studies. An exhaustive search was performed over constrained domains to explore the optimum combination of parameters to predict GPP. This led to identification of parameter values for best case and ensemble mean (of the ten best cases) cases optimized for the LS and WBS EC sites, using the NSE. Even though the model predicted daily GPP quite well, mostly negative bias was observed in predictions, and there was mismatch during the spring months. Validation results showed better performance by parameters optimized for WBS site than those done for LS site in GPP prediction. The difference in the local site vegetation community and the overall dominance of Wyoming big sagebrush in the study area and in the Great Basin may explain why the GPP predictions were closest to the WBS site. Similarly, the limitation of EDv2.2 in incorporating seasonal variation of parameters like V_{m0} and SLA, could also be attributed to its poor predictions for spring seasons.

Our identification of coefficients for allometric equations coupled with the other parametrization of a semiarid shrub PFT for EDv2.2 will permit exploration of additional research questions. For instance, ~~we can run~~ EDv2.2 could be run at regional scales with optimized parameters to model the spatiotemporal dynamics of the sagebrush community composition and ecosystem flux, under different climate and ecological restoration scenarios. With additional time and computing resources (to facilitate large numbers of simulations), we can further refine sagebrush parameters to explore variance decomposition and non-linear dependencies using different sensitivity and optimization methods. Optimization of associated or co-occurring PFTs (C3 grass and conifers) in the region spanning out to include additional study sites, would also help to better understand and constrain uncertainties in estimating the complex dynamics of the sagebrush-steppe ecosystem. Another direction is to optimize C3 grass PFT parameters in EDv2.2, simultaneously with shrub PFT parameters, by using multiple years of observation data to characterize inter-annual variation.

Code & data availability. Original EDv2.2 is available at Github (<https://github.com/EDmodel/ED22>), which is maintained and continuously updated by the owners of the repository. Modified source codes for EDv2.2 with shrub PFT parameters used in this paper and input data are available at <https://doi.org/10.5281/zenodo.2631988> (Last access: 08 April, 2019) ~~<https://doi.org/10.5281/zenodo.2144044> (Last access: 12 December, 2018).~~

Author contribution. KP led the model simulation and manuscript preparation with significant contributions from all co-authors. KP, HD, NFG, ANF, KCM, and DJS conceived the idea and contributed in research design. KP, KCM, and HD led

work on fitting shrub allometric equations and sagebrush parameters, with feedback from all other authors. GNF and AWF processed EC tower data to use in the analysis.

Competing interests. The authors declare that they have no conflict of interest.

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References

- [Ahrends, H. E., S. Etzold, W. L. Kutsch, R. Stockli, R. Bruegger, F. Jeanneret, H. Wanner, N. Buchmann, and W. Eugster. Tree phenology and carbon dioxide fluxes: use of digital photography for process-based interpretation of the ecosystem scale. *Climate Research* 39:261–274, 2009.](#) AmeriFlux: <http://ameriflux.lbl.gov>, last access: 7 May 2018.
- Antonarakis, A. S., Munger, J. W., and Moorcroft, P. R.: Imaging spectroscopy- and lidar-derived estimates of canopy composition and structure to improve predictions of forest carbon fluxes and ecosystem dynamics, *Geophys. Res. Lett.*, 41, 2535–2542, doi:10.1002/2013GL058373, 2014.
- Barnard, D. M., and Bauerle, W. L.: The implications of minimum stomatal conductance on modeling water flux in forest canopies, *Journal of Geophysical Research: Biogeosciences*, 118, 1322-1333, doi:10.1002/jgrg.20112, 2013.
- [Bonan, G. B., Williams, M., Fisher, R. A., and Oleson, K. W.: Modeling stomatal conductance in the earth system: linking leafwater-use efficiency and water transport along the soil–plant–atmosphere continuum, *Geosci. Model Dev.*, 7, 2193–2222, 2014.](#)
- Bond-Lamberty, B., Fish, J., Holm, J. A., Bailey, V. and Gough, C. M.: Moderate forest disturbance as a stringent test for gap and big-leaf models. *Biogeosciences Discuss*, 11, 11217-11248, 2014.
- Botkin, D. B., Janak, J.F., Wallis, J. R.: Rationale, Limitations, and Assumptions of a Northeastern Forest Growth Simulator. *IBM Journal of Research and Development*, 16(2), 101-116, 1972.
- 20
- 25
- 30

- Brabec, M. M.: Big Sagebrush (*Artemisia tridentata*) in a shifting climate context: assessment of seedling responses to climate, Master's Thesis. Boise State University, United States, 116pp., 2014.
- Bradley, B. A.: Assessing ecosystem threats from global and regional change: hierarchical modeling of risk to sagebrush ecosystems from climate change, land use and invasive species in Nevada, USA. *Ecography*, 33, 198-208, [2010](#)~~2014~~.
- 5 [Chambers, J. C., Miller, R. F., Board, D. I., Pyke, D. A., Roundy, B. A., Grace, J., Braswell, B. H., Sacks, W. J., Linder, E., and Schimel, D. S.: Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. *Global Change Biology*, 11, 335–355, doi:10.1111/j.1365-2486.2005.00897.x, 2005.](#)
- ~~Chambers, J. C., Miller, R. F., Board, D. I., Pyke, D. A., Roundy, B. A., Grace, J. B., Schupp, E. W., and Taush, R. J.~~
- 10 Resilience and Resistance of Sagebrush Ecosystems: Implications for State and Transition Models and Management Treatments. *Range Ecol Manage* 67: 440-454, 10.2111/REM-D-13-00074.1, [2014](#)~~2010~~.
- ~~Chen, J. M., Mo, G., Pisek, J., Liu, J., Deng, F., Ishizawa, M., and Chan, D.: Effects of foliage clumping on the estimation of global terrestrial gross primary productivity, *Global Biogeochem. Cycles*, 26, GB1019, doi:10.1029/2010GB003996, 2012.~~
- Cleary, M. B., Pendall, E., and Ewers, B. E.: Aboveground and belowground carbon pools after fire in mountain big sagebrush
- 15 steppe, *Rangel Ecol. Manag.*, 63, 187–96, [doi.org/10.2111/REM-D-09-00117.1](#), [2010](#)~~doi.org/10.2111/REM-D-09-00117.1, 2010.~~
- Cleary, M. B., Naithani, K. J., Ewers, B.E., and Pendall, E.: Upscaling CO₂ fluxes using leaf, soil and chamber measurements across successional growth stages in a sagebrush steppe ecosystem, *J. Arid Environ.*, 121, 43–51, 2015.
- Comstock, J.P. and Ehleringer, J.R.: Plant adaptation in the Great Basin and Colorado Plateau, *Great Basin Naturalist*, 52, 195-215, 1992.
- 20 Connelly, J. W., Knick, S. T., Schroeder, M. A., and Stiver, S. J.: Conservation Assessment of Greater Sage-grouse and Sagebrush Habitats. Western Association of Fish and Wildlife Agencies, Unpublished Report, Cheyenne, Wyoming, 2004.
- ~~Davidson, E., Lefebvre, P. A., Brando, P. M., Ray, D. M., Trumbore, S. E., Solorzano, L. A., Ferreira, J. N., Bustamante, M. M. da C., and Nepstad, D. C.: Carbon inputs and water uptake in deep soils of an eastern Amazon forest, *Forest Science*, 57, 51–58, doi.org/10.1093/forestscience/57.1.51, 2011.~~
- 25 ~~57, 51–58, doi.org/10.1093/forestscience/57.1.51, 2011.~~
- Dietze, M. C., Serbin, S. P., Davidson, C., Desai, A. R., Fend, X., Kelly, R., Kooper, R, LeBauer, D., Mantooth, J., McHenry, K., and Wang, D.: A quantitative assessment of a terrestrial biospheremodel's data needs across North American biomes, *J. Geophys. Res.Biogeosci.*, 119, 286 –300, doi:10.1002/2013JG002392, 2014.
- ~~Dong, J., Li, L., Shi, H., Chen, X., Luo, G., and Yu, Q.: Robustness and Uncertainties of the “Temperature and Greenness” Model for Estimating Terrestrial Gross Primary Production, *Scientific Reports*, 7, 44046, 2017.~~
- 30 ~~Model for Estimating Terrestrial Gross Primary Production, *Scientific Reports*, 7, 44046, 2017.~~
- Duursma, R. A., Blackman, C. J., Lopez, R., Martin-StPaul, N. K., Cochard, H., Medlyn, B. E.: On the minimum leaf conductance: its role in models of plant water use, and ecological and environmental controls, *New Phytologist*, online version, doi : 10.1111/nph.15395, 2018.
- Farquhar, G. D. and Sharkey T. D.: Stomatal conductance and photosynthesis, *Ann. Rev. Plant Physiol.*, 33, 317– 345, 1982.

Fellows, A. W., Flerchinger, G. N., Seyfried, M. S., and Lohse, K.: Data for Partitioned Carbon and Energy Fluxes Within the Reynolds Creek Critical Zone Observatory [Data set]. Retrieved from <https://doi.org/10.18122/B2TD7V>, 2017.

~~Fellows, A. W., Flerchinger, G. N., Lohse, K. A., and Seyfried, M. S.: Rapid Recovery of Gross Production and Respiration in a Mesic Mountain Big Sagebrush Ecosystem Following Prescribed Fire, *Ecosystems*, 1–12, doi.org/10.1007/s10021-017-0218-9, 2018.~~

Fisher, R., McDowell, N., Purves, D., Moorcroft, P., Sitch, S., Cox, P., Huntingford, C., Meir, P., and Woodward, F. I.: Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations, *New Phytologist*, 187, 666-681, doi: 10.1111/j.1469-8137.2010.03340.x, 2010.

Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C., Farrior, C. E. Holm, J. A., Hurtt, G. C., Knox, R. G., Lawrence, P. J., Lichstein, J. W., Longo, M., Matheny, A. M., Medvigy, D., Muller-Landau, H. C., Powell, T. L., Serbin, S. P., Sato, H., Shuman, J. K., Smith, B., Trugman, A. T., Viskari, T., Verbeeck, H., Weng, E., Xu, C., Xu, X., Zhang, T., and Moorcroft, P. R.: Vegetation demographics in Earth System Models: A review of progress and priorities, *Glob. Change Biol.*, 24, 35-24, DOI: 10.1111/gcb.13910, 2017.

Flores, A., Masarik, M., and Watson, K.: A 30-Year, Multi-Domain High-Resolution Climate Simulation Dataset for the Interior Pacific Northwest and Southern Idaho [Data set]. Retrieved from <http://dx.doi.org/10.18122/B2LEAFD001>, 2016.

Gill, R.A. and Jackson, R. B.: Global patterns of root turnover for terrestrial ecosystems, *New Phytol.*, 147, 13-31, doi.org/10.1046/j.1469-8137.2000.00681.x, 2000.

Glenn, N.F., Spaete, L. P., Shrestha, R., Li, A., Ilangakoon, N., Mitchell, J., Ustin, S. L., Qi, Y., Dashti, H., and Finan, K.: Shrubland Species Cover, Biometric, Carbon and Nitrogen Data, Southern Idaho, 2014. ORNL DAAC, Oak Ridge, Tennessee, USA. [Data set] retrieved from <https://doi.org/10.3334/ORNLDAAAC/1503>~~https://doi.org/10.3334/ORNLDAAAC/1503~~, 2017.

Groenendijk, M., Dolman, A. J., Ammann, C., Arneth, A., Cescatti, A., Dragoni, D., Gash, J. H. C., Gianelle, D., Gioli, B., Kiely, G., Knohl, A., Law, B. E., Lund, M., Marcolla, B., Van Der Molen, M. K., Montagnani, L., Moors, E., Richardson, A. D., Rouspard, O., Verbeeck, H., and Wohlfahrt, G. Seasonal variation of photosynthetic model parameters and leaf area index from global Fluxnet eddy covariance data, *J. Geophys. Res.*, 116, G04027, doi:10.1029/2011JG001742, 2011.

Gupta, H. V., Kling, H., Yilmaz, K. K., and Martinez, G. F.: Decomposition of the mean squared error and NSE performance criteria: Implications for improving hydrological modelling, *Journal of Hydrology*, 377, 80-91, doi:10.1016/j.jhydrol.2009.08.003, 2009.

Hoffman, E. O. and Gardner, R. H.: Evaluation of Uncertainties in Environmental Radiological Assessment Models, in: Till, J. E. and Meyer, H. R. (Eds.): *Radiological Assessments: a Textbook on Environmental Dose Analysis*. Washington, DC: U.S. Nuclear Regulatory Commission; Report No. NUREG/CR-3332, 1983.

~~Homer, C.G., Dewitz, J.A., Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N.D., Wickham, J.D., and Megown, K.: Completion of the 2011 National Land Cover Database for the conterminous United States Representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing*, v. 81, no. 5, p. 345–354, 2015~~

- Howard, J. L. 1999. *Artemisia tridentata* subsp. *Wyomingensis*, in: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Retrieved from <https://www.fs.fed.us/database/feis/plants/shrub/arttriw/all.html> Retrieved from <https://www.fs.fed.us/database/feis/plants/shrub/arttriw/all.html>, last access: 20 August 2018.
- 5 ~~Huntzinger, D. N., Post, W. M., Wei, Y., Michalak, A. M., West, T. O., Jacobson, A. R., Baker, I. T., Chen, J. M., Davis, K. J., Hayes, D. J., Hoffman, F. M., Jain, A. K., Liu, S., McGuire, A. D., Neilson, R. P., Potter, C., Poulter, B., Price, D., Raczka, B. M., Tian, H. Q., Thornton P., Tomelleri, E., Viovy, N., Xiao, J., Yuan, W., Zeng, N., Zhao, M., and Cook, R.: North American Carbon Program (NACP) regional interim synthesis: Terrestrial biospheric model intercomparison, *Ecol. Modell.*, 232, 144–157, doi:10.1016/j.ecolmodel.2012.02.004, 2012.~~
- 10 Kim, Y., Knox, R. G., Longo, M., Medvigy, D., Hutyrá, L. R., Pyle, E. H., Wofsy, S. C., Bras, R. L., and Moorcroft, P. R.: Seasonal carbon dynamics and water fluxes in an Amazon rainforest. *Global Change Biology*, 18, 1322–1334, doi: 10.1111/j.1365-2486.2011.02629.x, 2012.
- Knick, S. T. and Dobkin, D. S.: Teetering on the Edge or Too Late? Conservation and Research Issues for Avifauna of Sagebrush Habitats, *The Condor*, 105, 611–634, <https://doi.org/10.1650/7329>, 2003.
- 15 Knox, R. G., Longo, M., Swann, A. L. S., Zhang, K., Levine, N. M., Moorcroft, P. R., and Bras, R. L.: Hydrometeorological effects of historical land-conversion in an ecosystem-atmosphere model of Northern South America, *Hydrol. Earth Syst. Sci.*, 19, 241–273, doi:10.5194/hess-19-241-2015, 2015.
- Krause, P., Boyle, D. P., and Baise, F.: Comparison of different efficiency criteria for hydrological model assessment. *Advances in Geosciences*, 5, 89–97, <https://doi.org/10.5194/adgeo-5-89-2005>, 2005.
- 20 Kwon, B., Kim, H. S., Jeon, J., and Yi, M. J.: Effects of Temporal and Interspecific Variation of Specific Leaf Area on Leaf Area Index Estimation of Temperate Broadleaved Forests in Korea. *Forests*, 7, 215, doi:10.3390/f7100215, 2016.
- ~~[Lambrecht, S. C., Shattuck, A. K., and Loik, M. E.: Combined drought and episodic freezing effects on seedlings of low- and high-elevation subspecies of sagebrush \(*Artemisia tridentata*\), *Physiologia Plantarum*, 130: 207–217, 2007.](#)~~
- LCC: Landscape Conservation Cooperatives: 2015 LCC Network Areas OGC Webservices—: <https://www.sciencebase.gov/catalog/item/55c52e08e4b033ef5212bd75>, last access, 21 April, 2018
- 25 LeBauer, D. S., Wang, D., Richter, K. T., Davidson, C. C., and Dietze, M. C.: Facilitating feedbacks between field measurements and ecosystem models. *Ecological Monographs*, 83, 133–154, <https://doi.org/10.1890/12-0137.1>~~<https://doi.org/10.1890/12-0137.1>~~, 2013.
- 30 Leuning, R.: A critical appraisal of a combined stomatal-photosynthesis model for C3 plants, *Plant Cell Environ.*, 18, 339–355, 1995.
- Li, C., Sun, O. J., Xiao, C., and Han, X.: Differences in Net Primary Productivity Among Contrasting Habitats in *Artemisia ordosica* Rangeland of Northern China. *Rangeland Ecol Manage.*, 62, 345–350, <https://doi.org/10.2111/07-084.1>, 2009.
- McArthur, E. D. and Plummer, A. P.: Biogeography and management of native western shrubs: a case study, Section *Tridentatae* of *Artemisia*, *Great Basin Naturalist Memoirs*, 2, 15, <https://scholarsarchive.byu.edu/gbnm/vol2/iss1/15>, 1978.

- McIver, J. and Brunson, M.: Multidisciplinary, Multisite Evaluation of Alternative Sagebrush Steppe Restoration Treatments: The SageSTEP Project, *Range Ecol. Manage.*, 67, 435-439, <https://doi.org/10.2111/REM-D-14-00085.1>, 2014.
- Medvigy, D. M.: The state of the regional carbon cycle: Results from a coupled constrained ecosystem-atmosphere model, Ph.D. Thesis, Harvard Univ., Cambridge, Mass., 2006.
- 5 Medvigy, D. M., and Moorcroft, P. R.: Predicting ecosystem dynamics at regional scales: an evaluation of a terrestrial biosphere model for the forests of northeastern North America, *Phil. Trans. R. Soc. B*, 367, 222–235, [doi:10.1098/rstb.2011.0253](https://doi.org/10.1098/rstb.2011.0253), 2012.
- Medvigy, D., Wofsy, S. C., Munger, J. W., Hollinger, D. Y., and Moorcroft, P. R.: Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2, *J. Geophys. Res.*, 114, G01002, [doi:10.1029/2008JG000812](https://doi.org/10.1029/2008JG000812), 2009.
- 10 Medvigy, D., Jeong, S. J., Clark, K. L., Skowronski, N. S., and Schäfer, K. V. R.: Effects of seasonal variation of photosynthetic capacity on the carbon fluxes of a temperate deciduous forest, *Journal of Geophysical Research: Biogeosciences*, 118, 1703–1714, , [doi:10.1002/2013JG002421](https://doi.org/10.1002/2013JG002421), 2013.
- Miller, P. A. and Smith, B.: Modelling Tundra vegetation response to recent Arctic warming, *Ambio*, 41, 281–291, 2012.
- 15 Miller R.F., Knick, S.T., Pyke, D. A., Meinke, C. W., Hanser, S. E., Wisdom, M. J., Hild, A. L.: Characteristics of sagebrush habitats and limitations to long-term conservation, Knick S.T., J.W. Connelly (Eds.), *Greater sage-grouse—ecology and conservation of a landscape species and its habitats. Studies in avian biology no. 38, University of California Press, Berkeley, CA, USA, 145–185, 2011.*
- Mo, X., Chen, J. M., Ju, W., and Black, T. A.: Optimization of ecosystem model parameters through assimilating eddy covariance flux data with an ensemble Kalman filter, *Ecological Modelling*, 217, 157–173, <https://doi.org/10.1016/j.ecolmodel.2008.06.021>~~<https://doi.org/10.1016/j.ecolmodel.2008.06.021>~~, 2008.
- 20 Moorcroft, P. R.: Recent advances in ecosystem-atmosphere interactions: an ecological perspective, *Proceedings of the Royal Society B-Biological Sciences*, 270, 1215–1227, DOI: 10.1098/rspb.2002.2251, 2003.
- Moorcroft, P. R., Hurtt, G. C., Pacala, S. W.: A method for scaling vegetation dynamics: the Ecosystem Demography model (ED), *Ecol. Monogr.*, 71, 557–586, [https://doi.org/10.1890/0012-9615\(2001\)071\[0557:AMFSVD\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2001)071[0557:AMFSVD]2.0.CO;2), 2001.
- 25 Nash, J. E. and Sutcliffe, J. V. River flow forecasting through conceptual models, Part I - A discussion of principles, *J. Hydrol.*, 10, 282–290, 1970.
- ~~NPS, 2018. Great Basin: Trees and Shrubs. National Park Service: <https://www.nps.gov/grba/learn/nature/treesandshrubs.htm>, last access: 26 July 2018.~~
- 30 Oleson, K., Lawrence, D. M., Bonan, G. B., Drewniak, B., Huang, M., Koven, C. D., Levis, S., Li, F., Riley, W. J., Subin, Z. M., Swenson, S. C., Thornton, P. E., Bozbiyik, A., Fisher, R., Heald, C. L., Kluzek, E., Lamarque, J.-F., Lawrence, P. J., Leung, L. R., Lipscomb, W., Muszala, S., Ricciuto, D. M., Sacks, W., Sun, Y., Tang, J., and Yang, Z.-L.: Technical Description of version 4.5 of the Community Land Model (CLM), NCAR Technical Note NCAR/TN-503+STR, Boulder, Colorado, 420 pp., 2013.

- Olsoy, P. J., Mitchell, J. J., Levia, D. F., Clark, P. E., Glenn, N. F.: Estimation of big sagebrush leaf area index with terrestrial laser scanning, *Ecological Indicators*, 61, 815–821, <https://doi.org/10.1016/j.ecolind.2015.10.034>, 2016.
- Pacala, S. W., Canham, C. D., Silander Jr, J. A.: Forest models defined by field measurements. I. The design of a northeastern forest simulator, *Can. J. For. Res.*, 23, 1980-1988, 1993.
- 5 Pereira, F. F., Farinosi, F., Arias, M. E., Lee, E., Briscoe, J., and Moorcroft, P.R.: Technical note: A hydrological routing scheme for the Ecosystem Demography model (ED+R) tested in the Tapajós River basin in the Brazilian Amazon, *Hydrol. Earth Syst. Sci.*, 21, 4629–4648, <https://doi.org/10.5194/hess-21-4629-2017>, 2017.
- Qi, Y., Dennison, P. E., Jolly, W. M., Kropp, R. C., and Brewer, S. C.: Spectroscopic analysis of seasonal changes in live fuel moisture content and leaf dry mass, *Remote Sensing of Environment*, 150, 198-206, <https://doi.org/10.1016/j.rse.2014.05.004>, 2014.
- 10 <https://doi.org/10.1016/j.rse.2014.05.004>, 2014.
- [Qi, Y., Ustin, S. L., and Glenn, N. F.: Imaging Spectroscopic Analysis of Biochemical Traits for Shrub Species in Great Basin, USA, *Remote Sens.*, 10, 1621; doi:10.3390/rs10101621, 2018.](https://doi.org/10.1016/j.rse.2014.05.004)
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet M., Berbigier P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D.,
- 15 Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J. M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., and Valentini, R.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm, *Glob. Change Biol.*, 11, 1424–39, <https://doi.org/10.1111/j.1365-2486.2005.001002.x>, 2005.
- Richardson, A. D., Williams, M., Hollinger, D. Y., Moore, D. J. P., Dail, D. B., Davidson, E. A., Scott, N. A., Evans, R. E.,
- 20 Hughes, H., Lee, J. T., Rodrigues, C., Savage, K.: Estimating parameters of a forest ecosystem C model with measurements of stocks and fluxes as joint constraints, *Oecologia*, 164, 25–40, doi:10.1007/s00442-010-1628-y, 2010.
- Schlaepfer, D. R., Lauenrotha, W. K., and Bradford, J. B.: Modeling regeneration responses of big sagebrush (*Artemisia tridentata*) to abiotic conditions, *Ecological Modelling*, 286, 66-77, <https://doi.org/10.1016/j.ecolmodel.2014.04.021>, 2014.
- Schroeder, M. A., Aldridge, C. L., Apa, A. D., Böhne, J. R., Braun, C. E., Bunnell, S. D., Connelly, J. W., Deibert, P. A.,
- 25 Gardner, S. C., Hilliard, M. A., Kobriger, G. D., McAdam, S. M., McCarthy, C. W., McCarthy, J. J., Mitchell, D. L., Rickerson, E. V., and Stiver, S. J.: Distribution of Sage-Grouse in North America, *The Condor*, 106, 363-376, <https://doi.org/10.1650/7425>, 2004.
- Sellers, P. J., Berry, J. A., Collatz, G. J., Field, C. B., and Hall, F.G.: Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme, *Remote Sensing of Environment*, 42, 187-216, [doi.org/10.1016/0034-4257\(92\)90102-P](https://doi.org/10.1016/0034-4257(92)90102-P), 1992. ~~[doi.org/10.1016/0034-4257\(92\)90102-P](https://doi.org/10.1016/0034-4257(92)90102-P), 1992.~~
- 30 Seyfried, M. S., Harris, R., Marks, D., and Jacob, B.: A geographic database for watershed research: Reynolds Creek Experimental Watershed, Idaho, USA, Tech. Bull. NWRC 2000-3, 26 pp., Northwest Watershed Res. Cent., Agric. Res. Serv., U.S. Dep. of Agric., Boise, Idaho, 2000

- Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplans, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K. and Venevsky, S.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic vegetation model, *Global Change Biol.*, 9, 161 – 185, 2003.
- 5 [Skamarock, W. C., Klemp, J. B., Dudhia, J., Gill, D. O., Barker, D. M., Duda, M. G., Huang, X., Wang, W., and Powers, J. G.: A Description of the Advanced Research WRF Version 3. NCAR Technical Note NCAR/TN-475+STR, doi:10.5065/D68S4MVH, 2008.](#)
- Smith, B., Trentice, C.I., and Sykes, M. T.: Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Global Ecology & Biogeography*, 10, 621-637, 2001.
- 10 Stephenson, ~~G. R.~~ GR (Ed.): CZO Dataset: Reynolds Creek - Geology, Soil Survey, Vegetation, GIS/Map Data (1960-1970), Retrieved from <http://criticalzone.org/reynolds/data/dataset/3722/>, last access: 18 May 2018.
- [Sturges, D. L.: Soil water withdrawal and root characteristics of Big Sagebrush. *The American Midland Naturalist*, 98, 257-274, 1977.](#)
- [Tabler, R. D.: The root system of *Artemisia tridentata* at 9,500 feet in Wyoming. *Ecology* 45 \(3\), 633-636, 1964.](#)
- 15 Trugman, A. T., Fenton, N. J., Bergeron, Y., Xu, X., Welp, L. R., and Medvigy, D.: Climate, soil organic layer, and nitrogen ~~jointly drive~~ jointly drive forest development after fire in the North American boreal zone, *Journal of Advances in Modeling the Earth System*, 8, 1180–1209, doi:10.1002/2015MS000576, 2016.
- ~~Turner, D. P., Ritts, W. D., Cohen, W. B., Gower, S. T., Running, S. W., Zhao, M., Costa, M. H., Kirschbaum, A. A., Ham, J. M., Saleska, S. R., Ahl, D. E.: Evaluation of MODIS NPP and GPP products across multiple biomes, *Remote Sens. Environ.*, 102, 282–292, doi:<http://dx.doi.org/10.1016/j.rse.2006.02.017>, 2006.~~
- 20 USDA: Plant materials Technical Note No. MT-114. Natural Resources Conservation Service, United States Department of Agriculture, August 2016, 2016.
- USDA: Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Retrieved from <https://websoilsurvey.sc.egov.usda.gov/>, last access: 28 March 2018, [2018a.](#)
- 25 USDA: The PLANTS Database (<http://plants.usda.gov>~~http://plants.usda.gov~~, 20 August 2018). National Plant Data Team, Greensboro, NC 27401-4901 USA, 2018, [2018b.](#)
- [Wambura](#)~~Wamburaa~~, F. J., Ndombab, P. M.,~~-~~ Kongob, V., Tumboc, S. D.: Uncertainty of runoff projections under changing climate in Wami River sub-basin, *Journal of Hydrology: Regional Studies*, 4, 333–348, 2015.
- Wang, D., LeBauer, D., Dietze, M.: Predicting yields of short-rotation hybrid poplar (*Populus* spp.) for the United States through model–data synthesis, *Ecological Applications*, 23(4), 944-958, 2013.
- 30 Waring, B. G., Averill, C., Hawkes, C. V.: Differences in fungal and bacterial physiology alter soil carbon and nitrogen cycling: insights from meta-analysis and theoretical models, *Ecology Letters*, 16, 887-894, doi: 10.1111/ele.12125, 2016
- Weiss, A. and Norman, J. M.: Partitioning solar radiation into direct and diffuse, visible and near-infrared components. *Agric. Forest Meteorol.*, 34, 205–213, 1985.

[Wolf, A., Callaghan, T. V., and Larson, K.: Future changes in vegetation and ecosystem function of the Barents Region, *Climate Change*, 87, 51-73, 2008.](#)

Zaehle, S., Sitch, S., Smith, B., and Hatterman, F.: Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics, *Global biogeochemical cycles*, 19, 3, DOI: [10.1029/2004GB002395](#)~~10.1029/2004GB002395~~, 2005.

- 5 Zhang, K., de Almeida Castanho, A. D., Galbraith, D. R., Moghim, S., Levine, N. M., Bras, R. L., Coe, M. T., Costa, M. H., Malhi, Y., Longo, M., Knox, R. G., McKnight, S., Wang, J., and Moorcroft, P. R.: The fate of Amazonian ecosystems over the coming century arising from changes in climate, atmospheric CO₂, and land use, *Glob. Change Biol.*, 21, 2569–2587, <https://doi.org/10.1111/gcb.12903>, 2015.

- 10 Zhang, K., Ma, J., Zhu, G., Ma, T., Han, T., Feng, L. L.: Parameter sensitivity analysis and optimization for a satellite-based evapotranspiration model across multiple sites using Moderate Resolution Imaging Spectroradiometer and flux data, *J. Geophys. Res. Atmos.*, 122, 230–245, doi:10.1002/2016JD025768, 2017

Zhang, Y., Guanter, L., Berry, J. A., Joiner, J., Tol, C. V. D., Huete, A., Gitelson, A., Voigt, M., and Kohler, P.: Estimation of vegetation photosynthetic capacity from space-based measurements of chlorophyll fluorescence for terrestrial biosphere models, *Global Change Biology*, 20, 3727–3742, doi: 10.1111/gcb.12664, 2014.

- 15 ~~Zhao, M. and Running, S. W.: Drought Induced Reduction in Global Terrestrial Net Primary Production from 2000 through 2009, *Science*, 329, 940–943, doi: 10.1126/science.1192666, 2010.~~

~~Zhao, M., Heinsch, F. A., Nemani, R. R., Running, S. W.: Improvements of the MODIS terrestrial gross and net primary production global data set, *Remote Sens. Environ.*, 95, 164–176, doi:http://dx.doi.org/10.1016/j.rse.2004.12.011, 2005.~~