

Anonymous Referee #1

The authors investigate in this very interesting paper the interannual and seasonal differences of carbon and water exchange between vegetation and atmosphere in a temperate forest ecosystem dominated by Scots Pine. By combining Eddy-Covariance-Data and a local process-based vegetation model (LPJ-GUESS) the authors show that environmental factor do not explain annual exchange rates, but can successfully for monthly and daily ones – except for winter seasons and droughts. By analyzing other temperature responses and different mechanisms of water uptake the authors emphasize the need for testing and developing modelling approaches in vegetation modelling. To my opinion this paper is well written and comprehensible, except for a couple of minor comments. I recommend publication of this paper.

Minor comments:

Page 270, line 17-21: These sentences are written a bit complicated (line 17) or too general (line 18-21). Please try to rewrite in order to better understand what you mean with “more direct” (line 17) and whether you used “factorial experiments” instead of one could do that.

AUTHORS:

We thank the reviewer for pointing out that this was not entirely clear. With more direct responses, we meant the response of vegetation, and in particular photosynthesis, to direct environmental variables (temperature, precipitation (drought), and radiation) which act on the carbon and water balance on an hourly or daily time scale. The first part of the paragraph describes the indirect responses (phenology, C allocation etc.). To illustrate this, we added the word ‘indirect’ before ‘short-term’ in line 11, and before the word ‘long-term’ in line 15. We further try to clarify the above issues by now writing (Page 270, line 16–21):

“Before addressing these complex process representations within models, however, it can be useful to test whether IAV_{cw} can be explained by rather simple relationships with direct environmental drivers, such as drought, temperature and radiation, which can affect, e.g., photosynthesis and soil respiration rather directly and instantaneously. Factorial experiments with a dynamic vegetation model can then be used to generate hypotheses concerning simple and/or complex interactions of processes driving IAV_{cw}.

These vegetation models can be expected to capture at least some of the complexity of real ecosystems, and the factorial experiments can be used, for example, to keep certain environmental drivers constant (i.e. switching of their effect, e.g. Hickler et al., 2005), or to implement different hypotheses concerning the most important processes within an ecosystem. The latter can also be achieved by data-model intercomparisons with several models, that differ in their process representation (e.g. Medlyn et al., 2015). In this study, the factorial model experiments refer to model setups with different process representations. With this purpose in mind, we used ...”

Reference:

Medlyn, B. E., Zaehle, S., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Hanson, P. J., Hickler, T., Jain, A. K., Luo, Y., Parton, W., Prentice, I. C., Thornton, P. E., Wang, S., Wang, Y.-P., Weng, E., Iversen, C. M., McCarthy, H. R., Warren, J. M., Oren, R., and Norby, R. J.: Using ecosystem experiments to improve vegetation models, *Nature Climate Change*, 5, 528–534, 2015.

REFeree:

Page 271, line 12: Please use another word for “model error”.

AUTHORS:

We changed this into:

“can explain differences between modelled values and observations for...”

REFEREE:

Page 273, line 4: Please be clear what you mean with “for all years”. Do you mean 1997, 1998 and 2009 or more years?

AUTHORS:

We meant the years considered in this study, and changed the text into:

“Soil moisture data are available for all years considered within this study (1997–2009), ...”

REFEREE:

Page 273, line 6: please explain “litter” in terms of “a depth” as it is written in this sentence! Is it the “aboveground litter layer” or the “soil surface”?

AUTHORS:

Indeed, this is unclear. The depth is at 0.00 m, so the aboveground litter layer. We clarified by now writing:

“In 2005 all sensors were replaced and positioned at different depths: 0.00 (aboveground litter), 0.03, 0.20, 0.50 and 1.0 m.”

REFEREE:

Page 273, line 9-10: Are exact dates known for these additional measurements? Please provide the years in brackets.

AUTHORS:

Yes, we can provide the years and changed the text into:

“Additional site measurements at less frequent intervals include the leaf area index (LAI) of trees (1997 – 2009, every few months at irregular intervals) and, to a lesser extent, the understory (1999, 2002, 2012).”

REFEREE:

Page 273, line 16: Please provide some references for forest gap models.

AUTHORS:

The gap model we refer to here is called FORSKA. It was published as a PhD thesis in 1989, by Leemans and Prentice. Model name and reference are now added:

“.. gap models (FORSKA, Leemans and Prentice, 1989).”

In case the reviewer would prefer a broader reference, we would like to suggest the extensive review of forest gap models by Bugmann et al. (2001) in Climatic Change.

References:

Bugmann, H.: A Review of Forest Gap Models, Climatic Change, 51, 259-305, 2001.

Leemans, R. and Prentice, I. C.: FORSKA, a general forest succession model, 1989.PhD, Institute of Ecological Botany, Uppsala University, Uppsala, Sweden, 70 pp., 1989.

REFEREE:

Page 273, line 18: Please explain what you mean with “main tree species”. Is it the dominant species or a mean species? Moreover, authors write that the study is based on main tree species rather than PFTs. However, on the next pages authors refer to PFT-specific parameters (e.g. page 275, line 12). Please try to avoid this inconsistency.

AUTHORS:

We agree this is not entirely clear. We meant dominant species here, and replaced 'main' with 'dominant' on page 273, line 18. In addition, we agree with the reviewer that we should clearly distinguish between single species and PFTs, as the latter represents a broad class that can contain multiple species. We therefore changed the document accordingly:

Page 275, line 12: 'PFT/species-specific' instead of 'PFT-specific'

Page 277, line 10-12: 'Only *Pinus sylvestris* and the PFT for herbaceous vegetation with C3 photosynthesis (to represent the understory) were allowed to establish.'

Page 277, line 13: 'species' instead of 'PFT'

Page 277, line 17: 'PFT/species-specific' instead of 'PFT-specific'

Page 277, line 18: 'PFT/species' instead of 'PFT'

Page 279, line 13: 'PFT/species-specific' instead of 'PFT-specific'

Page 279, line 18: 'PFT/species-specific' instead of 'PFT-specific'

Page 279, line 26: replaced 'PFTs' with '*P. sylvestris* and C₃ grasses,'

Page 285, line 8: replaced 'PFTs' with 'PFTs and species'

Page 290, line 10: 'PFT/species-specific' instead of 'PFT'

Table 1: Replaced 'Species PFT' with 'Species/PFT'

Figure 1: removed 'PFT' from caption

REFEREE:

Page 273, line 20: Please explain in more detail, what "neighboring individuals" means on a patch.

AUTHORS:

It means neighbouring individual trees, which we added to the text.

REFEREE:

Page 273, line 21: I would recommend switching "cohort" to the brackets and "age class" to the sentence for a better understanding.

AUTHORS:

Changed according to the reviewer's suggestion.

REFEREE:

Page 277, line 7: Did you check whether there is a significant trend in the climate data from 1997 to 2009?

AUTHORS:

We checked whether there is a significant trend in the climate data (linear regression in R) and did not find one for temperature or radiation. For precipitation and AET we do find a small but significant increase between 1997 and 2009, but this was to be expected because precipitation is known to have increased over the last century in the whole of The Netherlands (Buishand, 2011). So during the spin-up period, when we repeat the meteorological dataset this could have caused some IAV, but during the simulated result period this should not have an effect.

Reference:

Buishand, T.A., De Martino, G., Spreeuw, J.N., Brandsma, T., 2013. Homogeneity of precipitation series in The Netherlands and their trends in the past century. *International Journal of Climatology* 33, pp. 815-833. doi:10.1002/jov.3417.

REFEREE:

Page 278, line 10-11: Please also provide for this reference a location of that study.

AUTHORS:

The location is Creag Fhiaclach, situated in Cairngorms national park in Scotland. We have added this information to the text, in brackets.

Technical comments:

REFEREE:

Page 275, line 3: Please write “with” using lower case letter.

AUTHORS:

Changed according to the reviewer’s suggestion.

REFEREE:

Please use consistent labels in the figure and table captions concerning the change of the temperature response function (Fig. 3, 5, 6, Tab. 3).

AUTHORS:

We thank the reviewer for pointing out this inconsistency. We changed all labels (and, if necessary, captions) according to the descriptions used in Table 3.

REFEREE:

Fig. 7: In the figure captions, it should be stated (consistent to the figure) that solid lines are modelled values and the dotted line is the observation.

AUTHORS:

Thank you, reviewer, for finding this mistake! We completely missed that one ourselves.. Changed according to the reviewer’s suggestion.

REFEREE:

Page 284, line 11: A section number is missing.

AUTHORS:

This change was made by the ESDD editorial team. Our original manuscript referred to this paragraph as Section 3.3.1. We have added a remark in the revised manuscript regarding this matter.

REFEREE:

Please use “g” instead of “gram” consistently in all figures and tables.

AUTHORS:

We agree with the reviewer that consistency is important, and changed Figs 2, 3, 4, 5, 6, 7 and 10 accordingly.

Anonymous Referee #2

General comments:

The paper studies vegetation – atmosphere carbon and water exchange using multiple years of Eddy Covariance data from Loobos, a Dutch Scots pine forest and LPJ-GUESS, a process based ecosystem model. Specifically, the paper looks at multiple timescales (daily, monthly and yearly), and shows that interannual variability in carbon and water exchange (IAV_{cw}) is not well captured by models. Next, different model versions are used in order to explain and minimize the IAV_{cw}. Overall, I think the paper is well written, and interesting. The extension of the model with carbon uptake up to -10 degrees Celcius is interesting, even though it is not improving IAV_{cw} much. Also, the different water uptake routines show interesting results. I would recommend this paper for publication, with minor revisions. Please see comments below.

Specific comments:

Page 275, eq 1. What is $p_{stemhigh}$ and $p_{stemlow}$? This is not clear from the next, nor from figure 1. Also, I would recommend not just explaining the abbreviation in the figure caption, but also in the text.

AUTHORS:

We would like to point out that both parameters $p_{stemhigh}$ and $p_{stemlow}$, are described extensively on page 275, lines 14-18, as ‘the optimum temperature range for photosynthesis’, where we also refer to Figure 1. This optimum range for each species/PFT is taken from Table 3.7 in Larcher, 1980. In the caption of Figure 1, these optimum ranges per species/PFT are provided: for *P. sylvestris* it is 15–25°C, and for C₃ grass 10–35°C (Larcher, 1980).

We think that some confusion may have been caused in this paragraph by some edits from the ESDD editorial team. Our original submitted text was “Within the optimum range, t_{scalar} equals unity (1),...” and the editorial team changed this into “Within the optimum range, t_{scalar} equals unity (Eq 1),...”.

We try to be very exact in our meaning, by changing the sentences (page 275, lines 14-18) regarding the optimum temperature range into:

“This optimum range (i.e. the upper plateau in Fig. 1) represents an effective temperature response of many enzyme and transport related processes. Within this optimum range, t_{scalar} equals unity (i.e. t_{scalar} is equal to 1), and creates a slight rise in maximum carboxylation capacity (V_m), but reduces photosynthesis with increasing temperature. Outside this optimum range, both ...”

REFEREE:

Page 278, section 2.3.2. In this section, the authors show some results for the alternative temperature response function, also referring to the supplementary information, and in section 3.2.1 (page 281) more about the temperature response is shown. I would suggest to move large parts of section 2.3.2 to section 3.2.1 so the paper is better structured.

In the originally submitted manuscript this structure was as the reviewer suggests. On personal request of the handling editor (20-06-2014), we changed the structure to the current version. We would only make this change again with the specific consent of the handling editor.

REFEREE:

Page 283, line 20-22. Figure S3, the authors state that the soil moisture patterns are captured reasonably well compared to observations, but I see quite a distinct difference in the years 2000 and 2005-2008, with the model showing much more dynamics than the data. 2003, on the other hand, is captured much better where the data show much more rewetting in the beginning and the end of the year, which the model also simulates for the other years. However, the data don't follow this rewetting patterns. Could the authors please comment?

AUTHORS:

We thank the reviewer for pointing this out to us, and would like to clarify a bit more. The model's soil hydrology is a very simple, two-layer bucket model. Therefore, the description of soil moisture to a depth up to 1.5 m, is captured with only two layers. Our observation data (Section 2.1.3) are measured at 5 different depths. So, for the comparison of the modelled soil moisture to our measurements we averaged the data corresponding with the depths the first model soil layer (I_1 , 0–50 cm) and the second soil layer (I_2 , 50–150 cm). We agree that this is important information that should be included in the manuscript, and added it to the text, at line 21.

With this information in mind, we still think the model performed reasonable well in capturing the seasonal dynamics. The model, especially upper layer (I_1), shows more dynamics than the observation data because 1) it responds quickly and strongly to plant water uptake as most modelled roots are located in the upper soil layer (Table 1), and 2) it quickly and strongly responds to precipitation and soil evaporation (description in Supplement, Section 1, and Sitch et al. (2003)). The second soil layer (I_2), receives moisture through percolation and loses water through plant water uptake, but the changes in water contact are less strong than for the upper layer.

The data, on the other hand, are averaged to meet the modelled depth, and show less dynamics because there is not such a strong and direct link to water uptake in the top layer, especially because the soil is very sandy and water percolates to lower layers easily.

The last point the reviewer makes here is that the data do not show the rewetting patterns of the model. This is partly caused by the modelled winter temperature response of photosynthesis, where the model assumes a shutdown of photosynthesis and underestimates GPP and AET. When we look at Fig. 3, these are also the years where AET is underestimated by the model the most. The data do not show rewetting because vegetation is still actively assimilating and retracting water from the soil (in particular the understory remains active during mild winters), whereas the model keeps all the water in the soil as plants are not retracting much water from the soil.

REFeree:

Page 284, line 1-5. In figure 8, modeled transpiration versus observed sap flow is shown. In the text, the authors stress the good correlation in these figures. However, I would like to ask them to comment on the difference between S1 and S2-S3. The latter two have much less modeled transpiration (ranging from 0-1.5) than the observed sapflow (ranging from 0-3). However, S1 has a similar range in modeled and observed transpiration (except for 2009, where sapflow had a smaller range, up to 1.5 rather than 3 mm/day as in the other years). In the manuscript, the authors indicate the conservative water uptake by S3 (as is also shown in figure S1). Could they explain why we also see a smaller range in simulated values for transpiration for S2? Also, S2 indeed increases the r (table 3), but increases the RMSE at the same time.. How do these changes affect figure 2?

AUTHORS:

We would like to thank the reviewer for this keen observation. Unfortunately, we confused the reader by making a typing error in line 4-5. setups 'S1 and S2', should be replaced with 'S2 and S3'. This is now corrected in the text.

Furthermore, we find the reviewer's observation on the differences in range of modelled transpiration between setups S1 and S2-S3 very sharp and helpful, so we have added this information to the text on page 284, line 3:

“(Fig. 8, $r = 0.68-0.74$). For setup S2 and S3, the range of modelled plant transpiration is lower than the observed plant transpiration ($0-1.5 \text{ mm day}^{-1}$ and $0-3 \text{ mm day}^{-1}$ respectively). For setup S1, the range of modelled plant transpiration matches that of the observations for 1997 and 1998 ($0-3 \text{ mm day}^{-1}$). This relates directly to the shape of the response curve for each setup (Supplement, Fig. S1), where S2 and S3 reduce the water supply S more strongly than S1 in response to declining soil water. Correlations for individual years are lowest for 1997, especially for setups S2 and S3, where modelled transpiration...”

We would also like to address the reviewer's comment that for 2009, the observed data range is lower ($0-2 \text{ mm/day}$). Our site PI (J. Elbers, jan.elbers@wur.nl) acknowledges that since the installation of the new sap flow measurement system (data for 2009, Granier thermal dissipation probes on 6 trees, see section 2.1.3) all sap flow measurements have been slightly lower than those measured with the previous system (data for 1997 and 1998, tissue heat balance systems on 3 trees). There are several reasons why the new data read slightly lower than the old ones: the systems have different measurement uncertainties, and the spread in the older data may be larger because it was measured on fewer trees. Furthermore, the conversion method to calculate sap flow speed (meters s^{-1}) to tree transpiration (mm/day) is based, a.o., on the density and height of the trees which may cause additional errors. For sake of readability of the manuscript, we prefer not to include all this information in the results section of the paper.

Finally, we would like address the reviewer's last comment regarding the correlations and RMSE. For model setup S2, r only increases for GPP (Table 3), and not for AET. RMSE for AET actually decreases on the monthly and daily time scale. The reviewer asks how this would affect Fig. 2, and we would like to refer them to the bottom panel of Fig. S2 in the Supplement. This shows the effect of setup S1-S3 on the residuals of AET. At low soil water content, S2 and S3 underestimate AET much stronger than S1. A representation of these data, similar to Fig. 2, would therefore show more skewedness and a larger deviation from the 1:1 line.

REFeree:

Page 284, line 19-21: and to a lesser extend S2?

AUTHORS:

Yes, but only for the lower soil layer. We added this to line 21.

REFeree:

Page 288, line 25-26: Could the authors explain further? Because of drainage below the rootzone? Water that is not intercepted will enter the soil, correct? And then be available for AET? Unless it is drained?

AUTHORS:

Yes, we can explain this. Modelled AET is calculated as the sum of plant transpiration, soil evaporation and canopy evaporation. So yes, water that is not intercepted will enter the soil and be available for soil evaporation and plant transpiration. During winter, when the model simulates little or no photosynthetic activity because temperatures are low, simulated plant transpiration will also be low. Therefore, by not handling shower intensity explicitly, the model further underestimates interception evaporation which contributes to the underestimation of modelled AET. To clarify this issue, we changed the introduction of the paragraph (page 288, lines 17-18):

“Simulated AET is calculated as the sum of plant transpiration, soil evaporation and canopy evaporation. Underestimation of canopy evaporation, or interception loss, in relation to..”

REFEREE:

Page 289, line 26: the onset of drought, rather than drought? In figure S3, the 2003 drought seems to be captured well in general..

AUTHORS:

The reviewer is correct here that in Figure S3 the onset of drought is captured well in terms of soil moisture. In this paragraph, however, we meant the response in terms of simulated GPP and AET. To clarify, we changed the text into:

“However, none of the uptake parameterizations capture the observed response in terms of GPP and AET to a drought such as occurred in the summer of 2003 (Fig. 10).”

Technical corrections:

Finally, some minor grammatical and style suggestions:

REFEREE:

Page 272, line 21-22: Reichstein instead of Re-ichstein

AUTHORS:

Changed according to reviewer's suggestion.

REFEREE:

Page 275, line 6: change into ‘The scalar c_1 is ...’ and remove c_1 from the end of the sentence?

AUTHORS:

We apologise for the confusion, as we meant t_{scalar} here, and not c_1 . We clarified by rewriting the sentence to:

“The inhibition function t_{scalar} is used for...”

REFEREE:

Page 275, line 17: change) to be after V_m instead of after temperature

Page 275, line 21: add comma after kinetics

Page 278, line 13: change into: ‘than, but in a similar range as, observed..’

AUTHORS:

All these points were changed according to the reviewer's suggestion

REFEREE:

Page 280, line 24: add (2.4 and 1.6 respectively) after observed

We agree with the reviewer that this information should be added, but the value 1.6 the (s)he suggests here is incorrect, and should be 1.0 (please refer to Table 2). We therefore wrote (2.4 and 1.0 respectively) after observed.

REFEREE:

Page 284, line 6: add (S2) after ‘species specific uptake’

Page 284, line 7: add (table 3) after ‘coefficient’

Figure 6: add ‘winter’ in the beginning of caption, rather than at the end

AUTHORS:

All these points were changed according to the reviewer's suggestion

REFEREE:

Figure 9: add 2003 and 2005 in the figure itself (e.g. above the different figures, 2003 on the left and 2005 on the right)

AUTHORS:

Thank you, we agree this makes the figure more clear. We added the corresponding years to the top left of each subpanel.

AUTHOR corrections

We found some additional mistakes and inconsistencies while working on the revisions of this manuscript. The proposed changes are:

Page 275, line 9: replaced the period with a colon after (Haxeltine and Prentice, 1996)

Page 276, line 1: changed 'the supply of water' to 'water supply'

Page 277, line 2: added) after Haxeltine and Prentice, 1996b

Page 279, line 9: replaced 'Sylverstris' with 'sylvestris'

Page 279, line 22: replaced 'Sylverstris' with 'sylvestris'

Page 279, line 24: replaced 'Sylverstris' with 'sylvestris'

Page 283, line 22: changed 'observation' to 'observations'

Page 288, line 21: 'Elbers et al. 2010' instead of 'Elbers et al. 201'

Page 297, line 11: replaced 'Sylvestris' with 'sylvestris'

Page 298, line 25: replaced 'The' with 'the'

Page 298, line 26: replaced first author 'E.' with "E.J." (EndNote sorting algorithm)

Page 302, line 1-3: updated reference for Wolkovich *et al.* (2012)

Caption Fig. 8: added 'for' before 1997.

Figs. 2, 3, 4, 5, 6, 7, 8, 10: For consistency with the text and figure captions, we changed all units in these figures, using superscript instead of ' / '. For example, AET in 'mm day⁻¹' instead of mm/day.



Modelling short-term variability in carbon and water exchange in a temperate Scots pine forest

M. H. Vermeulen et al.

Modelling short-term variability in carbon and water exchange in a temperate Scots pine forest

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Abstract

Vegetation – atmosphere carbon and water exchange at one particular site can strongly vary from year to year, and understanding this interannual variability in carbon and water exchange (IAV_{cw}) is a critical factor in projecting future ecosystem changes.

5 However, the mechanisms driving this IAV_{cw} are not well understood. We used data on carbon and water fluxes from a multi-year Eddy Covariance study (1997–2009) in a Dutch Scots pine forest and forced a process-based ecosystem model (LPJ-GUESS) with local data to, firstly, test whether the model can explain IAV_{cw} and seasonal carbon and water exchange from direct environmental factors only. Initial model runs showed

10 low correlations with estimated annual gross primary productivity (GPP) and annual actual evapotranspiration (AET), while monthly and daily fluxes showed high correlations. The model underestimated GPP and AET during winter and drought events. Secondly, we adapted the temperature inhibition function of photosynthesis to account for the observation that at this particular site, trees continue to assimilate at very low

15 atmospheric temperatures (up to daily averages of -10°C), resulting in a net carbon sink in winter. While we were able to improve daily and monthly simulations during winter by lowering the modelled minimum temperature threshold for photosynthesis, this did not increase explained IAV_{cw} at the site. Thirdly, we implemented three alternative hypotheses concerning water uptake by plants in order to test which one best corresponds with the data. In particular, we analyse the effects during the 2003 heat-

20 wave. These simulations revealed a strong sensitivity of the modelled fluxes during dry and warm conditions, but no single formulation was consistently superior in reproducing the data for all time scales and the overall model-data match for IAV_{cw} could not be improved. Most probably access to deep soil water leads to higher AET and GPP simulated during the heat wave of 2003. We conclude that photosynthesis at lower

25 temperatures than assumed in most models can be important for winter carbon and water fluxes in pine forests. Furthermore, details of the model representations of wa-

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ter uptake, which are often overlooked, need further attention, and deep water access should be treated explicitly.

1 Introduction

Carbon and water fluxes at one particular site can strongly vary from year-to-year (e.g. Goulden et al., 1996; Yamamoto et al., 1999; Baldocchi et al., 2001). This interannual variability in net ecosystem exchange (NEE) and actual evapotranspiration (AET) is observed across different geographical regions and ecosystem types, and understanding interannual variability in carbon and water fluxes (IAV_{cw}) is crucial for projections of future ecosystem changes and feedbacks on climate. However, little is known about the processes determining this year-to-year variation. Numerous studies have tried to relate IAV_{cw} to climatic variables and local ecosystem responses to droughts, fires or deforestation (e.g. Goulden et al., 1996; Yamamoto et al., 1999; Aubinet et al., 2002; Hui et al., 2003; Williams et al., 2008; Sierra et al., 2009; Weber et al., 2009; Yuan et al., 2009), but no clear picture has yet emerged.

Process-based biogeochemical and vegetation models capture the response of terrestrial ecosystems to mean climatic drivers reasonably well at diurnal and seasonal time scales, but not at yearly and longer time scales (Keenan et al., 2012). At the global scale, some vegetation models reproduce interannual variability in terrestrial net primary production and atmospheric CO_2 growth rates well (Peylin et al., 2005; Ahlström et al., 2012; Sitch et al., 2013), but large uncertainty exists at smaller spatial scales. Only few studies have quantified the extent to which these models can reproduce observed IAV_{cw} at the regional and site scale (Peylin et al., 2005; Keenan et al., 2012). Despite the uncertainties, such models are widely used to project future changes in vegetation and ecosystem functioning. Some of these model simulations suggest the potential for severe vegetation changes across major global biomes in the future: for example Amazon forest die-back/greening, as well as substantial shifts in potential natural vegetation distributions for boreal and Mediterranean forests (e.g. Lenton et al., 2008;

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Rammig et al., 2010; Hickler et al., 2012), and alternative vegetation states under elevated atmospheric CO₂ (e.g. Higgins and Scheiter, 2012). Such vegetation changes would also feed back on regional and global climate (e.g. Cox et al., 2000; Naeem, 2002; Sitch et al., 2003; van den Hurk et al., 2003; Arora and Boer, 2005; Bonan, 2008; Pitman et al., 2009; Wramneby et al., 2010), and can affect the long-term terrestrial carbon balance profoundly. Therefore it is crucial that these models accurately reproduce IAV_{cw} across all spatial scales.

To provide insight in the climate change impacts on the terrestrial carbon balance in the long term, both short- and long-term vegetation responses to a constantly changing environment should be better understood and represented. This implies better model representations of short-term processes such as the mechanisms governing vegetation phenology (Cleland et al., 2007; Kramer and Hänninen, 2009; Wolkovich et al., 2012), dynamic carbon and nutrient allocation (Litton et al., 2007; Epron et al., 2012; Franklin et al., 2012), photosynthetic temperature acclimation (Gea-Izquierdo et al., 2010), as well as better representing long-term processes such as soil, nutrient and carbon dynamics. ~~Before addressing these process representations, however, it should be established that IAV_{cw} cannot be explained by more direct environmental responses such as to drought, temperature and radiation. Factorial experiments with a dynamic vegetation model can be used to generate hypotheses concerning the main drivers of IAV_{cw} (e.g. Hickler et al., 2005), whereby vegetation models capture at least some of the complexity of real ecosystems. In this study, we used~~ a long time series of Eddy Covariance measurements at a well-researched forest site (Loobos, a Scots pine forest on sandy soils in the Netherlands) and a DGVM (LPJ-GUESS; Smith et al., 2001) parameterized for the site. The observed interannual variability in NEE at Loobos is comparable to that found at sites with similar vegetation composition and climate (Carrara et al., 2003), but this interannual variability cannot be explained directly from climate variables (Jacobs et al., 2009; Kruijt et al., 2009). Previous analyses suggest that temperature is an important driver of ecosystem respiration at this site, and the remaining variation can be related to local extremes, such as drought, storm damage, and snow-

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fall in winter (Moors et al., 2014). Luyssaert et al. (2007) thoroughly analysed observational Loobos data and proposed that photosynthesis variability is the main driver of interannual variability in NEE, suggesting that short-term ecophysiological responses play an important role.

In this study, we first tested whether LPJ-GUESS can reproduce the observed IAV_{cw} and seasonal carbon and water exchange at the Loobos site from direct environmental factors only. LPJ-GUESS combines detailed vegetation demographics and dynamics, with mechanistic representations of short-term plant physiological processes. This combination makes the model a good platform to study IAV_{cw} , because we can simultaneously study the effects of environmental and ecosystem drivers on modelled IAV_{cw} . Secondly, we tested whether using alternative model formulations and parameters can explain model error for this single site. We performed these secondary tests, because in the first test we observed systematic biases during winter periods and drought events. Therefore, we analysed the photosynthesis response to temperature during winter periods, and we analysed the response to drought events by comparing alternative plant water uptake parameterizations.

2 Methods

2.1 Study site and observation datasets

2.1.1 Study site

Loobos (coord: 52°10'04" N, 05°44'38" E) is a planted Scots pine forest that is approximately 100 years old and located in bare sandy soil at the Veluwe forest in central Netherlands. The dominant tree species is *Pinus sylvestris* and understory vegetation consists mostly of the grass *Deschampsia flexuosa* and mosses. *Vaccinium myrtillus* and various species of lichen make up the remaining understory vegetation, and the site "suffers" from encroachment of *Prunus serotina*. The landscape consists of veg-

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etated sand dunes that create a bumpy topography with elevations varying several meters and the local groundwater levels are strongly influenced by this local topography (Moors, 2012). The average tree height is approximately 17 m, and tree density is 478 ha^{-1} . For more information on the site, and a complete overview of its measurement instrumentation and description, see <http://climatexchange.nl/sites/loobos/>, Dolman et al. (2002), Schelhaas et al. (2004) and Elbers et al. (2011).

2.1.2 Eddy covariance data

Eddy covariance (EC) and meteorological measurements have been continuously collected at this site since 1995 and these data are part of the FLUXNET database (Baldocchi et al., 2001). EC instrumentation is positioned on a mast extending 3 m above a 23 m scaffolding tower. In addition to EC and meteorological measurements, CO_2 -concentrations are measured at five levels in the canopy: 24.4, 7.5, 5.0, 2.5 and 0.4 m above ground. The tower footprint stretches to several hundred meters, while the forest extends for more than 1.5 km in all directions from this point. EC data are processed to half-hourly corrected fluxes with the instrumentation and method described in Elbers et al. (2011). These data are quality checked, flagged and, if necessary, gap filled and split up in gross primary productivity (GPP) and ecosystem respiration (R_{eco}), using the online EC gap-filling and flux partitioning tool at <http://www.bgc-jena.mpg.de/~MDIwork/eddyproc/> (7 April 2014). We used this gap-filled dataset to calculate all EC and meteorological variables on a daily time step. Flux partitioning of measured Net Ecosystem Exchange (NEE) to estimate GPP follows Reichstein et al. (2005), i.e., $\text{GPP} = R_{\text{eco}} - \text{NEE}$. Since our dataset follows the standard FLUXNET database format, R_{eco} and GPP are both positive quantities whereas negative NEE represents a net carbon uptake by the vegetation. As a result, GPP estimates can have a negative sign in this dataset and represent a net carbon loss of the vegetation. By definition, negative GPP cannot occur in a biological sense, but negative GPP values were not omitted from the dataset to preserve original scatter.

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2.1.3 Additional site data

Sap flow measurements on *Pinus sylvestris* are available for 1997 and 1998 using tissue heat balance systems (details in Moors et al., 2012), and for 2009 using Granier thermal dissipation probes. Soil moisture data are available for all years, and measured with frequency domain sensors at 5 different depths: 0.03, 0.10, 0.25, 0.75 and 2.0 m. In 2005 all sensors were replaced and positioned at different depths: litter, 0.03, 0.20, 0.50 and 1.0 m. For comparison with model data, available soil moisture (excluding the litter sensor) was averaged for an upper soil layer (0–50 cm), and a lower layer (50–150 cm). Additional site measurements at less frequent intervals include the leaf area index (LAI) of trees and, to a lesser extent, the understory.

2.2 Model description

LPJ-GUESS (Smith et al., 2001) is a flexible, modular modelling platform to simulate vegetation dynamics and biogeochemical cycles from local to global scales. It combines mechanistic representations of physiological and biogeochemical processes from LPJ-DGVM (Sitch et al., 2003), with the more detailed descriptions of vegetation dynamics and vegetation structure of forest gap models. The model version used in this study includes an improved hydrological scheme (Gerten et al., 2004) and an adaptation for European vegetation which is mainly based on main tree species rather than plant functional types (PFTs) (Hickler et al., 2012). Vegetation growth is simulated on patches of 1000 m², where neighbouring individuals compete for space, light and water. On a patch, each tree individual is simulated, but individuals of the same cohort (age class) are identical. Several replicate patches (here 100) are calculated to characterise vegetation over a larger area and account for stochastic processes (establishment, mortality and disturbance events). The model is driven by daily values of temperature, precipitation and radiation, and information on atmospheric CO₂-concentrations and soil texture. The daily calculations of carbon and water fluxes between vegetation and atmosphere are mechanistically simulated in one “canopy exchange” module.

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2.2.1 Photosynthesis calculation

Photosynthesis – with distinction between C_3 and C_4 plants – is based on the original scheme proposed by Farquhar, as simplified by Collatz et al. (1991, 1992), and adapted from the BIOME3 model (Haxeltine and Prentice, 1996b; Haxeltine and Prentice, 1996a). Daily gross and net leaf-level daytime photosynthesis are calculated as a function of atmospheric CO_2 concentrations, air temperature, photosynthetically active radiation (PAR), day length, and canopy conductance. APAR, the fraction of absorbed PAR captured by the vegetation, is calculated from the leaf area index with Beer's law. Leaf respiration linearly scales with Rubisco enzyme capacity. In the absence of water stress, photosynthesis is limited by two main processes that co-vary: the response of photosynthesis to APAR (J_e), and the limitation of photosynthesis by Rubisco enzyme activity and CO_2 (J_c). The rate of carbon assimilation linearly scales with APAR until maximum Rubisco activity is reached. Maximum Rubisco activity is calculated daily under the assumption that sufficient leaf nitrogen is available at the point that the marginal cost by respiration of enhanced carbon gain is zero. This leads to Rubisco activity itself also being proportional to daily APAR (the optimality hypothesis, Haxeltine and Prentice, 1996a). Two environmental stressors that can directly affect modelled daily photosynthesis are temperature and water availability. These are discussed in more detail below.

2.2.2 Temperature dependence of photosynthesis

The parameters governing maximum carboxylation capacity (V_m), as well as parameters describing saturation of Rubisco, oxygen consumption and photorespiration, follow enzyme kinetics and are thus temperature dependent. In addition, when water is not limiting, photosynthesis is made temperature dependent through a temperature scalar

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2.2.3 Photosynthesis under water stress

Plants experience water stress when the supply of water (S) is smaller than the demand (D). Supply is proportional to the available soil moisture in the rooting zone (w_r) and the maximum possible transpiration rate under well watered conditions (E_{\max} ; 5 mm day⁻¹ following Haxeltine and Prentice, 1996b):

$$S = E_{\max} \times w_r \tag{4}$$

The demand is simulated with an empirically calibrated hyperbolic function of non-water stressed canopy conductance and the equilibrium transpiration (Huntingford and Monteith, 1998; Gerten et al., 2004). If the water supply is lower than the demand, canopy conductance is reduced until evapotranspiration (transpiration and evaporation from the canopy and the soil) equals the demand. This limits CO₂ diffusion into the leaves, expressed in a reduction of the ratio of internal to atmospheric CO₂-concentration, c_i/c_a . A lower c_i/c_a ratio leads to a reduction of photosynthesis.

2.2.4 Plant water uptake parameterizations

The soil hydrology is represented by a simple bucket model with two layers. The upper layer (l_1) is 50 cm deep, and the lowest layer (l_2) is 100 cm deep. Available soil moisture w_r is the ratio between current soil water content and plant-available water capacity. The latter is dependent on soil type and texture (Sitch et al., 2003). The model offers the following three methods to calculate available soil moisture in the rooting zone (Supplement, Fig. S1): Method 1: w_r is independent of soil water content until wilting point ($w_{r, \text{rootdist}}$). This is the current standard used in most studies with LPJ-GUESS (T. Hickler, personal communication, 2013), Method 2: w_r is influenced by a species specific drought tolerance value (Table 1). In response to declining soil water, drought-tolerant species reduce transpiration less than drought-sensitive species, and therefore have greater relative uptake rates ($w_{r, \text{species specific}}$; see Schurgers et al. (2009) for an application of LPJ-GUESS using this formulation), and Method 3: w_r declines linearly

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as a function of soil water content ($w_{r_{wcont}}$, which is used in most studies with LPJ-DGVM (description in Haxeltine and Prentice, 1996b)). A more detailed description of each method with equations is provided in the Supplement.

2.3 Modelling setups

2.3.1 Default modelling setup

As a driver, we used the site-specific meteorological dataset of daily averages from 1997 to 2009, and this dataset was repeated consecutively during the model run. To simulate the establishment of a Scots pine forest on a bare sand soil, we ran the model for 105 years (as a “spin up” period), so that the simulated forest would have a stand age and soil carbon pools comparable to our study site. Only the two PFTs representing *Pinus sylvestris* and herbaceous vegetation with C_3 photosynthesis (to represent the understory) were allowed to establish. Since *Prunus serotina* encroachment is relative recent and actively suppressed, we did not include this PFT in the model. Furthermore, the site has not been disturbed by fire since its establishment so we also did not include fire disturbance in the model. Finally, we used the averaged results of 100 replicate patches to account for any stochastic effects on vegetation establishment. All PFT-specific parameters for this study were taken from Hickler et al. (2012), except for two parameters (Table 1, bold values). Maximum coldest month temperature for PFT establishment ($T_{c,max_{est}}$) was set to limitless for *P. sylvestris*, to ensure establishment of these planted trees at the temperate climate of Loobos. Specific leaf area (*sla*) for *P. sylvestris* was set to a site-specific value based on measurements (Table 1). For comparison of modelled carbon and water fluxes to EC data, modelled daily GPP, NEE, R_{eco} , plant transpiration, soil evaporation and canopy interception are available. Modelled AET was calculated as the sum of plant transpiration plus evaporation from the soil and canopy. Water uptake was set to the default used in previous studies with this model: $w_{r_{rootdist}}$.

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2.3.2 Alternative temperature response function

Based on the results of the default model run (Sect. 3.1), we decided to decrease the lower temperature limit ($p_{\text{temp}_{\text{min}}}$, Eqs. 1 and 2) for Scots pine to allow photosynthesis on frost days. To compare our findings with existing data, and to determine a suitable lower temperature threshold for photosynthesis of mature Scots pine forests at temperate sites, we identified a limited number of previous studies relevant to the situation at Loobos. For example, James et al. (1994) measured photosynthesis and growth of Scots pine along a latitudinal gradient in Scotland, and found that valley trees displayed higher photosynthesis rates in winter compared to those growing at higher latitudes. Teskey et al. (1994) report net photosynthesis in winter when there are no severe frosts and the soil is not frozen. Linder and Troeng (1980) report minimum atmospheric temperatures of -7°C for net photosynthesis for *P. sylvestris* in southern Sweden, which is slightly higher than but in a similar range as that observed at our study site Loobos. Sevanto et al. (2006) show net uptake of carbon for many freezing days during the winter of 2002/03, and positive uptake in all previous 7 years except during January in southern Finland. At Brasschaat, a slightly younger (compared to Loobos) temperate mixed-deciduous-coniferous forest in Belgium, net carbon uptake was observed only in the winter of 2001 (Carrara et al., 2003). At this site, however, not all trees are evergreen so winter LAI is lower compared to our study site.

In addition to the literature review, we analysed several types of available observation data in three different ways to determine a suitable lower temperature threshold. Analysis 1: we selected days from the EC dataset between late November and late February, with average daily temperatures below 0°C ($n = 226$). In order to see the effect of temperature on observed GPP and AET, days with low radiation were excluded: total net shortwave radiation received $> 2 \text{ MJ day}^{-1}$, which is an average of about 75 W m^{-2} for a winter day with 6 h of daylight. For days that met these criteria ($n = 175$), modelled and observed data were binned to temperature classes of 2° ranging from ≤ -10 to 0°C ; Analysis 2: from a different study (Abreu, 2012), we included a fitted temperature

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response curve for maximum GPP (indicated as GPP_{1000}). Abreu calculated GPP_{1000} following Jacobs et al. (2007), using half-hourly EC data between 1997 and 2011. Due to the large number of data points needed to calculate GPP_{1000} , these results are only available for 5° temperature bins between -5 and 35 °C; Analysis 3: a two-day measurement campaign with a portable ADC-LCpro (ADC BioScientific, Hoddesdon, UK) was carried out at the study site in 2012 to measure leaf photosynthesis on days with temperatures below 0 °C (description and results in Supplement).

Based on the outcome of the literature review and observation data analysis, this model experiment uses a lower threshold for *P. sylvestris* photosynthesis ($p_{temp_{min}}$) of -10 °C. Other than this lower threshold, this model setup does not differ from the default model setup.

2.3.3 Alternative plant water uptake parameterizations

In this setup, PFT-specific parameter values remained unchanged compared to the default setup, but we ran the model for all three available water uptake parameterizations (Sect. 2.2.3): (1) the default run (S1), using the standard “ $w_{rootdist}$ ” uptake, (2) a species specific water uptake run (S2), and (3) a linear uptake run (S3). Figure S1 shows the different water uptake response curves for *P. sylvestris* and C_3 grasses. Response curves differ between species as a result of PFT-specific root distributions ($root_{distr}$, Table 1): C_3 grass has 90 % of its roots prescribed in the upper soil layer (0–50 cm), and 10 % in the lowest layer (50–150 cm), for *P. sylvestris* this is 60 and 40 %, respectively. In the case of species specific water uptake, the response curves also differ because grass and *P. sylvestris* have different assumed drought tolerance ($drought_{tol}$, Table 1). Species specific water uptake is represented with response curves S2a and b, with C_3 grass having larger relative uptake rates than *P. sylvestris* under declining soil water content. Linear decline of supply with decreasing soil water results in similar uptake rates for both PFTs since modelled water uptake is independent of root distribution in this parameterization (Supplement, Fig. S1, response curve S3).

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As a control, we include one additional model run (S4) using the standard water uptake method ($w_{r_{\text{rootdist}}}$), but eliminated plant water stress by fixing w_r to 1.0 so that supply is always equal to E_{max} (Eq. 4). Model results of setups S1–S4 were investigated in more detail for the summer period to determine the effect of a heat wave and corresponding drought on the observed and modelled carbon and water fluxes.

2.4 Statistical tests

To test how well the model is predicting the observed values of GPP and AET, we applied a linear regression through the origin as well as Pearson correlation tests. If the slope of the linear regression were equal to unity, our model would match the observed data with no systematic bias. Statistically significant differences from 1.0 in the regression slope were determined by a two-sided t test at a threshold of $P = 0.05$. The root mean squared error (RMSE) between model and data was calculated as a measure of prediction accuracy, i.e., “goodness-of-fit”. Additionally, a two-sided paired Wilcoxon ranking test was performed to determine if observed and modelled samples follow similar distributions. Only when P values of this test are larger than 0.05, we accept that the model produces a data distribution that is similar to the data distribution of the observations.

3 Results

3.1 Default modelling setup

The general site characteristics of Loobos are well represented by the default modelling setup (S1, Table 2): modelled LAI for Scots pine is 1.5, declining to 1.4 between 1997 and 2009. This LAI is just below the observed site average of 1.62 between 1997 and 2009 (minimum 1.44 in 2007, maximum 1.78 in 2009). Modelled LAI for C_3 grasses is higher than observed, but few measurements of understory grass LAI were available for

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validation and none for mosses. Modelled aboveground biomass estimates are close to available observations.

Figure 2 shows the interannual and monthly variability in GPP and AET. Table 3 summarizes the goodness-of-fit-values for GPP and AET. The model shows good correlations on daily and monthly time scales (Fig. 2c and d). Monthly correlations are significant (0.92 for GPP, and 0.87 for AET), indicating that the model is accurately capturing the seasonal pattern of both fluxes. This is also visible in Fig. 3a and b. In contrast, we find poor correlations on the annual time scale: annual totals for GPP and AET are of the same order of magnitude as observed values, but the observed IAV_{cw} is not captured well by the model for water nor for carbon (Fig. 2a and b). The modelled data distribution is similar to observations (Table 3, bold values), but correlation coefficients are low and not significant (0.22 and 0.20 for GPP and AET, respectively).

The monthly scatterplots (Fig. 2c and d) display systematic model biases during certain periods. Fluxes are underestimated in winter, overestimated in spring/early summer and slightly underestimated in fall (Fig. 2c and d). In summer (mainly in August and July), large deviations from the 1 : 1 line can be seen, which we could directly relate to periods with high atmospheric temperatures and low precipitation. Figure 3 shows these deviations per month in more detail.

3.2 Alternative temperature response function

3.2.1 Observed temperature response

According to the EC data, the vegetation at Loobos is able to keep assimilating carbon even at temperatures below 0°C (Fig. 4). In the fitted response curve of half-hourly EC fluxes, maximum GPP for the lowest temperature class (−5 to 0°C, Fig. 4a) is 1.8 μmol m^{−2} s^{−1}, which corresponds to 1.87 g C m^{−2} day^{−1}. Figure 4b shows temperature-binned daily GPP on sunny days, and the response to temperatures below −10°C. The lower temperature limit in our observation data, i.e., where average GPP approaches 0, is found when temperatures are below −8°C. Note that the num-

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simulation period. However, the Wilcoxon ranking test shows that for GPP the modelled data distribution is now matching the observed data distribution at monthly time scales more closely ($P < 0.05$). In addition, when data of only the winter months are included (Fig. 6), the slope of the regression substantially improves for GPP from 0.32 to 0.58, while keeping a similar correlation coefficient (0.80 vs. 0.78). This indicates a better match between modelled and observed results. By changing the temperature response, simulation of IAV_{cw} does not improve for the carbon fluxes, and only marginally for the water fluxes (Table 3).

3.3 Alternative plant water uptake parameterizations

Figure 7 shows modelled carbon and water fluxes on a monthly time scale for the three different water uptake parameterizations (S1–S3) and the control model setup without soil moisture stress (S4). All three uptake parameterizations appear to be equally strong in simulating the seasonal trend with correlations from 0.92–0.94 for GPP and 0.86–0.88 for AET (r , Table 3). During summer, the linear uptake response curve (S3) underestimates both AET and GPP more often than the species specific (S2) and default uptake (S1) parameterizations. Eliminating water stress (model setup S4), results in overestimation of fluxes during summer, increased error and lower RMSE. Moreover, using this setup both AET and GPP are overestimated in spring and summer for all years (Fig. 7a), indicating that water limitation does play an important role in Loobos.

Given the model's very simple two-layer soil hydrology (Sect. 2.2.4), seasonal soil moisture patterns are captured reasonably well between the different model setups when compared to observation (Supplement, Fig. S3). Modelled soil moisture in the upper soil layer changes more rapidly than observations suggest, and modelled moisture recharge in winter increases to higher values than observed for some years. Soil moisture measurements, however, were not always available during winter and completely absent from fall 2000 until summer 2002. Because plants are taking up water more conservatively in setup S3, modelled soil moisture is higher during the growing season for all years compared to the other two setups, and the bucket never com-

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pletely empties as is often the case for the other two setups. Available sap flow data for *P. sylvestris* (1997, 1998 and 2009) show good correlations with modelled transpiration (Fig. 8, $r = 0.68\text{--}0.74$). Correlations for individual years are lowest for 1997, especially for setups S1 and S2, where modelled transpiration is reduced too strongly in response to declining modelled soil water between day 100 and 300 (Supplement, Fig. S3).

On the annual time scale, species specific uptake leads to the best explanation of interannual variability in GPP in terms of correlation coefficient, while for AET there is a small decrease compared to the default setup. Using the model setup in which soil water is not a limiting factor (S4), the model also cannot accurately capture interannual variability in GPP and AET.

Comparing water uptake parameterizations during a dry and wet summer

The summers of 2003 and 2005 were very different, with the 2003 heat wave over Europe affecting both managed and natural vegetation systems but each ecosystem showing different responses to the extreme heat (e.g. see Granier et al., 2007; van der Werf et al., 2007; Teuling et al., 2010). The 2003 heatwave affected the Netherlands (KNMI, 2003) especially in August, which in combination with a prolonged period of low precipitation resulted in a drought. We compare the results of the extremely sunny, warm and dry August 2003 to those of August 2005, which was a regular but very wet month. Observed soil moisture at Loobos declined considerably during the 2003 heatwave, and modelled soil water runs out earlier than observations suggest (Fig. 9, for 2003), with the exception of setup S3. For 2005, modelled soil moisture is often too low when using the default setup (S1), and water content of the upper layer changes more rapidly than observations suggest.

When comparing daily carbon and water fluxes to observations (Fig. 10) during the wet period (2005), all uptake parameterizations perform well compared to observed data, with no striking differences between uptake parameterizations in simulating GPP and AET. During the 2003 heatwave and drought however, the parameterizations show different responses. During the first half of the heatwave period (indicated by the two

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vertical dotted black lines in Fig. 10), there is a gradual decline in observed daily GPP and AET at the site. Given the considerable drop in observed soil water during the heat-wave (Fig. 9), reductions in observed GPP and AET look considerably more gradual (Fig. 10). This suggests a possible access of the vegetation to water from deeper layers, or groundwater. The no-water stress control run (S4) clearly demonstrates there is some water stress at Loobos (both observed GPP and AET are lower than the model predicts), but all parameterizations fail to simulate the correct response. The default and species specific response curves (S1 and S2), allow PFTs to take up relatively more water at low soil water contents compared to the linear uptake parameterization, thereby not restricting photosynthesis as long as water remains available for uptake. We can observe this effect during the heatwave period, where the linear uptake function (S3) least underestimates GPP and AET, because there is more water available for uptake due to conservative water use, and the effects on the modelled supply are less strong at lower soil water contents (Figs. S1 and S2). The real observed response of the Loobos vegetation, however, is not reproduced using either uptake parameterization. The sensitivity of GPP and AET to declining soil moisture during the growing season is visible in Fig. S2 by plotting the residuals (modelled–observed values, so that an underestimation is depicted with a negative sign) against modelled available soil moisture (Θ). In general, the linear uptake parameterization seems to underestimate both GPP and AET more at higher soil moisture values, so with regard to the observations, this response curve imposes water stress on plants at this site too strongly.

A comparison of the three different plant water uptake response curves does not lead to identification of any setup that is clearly superior for simulating IAV_{cw} to the others (Table 3). Species specific uptake (S2) results in the smallest errors (RMSE, Table 3) on monthly and daily time scale, but on annual time scale the default uptake (S1) has the smallest error.

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4 Discussion

4.1 Default modelling setup

The model reproduced the daily and monthly carbon and water fluxes equally well as shown in previous studies with LPJ-GUESS (Sitch et al., 2003; Gerten et al., 2004; Morales et al., 2005; Zaehle et al., 2005; Hickler et al., 2006). Fatichi and Ivanov (2014), using a different process-based vegetation model, similarly found very high correlations on daily and low correlations on annual time scales for GPP and evapotranspiration. However, good correlations on shorter time scales can be expected, given the strong diurnal and seasonal cycles to climatic drivers (mainly radiation and temperature). While the model produces reasonable flux estimates at daily and monthly time scales, the small deviations on these time scales lead to poor estimates of IAV_{cw} and longer time scales, which Keenan et al. (2012) demonstrated for a wide range of terrestrial biosphere models.

At some sites where needle leaf evergreen vegetation is the dominant vegetation type, year-to-year variation in fluxes can be explained by climatic and environmental drivers (e.g. disturbances) only. For example, Sierra et al. (2009) applied a process-based stand vegetation model which showed that some forests are mostly affected by short term dynamics such as disturbances, and others are more influenced by climatic controls. Duursma et al. (2009) performed a model-data comparison using a calibrated empirical photosynthesis model, and found good fits for GPP on daily to seasonal time scales for several European FLUXNET sites and, similar to this study, comparably poor fits on the annual time scale. They attributed part of this mismatch to uncertainty in the EC data, variations in LAI, and reductions in GPP as a result of soil drought. Purely observational studies at temperate coniferous forests in Brasschaat (Carrara et al., 2003, 2004) and Vielsalm (Aubinet et al., 2002), showed that climatic and ecological drivers (such as changes in LAI, phenology shifts) explain the majority of interannual variability in observed carbon and water fluxes. Our results, as well as studies by Jacobs et al. (2009), Kruijt et al. (2009) and Luyssaert et al. (2007) suggest that, in addition to

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direct climatic and environmental factors, ecological drivers also operate at the Loobos site.

4.2 Uncertainties in the observation dataset

For this study, the mismatch between simulated and observed fluxes both at the monthly and at the annual time scale can only be partly attributed to uncertainties in the flux data. The magnitude of the error for this dataset is estimated by Elbers et al. (2011) as 8 % of annual NEE, which is a quarter of the standard deviation of annual NEE, and is small compared to other flux sites (Elbers et al., 2011, data from 1997–2010). Because GPP is estimated from NEE and night-time respiration, the errors in annual NEE, especially the notorious errors in night-time NEE due to low turbulence, propagate into GPP estimates. During winter, when relatively more data is gap-filled, this uncertainty in the data can contribute to a higher deviation between the modelled and observed results in this study.

4.3 Alternative temperature response function

4.3.1 Observed temperature response at Loobos and similar sites

We presented strong evidence that *Pinus sylvestris* continues to assimilate during winter in temperate climates, and even acts as a carbon sink during frost periods rather than as a source, as most DGVMs currently suggest (Morales et al., 2005). Falge et al. (2002) even suggest, based on their analysis of FLUXNET data, that temperate and boreal conifers should be seen as two separate classes. The observations at Loobos support this suggestion, as *Pinus sylvestris* clearly continues to assimilate in winter during all years, even when daily average temperatures drop below 0 °C. These pine trees grow in a temperate climate, and therefore experience relatively milder winters compared to the same species at boreal sites. Plants are known to acclimatize to their growing conditions, so differences in the seasonal carbon gain within species reflect to

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a large extent the light- and temperature environment in which they exist (Teskey et al., 1994). Plants native to a colder climate exhibit higher photosynthetic rates under colder temperatures, but, at higher latitudes, *Pinus sylvestris* is also known to display winter photo-inhibition as a result of lower winter temperatures (Berry and Bjorkman, 1980).

This winter inhibition of the photosynthetic capacity is thought to be a protective mechanism against damaging combinations of low atmospheric temperatures and exposure to high irradiances that can be enhanced by snow cover. If, however, winters are warm enough, photosynthesis in evergreen forest stands can continue if enough soil water is available to meet the transpirational demand (Sevanto et al., 2006 and references therein). How long it takes for the photosynthetic capacity to diminish during extended cold periods – and possibly recover when temperatures rise again (e.g. see Suni et al., 2003a, b; Kramer et al., 2008; Kramer and Hänninen, 2009) – is not known for this site and will be investigated in a winter measurement campaign of leaf photosynthesis over the next few years.

4.3.2 Modelled temperature response

The modelled changed temperature response function had a smaller effect on simulated AET than on simulated GPP (Fig. 5). ~~Underestimation of modelled interception loss in relation to~~ precipitation intensity in winter can play a role here. In general, measured AET fluxes during winter are high for this type of forest. At Loobos, measured AET peak values during winter are mainly the result of high interception evaporation (Elbers et al., 2011). Modelled LAI was slightly lower than observed (Table 2), which results in a lower precipitation storage capacity for the vegetation than in reality. Additionally, as the model does not explicitly handle shower intensity, and prolonged periods of low precipitation intensity occur often at the site during winter, the model underestimates interception evaporation. This underestimation of canopy interception likely contributes to underestimations of AET on the longer time scales as well.

Even when Scots pine is allowed to continue assimilating at lower temperatures, the difference between modelled and observed fluxes improves, but is not completely re-

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solved. The shape of the temperature response curve for *Pinus sylvestris* (Fig. 1), is modelled as a steep increase from the minimum temperature ($p_{\text{temp}_{\text{min}}}$) to the optimum temperature ($p_{\text{temp}_{\text{low}}}$), which, to our knowledge, is not supported by literature but purely empirical. For this study, we identified a lack of data and literature to verify the exact shape of this response curve and instead calculated the minimum temperature threshold from the available data. Smith and Dukes (2013) reviewed the latest available methods to incorporate photosynthesis temperature acclimation into global scale models, and suggest that instead of just looking at temperature optima, shifts in the slope/intercept of the initial instantaneous temperature response could be of equal or greater importance, especially at suboptimal temperatures, and that a combination of data collection and modelling studies, such as ours, is needed to improve our understanding and realistically simulate long term responses of vegetation to temperature shifts.

The small impact of changing the temperature response function on simulating IAV_{cw} is of course related to the fact that wintertime fluxes make up only a small part of the total annual flux (average observed annual GPP for this dataset is 1284 g C m^{-2}), usually less than 10 %. In contrast, the largest observed interannual difference in GPP for this period is almost twice as large at 200 g C m^{-2} . Therefore, small improvements in the winter estimates will not translate directly into good estimates and high correlation coefficients on the annual time scale.

4.4 Alternative plant water uptake parameterizations

The use of three different soil water uptake parameterizations revealed that the model can satisfactorily simulate GPP and AET during wet summers such as that of 2005. The model performed well for those years that plant transpiration for Scots pine could be compared with sap flow observations (Fig. 8). However, none of the uptake parameterizations capture the observed response to a drought such as occurred in the summer of 2003. In addition, none of the three parameterization consistently improved all results, nor improve simulated IAV_{cw} at Loobos.

Previous studies have demonstrated that LPJ-GUESS is sensitive to limitations in soil moisture, firstly because the parameters controlling stomatal conductance are very sensitive to plant water stress (Zaehle et al., 2005) and secondly, because the model does not account for plant ability to access water from deeper soil layers and aquifers in water-limiting situations (Hickler et al., 2006; Wramneby et al., 2008). The debate on how to improve modelling efforts in a mechanistic way, however, is still on-going. For example, Hickler et al. (2006) included plant hydraulic architecture in the global model version of LPJ, thereby changing the calculation of plant water supply to a more mechanistic scheme. This improved global simulations of AET, but the updated model requires additional PFT parameters that are often not available and the model still underestimates summer AET at one Mediterranean test site. Verbeeck et al. (2011) tried increasing soil depth and used locally varying root profiles to improve simulations of dry-season GPP for the tropics. Such an approach, however, does not lead to the desired mechanistic model improvements because it eliminates simulated water stress completely. Furthermore, high-quality data on effective rooting depth, soil volume and deep soil water are rarely available, and deriving model parameters representing deep tap roots, sometimes growing through rock fissures or compacted soil layers, is difficult. These challenges are probably the reason why access to deep water is, to our knowledge, not captured in any DGVM. Nevertheless, we think that further efforts should be devoted to improving the current state of the art in this respect, because access to deep water is probably crucial in many ecosystems around the world.

The 2003 summer drought simulations at Loobos confirm the strong model sensitivity to drought: under dry soil moisture conditions the vegetation shows a much more gradual response in flux reduction compared to the model runs (Fig. 10). Observed soil moisture values are low and gradually decline during the heatwave (Fig. 9), suggesting the vegetation can access water from deeper layers, or groundwater. *Pinus sylvestris* is known for its ability to create long tap roots, especially when growing on sandy soils, so that water uptake is also possible from sparsely rooted deep soil layers when water becomes limiting (Jarvis, 2011).

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The shape of the water uptake response curves in the model clearly has an effect on the water uptake (Supplement, Fig. S1). The exact shape of this curve, however, is both species and site specific, and remains poorly defined for global model studies that use broad PFT classifications. For *P. sylvestris*, Lagergren and Lindroth (2002) summarized uptake curves from several studies, and the reported shapes are very similar to the ones used in this study, most closely resembling $w_{r_{\text{rootdist}}}$ and $w_{r_{\text{speciespecific}}}$. Reality probably lies in between the original linear formulation and $w_{r_{\text{rootdist}}}$, because plants do not reduce transpiration immediately when soil water content declines: transpiration remains unaffected until the soil water potential reaches values at which the xylem can be damaged by cavitation. Next, depending on the strategy of the tree, transpiration is either reduced due to cavitation or to stomata closing to prevent cavitation (McDowell et al., 2008). During droughts, plants may reallocate carbon to roots instead of leaves or needles, thereby reducing their assimilation potential through reduced leaf area. Such seasonal changes in carbon allocation and phenology under drought are currently not explicitly handled in LPJ-GUESS because allocation occurs annually in the model (on the annual time scale, however, the leaf to fine root ratio adjusts to water availability). Model inaccuracies in reproducing this type of vegetation phenology and hence the simulation of seasonal cycle of CO_2 and water can lead to poorly simulated fluxes compared to observed ones. Future modelling efforts should focus on root dynamics, include the effects of groundwater uptake and shifts in carbon allocation under water stress.

5 Conclusions

Variability in ecosystem carbon and water exchange is a key aspect of ecosystem functioning, but, in many cases, the drivers are poorly understood. Here, we showed that a DGVM, when adapted to the local conditions, can reproduce daily to seasonal variability in carbon and water exchange with high correlation coefficients. Similar to other studies, however, the model cannot reproduce interannual variability. We tried to

improvement of the process-based modelling and confronting these results with observations is an important complementary approach. Accurate reproduction of site-level fluxes with such models on the seasonal to annual time scale is essential for our understanding of vegetation-climate interactions and for reducing uncertainties in future projections.

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Table 1. Parameter values for LPJ-GUESS. Values for this study are similar to Hickler et al. (2012), Table S1.1, except for values in bold font. $T_{c,max_{est}}$ = maximum coldest-month temperature for establishment; drought_{tol} = drought tolerance level of a species (0 = very tolerant, 1 = not at all tolerant); root_{distr[1]} = fraction of roots in first soil layer (the remainder being allocated to second soil layer); sla = specific leaf area.

| Species_PFT | Growth form | $T_{c,max_{est}}$ (°C) | drought _{tol} ^a (–) | root _{distr[1]} (–) | sla (m ² kg ^{–1} C) |
|---------------------------|-------------|---------------------------|--|---------------------------------|--|
| <i>Pinus sylvestris</i> | tree | limitless | 0.25 | 0.6 | 9.3^b |
| C ₃ herbaceous | herbaceous | limitless | 0.01 | 0.9 | 32.4 |

^a Similar to fAWC in Hickler et al. (2012), called drought tolerance here. Not always used by model, only when using species specific water uptake from the soil (model setup S2, $w_{r_{speciespecific}}$).

^b Value based on site measurements by Wilma Jans et al. (1997, unpublished data, available at: <http://www.climatexchange.nl/sites/loobos/>) and Katrin Fleischer (2013, unpublished data).

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Table 2. Modelled and observed site characteristics of Loobos. All modelled values for biomass are calculated for the period 1997–2009, and multiplied by a factor 0.82 to exclude root biomass (taken from Jackson et al. (1996) as a topical value for conifer forests).

| | Aboveground biomass (kg C m ⁻²) | LAI <i>Pinus sylvestris</i> | C ₃ grass |
|------------------|--|--------------------------------|----------------------|
| <i>Observed:</i> | 4.98 ^a | 1.62 ^b | 1.0 ^c |
| <i>Modelled:</i> | | | |
| Default/S1 | 5.95 ± 0.10 | 1.5 | 2.4 |
| pstemp | 7.18 ± 0.14 | 1.7 | 1.9 |
| S2 | 4.55 ± 0.11 | 1.1 | 3.6 |
| S3 | 4.72 ± 0.11 | 1.2 | 2.8 |
| S4 | 7.64 ± 0.19 | 1.8 | 2.6 |

^a 9.23 kg m⁻² standing biomass in 1997, annual growth increment of 0.124 kg m⁻² (data source: <http://www.climateexchange.nl/sites/loobos/>). To convert to carbon mass a factor of 0.5 was used (e.g. see Sandström et al., 2007; Thomas and Martin, 2012), resulting in an estimated average aboveground biomass between 1997–2009 of 4.98 kg C m⁻².

^b Measured average tree LAI from 1997–2009 (unpublished data), minimum 1.44 (2007), maximum 1.78 (2009), standard deviation is 0.10. Dolman et al. (2002) report maximum LAI of 1.9 for 1997.

^c Measurements between 1999 and 2002 ($n = 52$), standard deviation 0.4 m² m⁻² (unpublished data).

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Table 3. Goodness-of-fit values for model scenarios S1–S4 and changed temperature response function, “pstemp”. Correlation coefficient (r), and Root Mean Square Error (RMSE) for daily, monthly and annual data. Bold values represent data distributions that are identical using the Wilcoxon ranking test.

| Run | annual | | GPP monthly | | daily | | annual | | AET monthly | | daily | |
|------------|-------------|-------|----------------|------|-------|------|-------------|-------|----------------|------|-------|------|
| | r | RMSE | r | RMSE | r | RMSE | r | RMSE | r | RMSE | r | RMSE |
| Default/S1 | 0.22 | 125.9 | 0.92* | 35.7 | 0.79* | 2.20 | 0.20 | 77.7 | 0.87* | 19.7 | 0.62* | 1.27 |
| pstemp | 0.16 | 109.3 | 0.90* | 36.3 | 0.78* | 2.15 | 0.21 | 73.4 | 0.87* | 19.6 | 0.62 | 1.25 |
| S2 | 0.32 | 128.6 | 0.92* | 32.6 | 0.81* | 1.93 | 0.19 | 90.8 | 0.87* | 17.2 | 0.65* | 1.03 |
| S3 | 0.27 | 198.9 | 0.92* | 31.4 | 0.81* | 1.78 | 0.13 | 141.9 | 0.86* | 17.3 | 0.65* | 0.94 |
| S4 | 0.24 | 231.3 | 0.94* | 51.9 | 0.85* | 2.45 | 0.31 | 168.3 | 0.88* | 36.2 | 0.68* | 1.67 |

* Significance tests for Pearson correlation: P value < 0.05.

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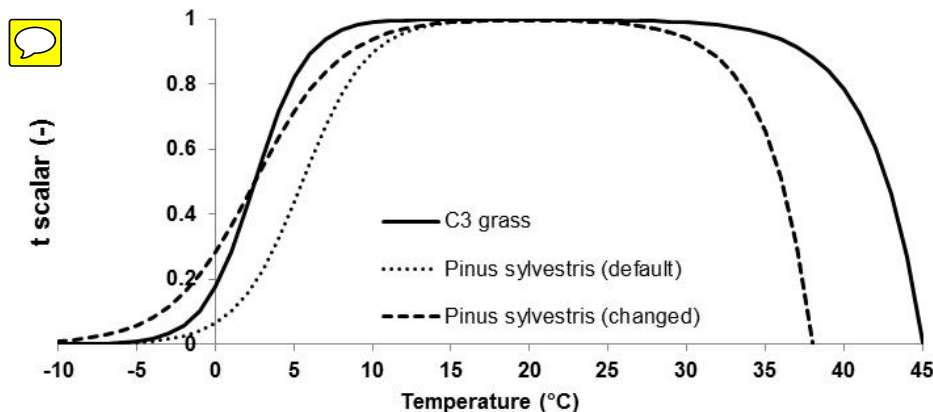


Figure 1. Temperature function (t_{scalar}) for ~~PFT~~ *Pinus sylvestris* and C_3 grass, values between 0 (photosynthesis maximally limited by temperature scalar) and 1 (photosynthesis not limited by temperature scalar). Default settings for *P. sylvestris* (dotted line: $\text{pstep}_{\text{min}} = -4^\circ\text{C}$, optimum $15\text{--}25^\circ\text{C}$, $\text{pstep}_{\text{max}} = 37^\circ\text{C}$) and C_3 grass (solid line: $\text{pstep}_{\text{min}} = -5^\circ\text{C}$, optimum $10\text{--}35^\circ\text{C}$, $\text{pstep}_{\text{max}} = 45^\circ\text{C}$). Changed parameterization for *P. sylvestris* ($\text{pstep}_{\text{min}} = -10^\circ\text{C}$, optimum $15\text{--}25^\circ\text{C}$, $\text{pstep}_{\text{max}} = 37^\circ\text{C}$).

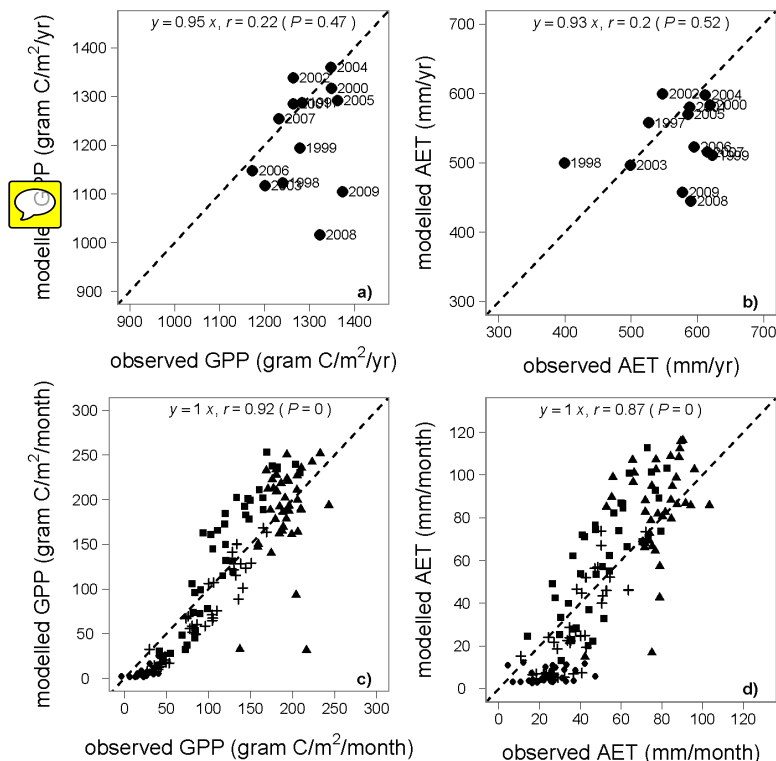


Figure 2. Observed vs. modelled variability in GPP (**a, c**) and AET (**b, d**) for the default model scenario (S1) on the annual time scale (**a, b**) and monthly time scale (**c, d**). Dotted line is the 1 : 1 line. The equation shows linear regression through the origin, with correlation coefficients. Fluxes are hatched per season for subpanels (**c**) and (**d**): • = winter (December, January, February); ■ = spring (March, April, May); ▲ = summer (June, July, August); + = fall (September, October, November).

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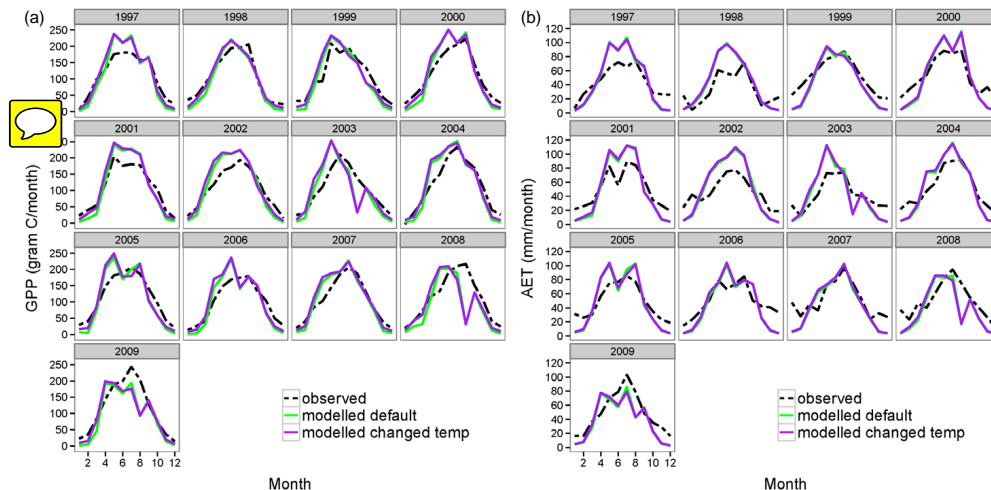


Figure 3. Observed (black dotted line) and modelled values for default/S1 (green line) and changed temperature response ptemp (purple line) runs. **(a)** Monthly values for GPP ($\text{gC m}^{-2} \text{ month}^{-1}$). **(b)** Monthly values for AET (mm month^{-1}).

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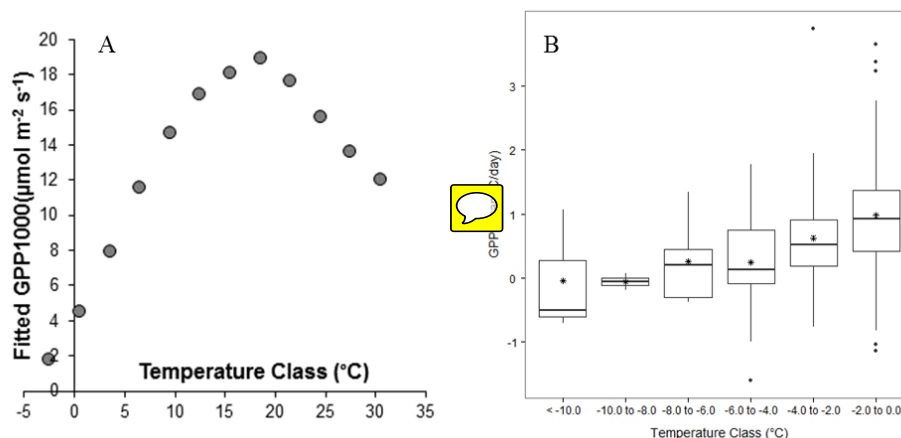


Figure 4. Observed temperature responses at Loobos. **(A)** Courtesy of P. Abreu: fitted GPP at a solar light intensity of 1000 Wm^{-2} (GPP1000, $\mu\text{mol m}^{-2} \text{s}^{-1}$) based on half-hourly EC measurements (1997–2011) following Jacobs et al. (2007); **(B)** daily GPP ($\text{gC m}^{-2} \text{day}^{-1}$) observed at Loobos calculated from site EC measurements, for days with average daily temperatures $< 0^{\circ}\text{C}$ and total net radiation received $> 2 \text{ MJ day}^{-1}$ ($n = 175$).

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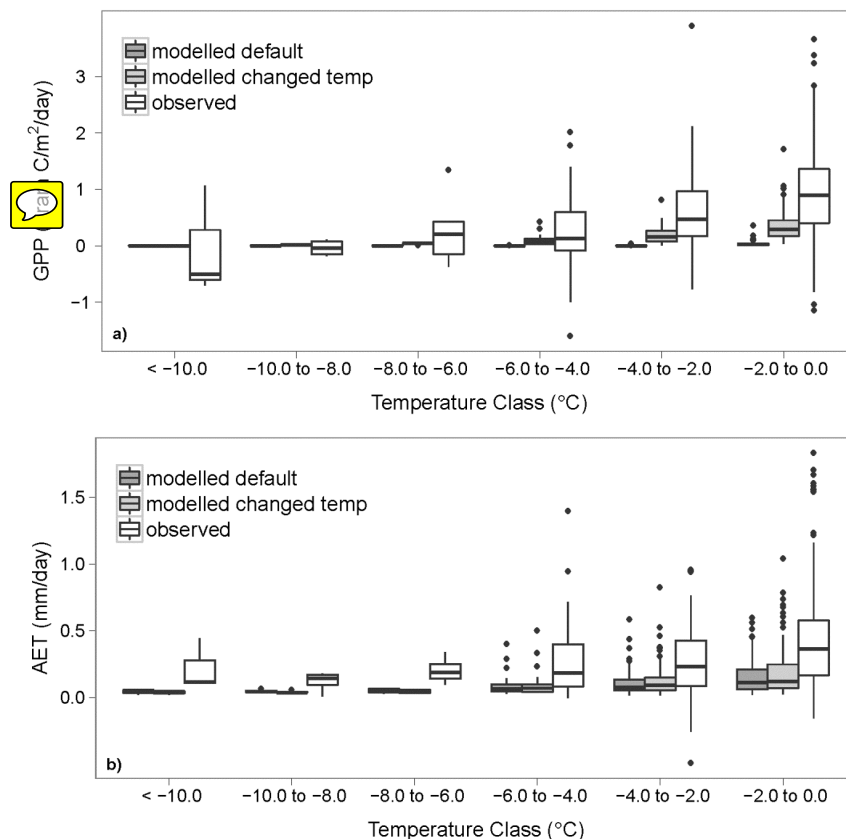


Figure 5. Effect of change in temperature scalar t_{scalar} on modelled estimates of **(a)** GPP ($\text{gC m}^{-2} \text{day}^{-1}$) and **(b)** AET (mm day^{-1}). $\text{pstemp}_{\text{min}}$ for *Pinus sylvestris* is set to -10°C , other values remain unchanged. (White: observed values, dark grey: modelled default, light grey: changed t_{scalar} function). Results for days with net radiation $> 2 \text{ MJ day}^{-1}$.

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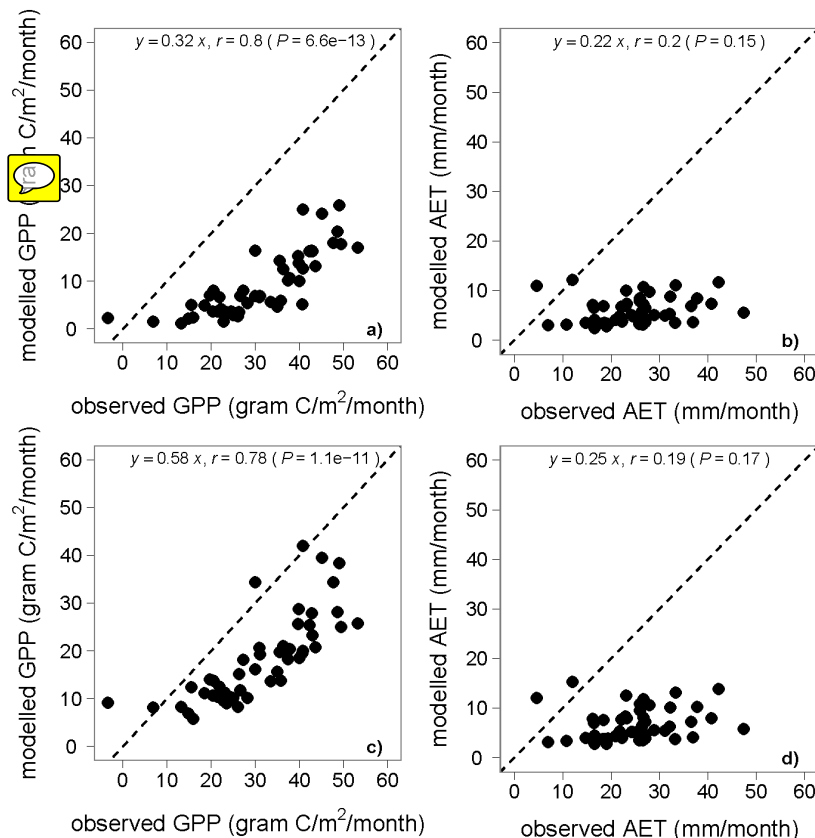


Figure 6. Variability on monthly time scale for **(a, b)** GPP ($\text{gC m}^{-2} \text{ month}^{-1}$); and **(c, d)** AET (mm month^{-1}), between default settings **(a and c)** and changed t_{scalar} **(b and d)** during winter. All days in December, January and February are included (i.e., no selection for radiation). All slopes significantly differed from 1.0 ($P < 0.05$). RMSE values: **(a)** 22.7, **(b)** 20.4, **(c)** 14.7, **(d)** 19.7.

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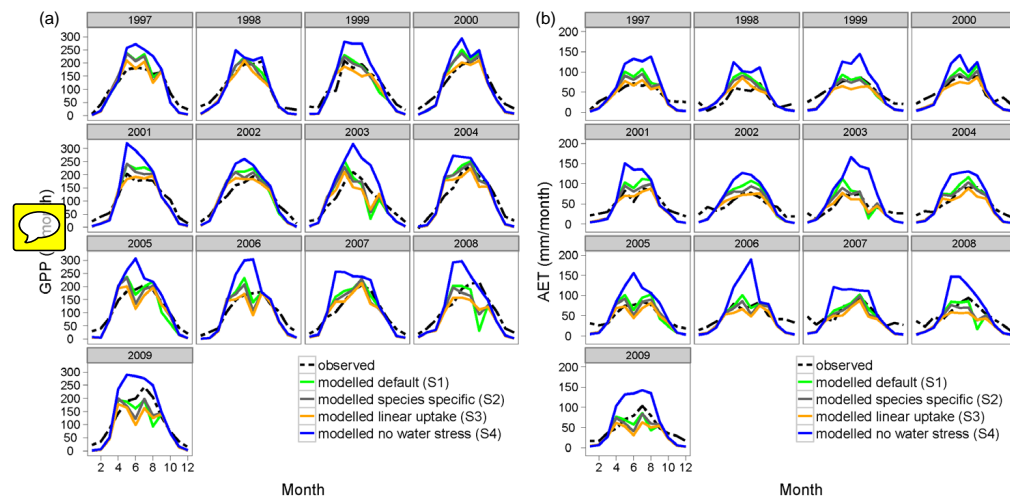


Figure 7. Comparison of fluxes for **GPP** (a) and **AET** (b) using different water uptake functions. Solid line: observed values. Dotted lines: modelled values for scenarios S1–S4.

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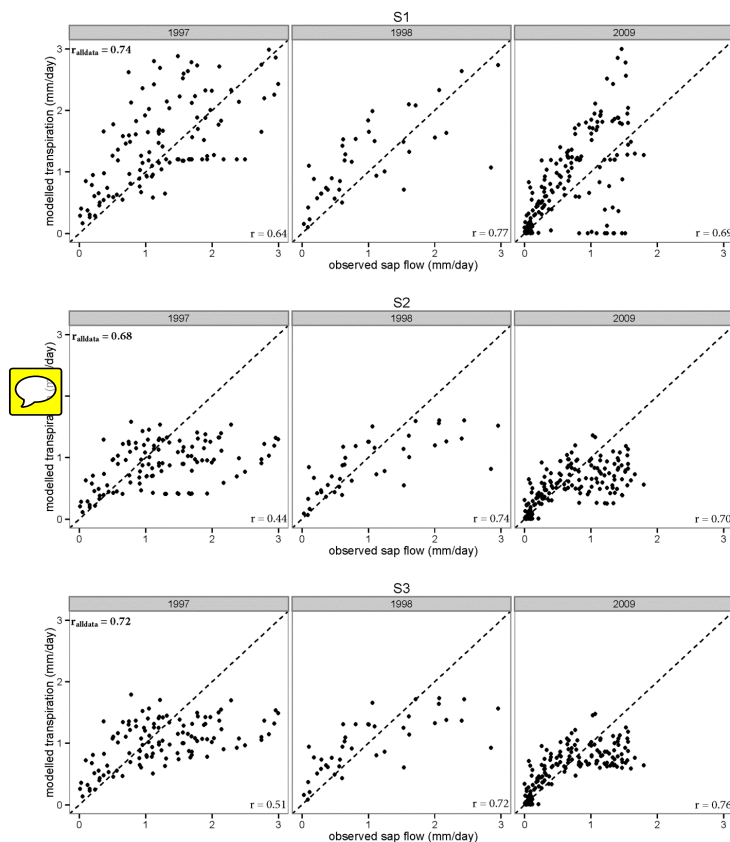


Figure 8. Modelled transpiration (mm day^{-1}) for *Pinus sylvestris*, compared to observed sap flow (mm day^{-1}). Pearson correlation coefficients significantly different from 0 ($P < 0.01$) for all separate years as well as all data points together ($r_{alldata}$). Sap flow measurements 1997 and 1998 acquired using tissue heat balance systems; and for 2009 using Granier thermal dissipation probes. S1 = default uptake, S2 = species specific uptake, S3 = linear uptake.

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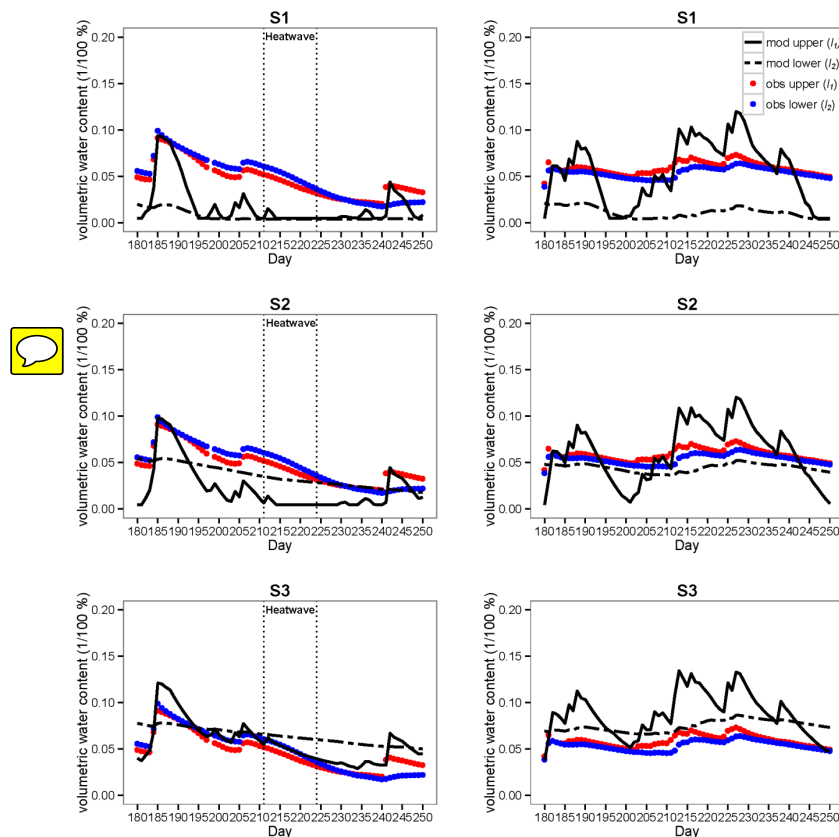


Figure 9. Daily modelled (mod, black lines) and observed (obs, red and blue) soil moisture (as volumetric water content, 1/100 %) for summer of 2003 and 2005. The two depths refer to the two soil layers in LPJ-GUESS: l_1 (0–50 cm) and l_2 (50–150 cm). For 2003, the heatwave period is indicated between the black lines.

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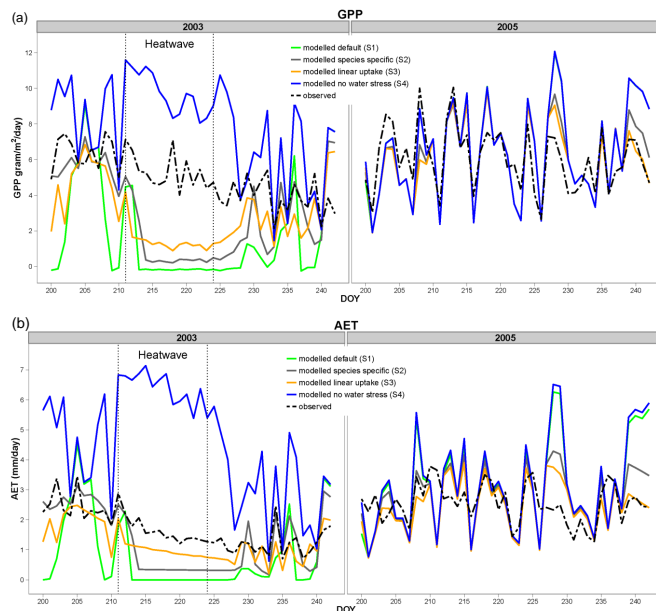


Figure 10. Daily observed and modelled fluxes for $\overline{\text{GPP}}$ (a) and $\overline{\text{AET}}$ (b) for July and August in two different climate years. In summer 2003 a heatwave and corresponding drought occurred in Europe (e.g. see Teuling et al., 2010). Based on long term averages of the Dutch Royal Meteorological Institute (KNMI), higher temperatures, more sunshine hours and much less precipitation was received during this summer, and an official heatwave took place in the Netherlands during August (KNMI, 2003). The KNMI defines a heatwave as a period of at least 5 consecutive days in which the maximum temperature exceeds 25°C , provided that on at least 3 days in this period the maximum temperature exceeds 30°C . Based on these criteria, heatwave duration was from 31 July to 13 August and is marked in the graph by two dotted black vertical lines. The summer of 2005 had average temperatures and sunshine but was much wetter, and August was a month with particularly high precipitation compared to long term averages (KNMI, 2005).

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