

We are very happy that all reviewers appreciated our work and that our paper has already been used for teaching purposes (see the interactive comment #1). We also acknowledge the reviewers for their constructive comments that improved the paper. Here below you will find a point-by-point response for all comments of the reviewers.

Reviewer #1:

Comment 1

0. Abstract:

0.1. clarify/revise results statement, what is meant by 'full spectrum', give specifics.

Response

We reformulated the sentence:

P 1 L 17 "MAIDEN explains 90% of the observed daily gross primary production variability, 73% of the annual ring width variability and 20-30% of its high frequency component (i.e. when decadal trends are removed)."

Comment 2

Introduction:

1. pg 2, l. 1: define 'secondary growth' at first use.

Response

We added the definition.

P 1 L 30 "secondary growth is the increase of the girth of the plant roots and stems"

Comment 3

2. pg 2, l. 5: also roots; e.g. Moorcroft (2006) and description in section 2.1.

Response

We modified the sentence and added the reference:

P 2 L 3 "Indeed, carbon allocated in different tree components (e.g. canopy, stem or roots) has a specific function and is stored for a different length of time (Moorcroft, 2006)"

Comment 4

3. pg 2, l. 25: I think you mean to say that these models should be able to simulate the following observed phenomena: (i,ii,iii).

Response

We modified as suggested.

P 2 L 23 "Such models should be able to simulate the following observed phenomena: ..."

Comment 5

4. pg 2, l. 31-32: briefly explain for those unfamiliar with its development, why MAIDEN is an ideal model with which to work for the purposes of this study. For instance, in the sentence prior, you've noted that it was developed for Mediterranean and temperate climates; why should it be suitable for simulations in boreal climates? Here you can borrow from section 2.1 the salient descriptive points, saving for section 2.1 the description of the modifications and the experiments performed for this study. But make the argument why the model should be suitable for the present study (noting also your point that it has never been applied in 'environments mostly sensitive to cold temperatures').

Response

We added a sentence:

P 2 L 29 "MAIDEN offers an ideal framework to analyze the impact of introducing in the model relevant processes for carbon assimilation and allocation in temperature sensitive boreal trees. Indeed, the model simultaneously simulates the course of photosynthesis and sets different

phenological phases to determine the allocation of carbon to different plant compartments in a dynamical manner.”

Comment 6

Materials and Methods:

5. pg 3, l. 21: I think you mean here: model has not been used to simulated forest growth in boreal conditions. See also note 4.

Response

We modified as suggested.

P 3 L 16 “Up to now, the model has never been used to simulate forest growth in boreal conditions.”

Comment 7

6. pg 3, l. 19-21: "Drought and water stresses are well take into account": support this statement with citations and references, but otherwise I suggest to save such statements for the Results section.

Response

We deleted the sentence.

Comment 8

0. Abstract:

0.2. use of the word robust means you have done validation or out-of-sample tests of the model. Have the authors done so?

7. pg. 3, l. 29: describe how the parameter estimates are cross-validated. To determine 6 or 12 parameters simultaneously, conditioned on two variables, must require a lot of data but also out-of-sample testing [to revisit after reading Supplement 1].

Response

We added a cross-validation exercise of parameter values:

Figs. S5, S9 and S10.

Supplement P 2 L 12 “The robustness of the parameters’ posterior distributions was tested with a cross-validation exercise. Firstly, we compared the parameters’ posterior densities, when the optimization was executed on the full period with observed data, to those obtained with half data (Figs. S5 and S9). However, we have to recall that in total we have 2920 observed daily data between 2003 and 2010 to optimize the 6 parameters influencing the GPP, and only 61 observed ring width annual data between 1950 and 2010 to optimize the 12 parameters influencing Dstem. Subsequently, the distributions of the parameters influencing Dstem were also compared to those obtained independently with data from specific sites (the used black spruce ring width data comes from five different riparian forests; Fig. S10).”

Comment 9

[to delete? 8. pg. 4, l. 1-30: please revise to better distinguish prior formulation of MAIDEN and the modifications introduced here. What is existing, what is new here?]

Response

We added a sentence:

P 4 L 8 “The computations of V_{cmax} and θ_g used here are identical to those of the prior formulation of MAIDEN (Gea-Izquierdo et al., 2015).”

Comment 10

9. pg 4, l. 30: Euler’s method might not be suitable in the case of a large time step, large change in the rate of change, or both; consider a Runge-Kutta solver, relatively straightforward to implement.

Response

We understand the reviewer comment. However, the Euler's method is a particular case of the Runge–Kutta family of methods and we think that a different solver will not change significantly our results and interpretations concerning the need to take into account acclimation of photosynthesis to temperature for boreal trees.

Comment 11

10. pg 5, l. 10-15, 16-20, 21-25: the determination of phenological phases seems highly specified for a modeling striving to be more ecophysiologicaly based (Introduction). Instead of basing these phases on correlation studies (empirical), could they be estimate from other properties of the environment, or prognostic variables within the existing model? In addition, please justify all choices of hard parameters, for instance, pg 5, l. 19, pg 6, l. 22.

Response

We modified the text to better justify our choices.

P 5 L 9 “Based on previous studies on black spruce forests (Girardin et al., 2016; Ols et al., 2016; Mamet and Kershaw, 2011), we modified the model to consider the effect of the previous year April precipitation and July-August temperature likely influencing the length and the thermal-hydraulic stress of the previous growing season, respectively. Previous year climate conditions of specific months are known to influence shoot extension of boreal trees likely because they control accumulation of resources in the buds (Salminen and Jalkanen, 2005).”

P 5 L 22 “In this way, *AlloCcanopy_j* may vary between the 70% and the 100% of *MaxCcanopy* as in the previous version of the model (Gea-Izquierdo et al., 2015).”

P 6 L 20 “The value 0.8 was chosen to force a minimum threshold of C allocation to the stem in this phase (at least 20%) and to guarantee the correspondence between the inflection point and the temperature where roughly 50% of CT_i is allocated to the stem.”

Comment 12

Results/Discussion:

11. General remark, section 2.3: if the simulation produces a good out-of-sample or independent fit to observed predictors, then it would be good to diagnose the model: what factors are most important controls on the fidelity of the simulations? Because this is an ecophysiological modeling study, this would be much more instructive than the statistical regression analysis, although the latter may be used to support the interpretation with respect to modeled variables. Therefore, please add ecophysiological diagnostics to this section or a new section 2.4.

18. Section 3.2: Revise the title for English; perhaps: Mechanistic diagnostics? And consolidate mechanistic results here, with their discussion in the Discussion section. Moving the Supplemental Figures that are most relevant for the central elements of the argument into the main text, and by expanding this part of the results, this may address my previous comment #11 on Section 2.3. This will help the reader understand what is going on in the simulation that explains the consistency with observations.

Response

We modified the title of section 3.2 as suggested. We believe that mechanistic results for GPP are already shown and discussed in depth (see Figs. 6, S4, and S12 to S18). We consolidated results and discussion of mechanistic rules for Dstem. Figs. 7 and 8, illustrating how specific processes impact the MAIDEN simulations, were indeed modified to show how the parameter selection of those processes alters the correlation with observed data. We also added Figs. S6, S7, S11, S20 in addition to the already existing Figs. S8, S19 and S21.

Comment 13

12. Section 3.1, pg 9, l. 3: explain here and/or in the Table 1 caption the definition and how to interpret the series of numbers that are in the last column of the Table. What exactly do you mean

by "sharp" here and on pg 11 (I think I know, but give a more objective description of what you mean for the reader).

Response

We added a sharpness definition in the text:

P 8 L 20 "The posterior distributions of the parameters were quite sharp (Fig. S4; Table 1; by sharpness we mean the shrinking of the distribution relative to the prior acceptable range toward a posterior distribution with a well-defined, narrow peak). Sharp distributions with small posterior ranges relative to the prior ones indicate sensitive parameters."

We added how to interpret prior and posterior ranges in the caption of Table 1:

"Small posterior ranges relative to the prior ones indicate sensitive parameters."

Comment 14

13. pg 9, l. 7-12: "However, the ensembles of daily and annual time series retained by the MCMC sampling were not always centered on the observed time series (Fig. 5)..." Revise and expand to reflect that the simulated annual GPP values overestimate the actual GPP at low observed GPP. This will better reflect the excellent information content of this figure.

Response

We modified as suggested.

P 8 L 29 "However, the ensembles of daily and annual time series retained by the MCMC sampling were not always centered on the observed time series (Fig. 3), in particular the simulated annual GPP values often underestimated the actual GPP especially at low observed GPP."

Comment 15

14. pg. 9, l. 13-17: Put uncertainty estimates on Fig 6 and use them in the description of results and in discussion later.

Response

We modified the figure adding the thresholds of significance ($p < 0.05$).

Comment 16

15. pg 9, l. 13-17: "The model explained about 20-30% of the 15 observed yearly R_{WHighF} variability corresponding to correlations of 0.58-0.66 (Fig. 4b). This is a good result because simulated detrended annual GPP values (i.e. photosynthetic assimilation before any carbon allocation) had only negative R² with R_{WHighF} (Fig. 4c; meaning performance worse than a straight line centered on R_{WHighF}). This suggests that the modified MAIDEN daily partition of carbon in the plant compartments significantly improved the concordance with tree-ring observations." Although I am not sure I understand this result (and its discussion; please clarify, in mechanistic terms, why we see the results in fig 4c?): If the correlations in Fig 4c are statistically significant (estimate p-values), then this is an even more important result than described, because not only are the model improvements an important advance, but they correct a result that would otherwise produce the opposite correlation.

Response

Correlations between GPP and R_{WHighF} are positive ($r = 0.3$, see text over Fig. 2c), such as those between D_{stem} and R_{WHighF} ($r = 0.65$, see text over Fig. 2b). However, R² values between GPP and R_{WHighF} are negative (see Fig. 2c), while those between D_{stem} and R_{WHighF} are positive (see Fig. 2b). To clarify this point, we have shown the equation to compute the R² (Eq. 8) and a comparison between GPP, D_{stem} and R_{WHighF} (Figs. S6 and S7).

Comment 17

16. pg 9, l. 20-24: Fig 7b, here and elsewhere: it is an interesting result! But where r is given, also give effective degrees of freedom and p-value; interpret based on the p-value as statistically significant or nonsignificant.

Response

We now provide all df and p-values of correlation coefficients in the text.

Comment 18

17. General remarks on sections 2 and 3: Reorganize the content in these sections into separate Results (section 3) and Discussion Sections (new Section 4), with subsections as appropriate. Results are what was objectively found and will be discussed; Discussion is for interpretation of the results. As it is, Results and Discussion are entwined, but it would clarify for the reader to separate and distinguish them. I would suggest to focus the Results on the following items of interest: (1) sensitivity of the simulations to specified parameters; (2) mechanistic and regression-based diagnostics. I would then put in the Discussion the following argument: (1) The results are sensitive to parameter estimation in the following ways: but: (2) Comparison with independent observations suggest MAIDEN as revised produces more accurate simulation of GPP, TRW, intra-growing season dynamics ... which are (3) consistent with response function analysis, and (4?) here are some predictions made by the model/simulations, that could be tested with additional observations.

Once these revisions help to reorganize the essential content of the paper, it will be easier to evaluate the expanded ecophysiological interpretation, which I think should be more central to the main thrust of the paper than the response function analysis (Abstract; section 3.3).

Response

We did not modified the paper as the reviewer suggested because the proposed modifications are much more than a reorganization and because the current structure is already well defined according to us:

3. Results and Discussion

3.1 GPP and tree-ring growth variability explained by MAIDEN

3.2 Mechanistic diagnostics

3.3 Comparison between MAIDEN and response functions

3.4 Limits and error sources of the study

Furthermore, the ecophysiological interpretation is already central in the Results and Discussion section (subsection 3.3 on the comparison with response functions is only approximately 1/6 of section 3).

Comment 19

19. p. 9, l. 30: "...is sensitive to all..." Discuss how the sensitivity of the results to parameter estimates related to "Vcmax or thetaG, except soilb", complicate the diagnostic interpretation. Are there multiple controls that all could produce a similar result and good fit to observations?

21. I would appreciate more discussion of fig S2. Interpret the bimodal structure of the posterior probabilities; connect to the plausible value descriptions in the last column of Table 1.

Response

The impact of the parameters on the simulations is already shown on Figs. 6 and S14-S18. We added and modified some text related to this reviewer's comment:

P 8 L 20 "The posterior distributions of the parameters were quite sharp (Fig. S4; Table 1; by sharpness we mean the shrinking of the distribution relative to the prior acceptable range toward a posterior distribution with a well-defined, narrow peak). Sharp distributions with small posterior ranges relative to the prior ones indicate sensitive parameters. This means that the model posterior probability (i.e. model plausibility) increased significantly with the specific values of the selected parameters retained by the MCMC sampling. The slightly bimodal structures of the

posterior distributions of Vmax, Vb and Vip were likely a consequence of their significant cross-correlations (Table S1). However, the posterior distributions of these three parameters were robust and consistent even when the Bayesian optimization was executed on independent periods (Fig. S5)."

Comment 20

Conclusions:

20. General remarks on Section 4: some of the points are speculative (e.g. p 12, l. 24-26; paragraph starting at l. 30); these belong in Discussion rather than Conclusions (see note 17, last sentence).

Response

We moved the indicated paragraph in the discussion.

Comment 21

22. Is MAIDEN publicly available (it was first introduced in 2004), and if not, could it be made so, to encourage experimentation in other environments, species, applications? This would be a great contribution and it would be consistent with the open data access policies of CP.

General comment

publication of MAIDEN code in the public domain such that others may experiment with this well-studied and highly valuable model

Response

The used MAIDEN version will be made publicly available upon the paper acceptance on "Figshare". The DOI will be updated at the next step of the reviewing process.

P 13 L 26 "The used MAIDEN version is publicly available on "Figshare": DOI: to be obtained."

Comment 22

23. Fig S12: this is not isoMAIDEN as in the caption, correct?

Response

We corrected our mistake.

Comment 23

24. Trivia: for future revisions if necessary, make line numbers cumulative rather than by page

Response

We used the Copernicus "Word" template.

Comment 24

25. Trivia: p. 9, l. 30: "...is sensitive to all..."

Response

We corrected the mistake.

Comment 25

26. Trivia: Slight revisions for English grammar and usage: pg 3 l. 3-5; please go through entire manuscript to revise for grammar as well.

Response

We revised the sentence:

P 3 L 2 "This comparison allows to verify that the process-based ecophysiological model satisfactorily reproduces the variability of the observed data and that its simulations keep robust relationships with the most significant climate variables."

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Reviewer #2:

Comment 1

1. Page3 last paragraph: About parameter tuning, there are 6 (reference: daily GPP) + 12 (reference: annual ring width) parameters tuned in this application. It is very smart of using Bayesian optimization for such a large number of parameters tuning. However, there are only 2 references (GPP and detrended tree ring). This might have impact on the final choice of the parameter value. Some solid check about the relationship among different parameters (correlation or interaction), and sensitivity analysis for Dstem parameters is needed.

Response

We added a cross-correlation analysis of the parameters' values (Tables S1 and S2; see also discussion of these tables in the main text), a sensitivity analysis of some central Dstem parameters (Figs. 7, 8 and S20), and a cross-validation of parameters' distributions (Figs. S5, S9 and S10; see also discussion in the main text).

Comment 2

2. Page 7 line 18: Typo "Ring with" should be "Ring width"

Response

We corrected the mistake.

Comment 3

3. Page 8 line 5: The input data for MAIDEN include daily temperature and precipitation, as well as CO₂. Is the solar-related parameter needed, e.g. sunshine hour, cloud cover fraction? If not, please briefly demonstrate how photosynthesis was estimated.

Response

MAIDEN can use two different meteorological input data: (1) a complete dataset composed of daily temperature, precipitation, CO₂, radiation, relative humidity and wind speed; (2) a reduced dataset composed of daily temperature, precipitation and CO₂. We used MAIDEN with the reduced input data and letting the model estimate the other variables as explained by Misson (2004).

In the case of radiation, Misson (2004) explains:

"Climatic driving variables are daily minimum and maximum temperatures, precipitation, global radiation, and atmospheric vapor pressure deficit (Table 1). Since radiation and humidity variables are usually not available for large temporal and spatial scale applications, we coupled the MT-CLIM model (Running et al. 1987) to MAIDEN to estimate these variables from observations of daily maximum and minimum temperatures and precipitation. In MT-CLIM, humidity estimates are based on the fact that daily minimum temperature is usually very close to the dew point (Running et al. 1987). Radiation estimates are based on the fact that the diurnal temperature range is closely related to the daily mean atmospheric transmittance (Running et al. 1987; Thornton et al. 2000)."

We modified our text to better clarify the input data required by MAIDEN while we refer to Misson (2004) for a more in detail description of the estimation of the micrometeorological covariates:

P 3 L 8 "Starting from daily minimum-maximum air temperature, precipitation and CO₂ atmospheric concentration (these are the minimum required input variables which are completed by radiation, relative humidity and wind speed when additional meteorological data are available; Misson, 2004), MAIDEN models the phenological and meteorological controls on GPP and carbon allocation (Fig. 1; see also flowcharts in Misson, 2004 and Gea-Izquierdo et al., 2015)."

The MAIDEN code will also be freely available upon the paper acceptance and the readers can directly verify on the code the used equations. The DOI will be updated at the next step of the reviewing process.

P 13 L 25 "The used MAIDEN version is publicly available on "Figshare": DOI: to be obtained."

Running, S. W., Nemani, R. R., and Hungerford, R. D.: Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis, *Can. J. Forest Res.*, 17, 472-483, doi:10.1139/x87-081, 1987.

Thornton, P. E., Hasenauer, H., and White, M. A.: Simultaneous estimation of daily solar radiation and humidity from observed temperature and precipitation: an application over complex terrain in Austria, *Agr. Forest Meteorol.*, 104, 255-271, doi:https://doi.org/10.1016/S0168-1923(00)00170-2, 2000.

Comment 4

4. Page 8 last paragraph: In the third step of this research (evaluation of the model performance), the indirect comparison between variance explanation (R²) of model simulation and climate response function was applied. It would be helpful to verify the model performance by showing the same climate response function analysis for the model simulation, e.g. combined Table 2 and 3 for the both observed and simulated GPP and Dstem. And it would be even more convincing to show the moving correlation analysis (figure 6) between simulated Dstem and monthly climate.

12. Figure 6: Is it possible to add the same moving correlation for simulated Dstem?

Response

We modified the figure (Fig. 4) as suggested, showing the moving correlations for simulated Dstem.

Comment 5

5. Page 9 line 3: R² was widely used in this model-data comparison. a) The calculation method for R² is needed here. b) Was model (parameter) was tuned using the same whole observation, or only a portion of the observation? A bit curious about the not small negative value of R².

10. Figure 4: The method of calculating R² need to be specified, either in the method part or the figure caption part. Is there any constraint when R² was calculated, especially for the negative R²?

Response

A cross-validation of parameters' distributions can be found on Figs. S5, S9 and S10 (see also discussion in the main text).

We added the R² computation method.

P 7 L 5 "The proportion of the observed variability explained by MAIDEN was evaluated with the coefficient of determination (R²), which compares the performance of simulated time series relative to that of straight horizontal lines centered on the data:

$$R^2 = 1 - \frac{\sum_i (Obs_i - Sim_i)^2}{\sum_i (Obs_i - \overline{Obs})^2}$$

Comment 6

6. Page 9 line 15: It makes sense that the annual GPP has a very poor correlation with ring width. One of the obvious reason is the definition of "annual" and the carbon carry over from previous year, which is the stored carbon in MAIDEN. I guess "annual" in the paper means the calendar year (Jan to Dec). It would be very useful to check the correlation between GPP in effective carbon year (or growth year, e.g. previous July to current June or from previous Phase 4 to Phase 3) and ring width observation.

Response

We checked the reviewer suggestion and produced a new figure (Fig. S6).

Comment 7

7. Page 12 line 23: Does increasing CO₂ contributed to this positive relation between summer temperature and Dstem? Is there any CO₂ fertilisation signal in both the simulated Dstem and the observed ring width?

Response

We added Figure S11 and some text.

P 9 L 17 “Indeed, the positive trend in response to the warming of the last few decades was well captured by the model simulations of stem increments, which included some CO₂ fertilization contribution (Fig. S11).”

Comment 8

8. Page 11 line 1: Does this stored carbon include previous year's stored carbon? What would happen, if the stored carbon was used up, e.g. carbon was stored very little during previous year?

Response

Yes, the stored carbon include previous year's stored carbon. If no stored carbon is used in the budburst phase the correlations between Dstem and RWhighF drop down (Fig. S20). We modified some text accordingly:

P 10 L 33 “In phase 3, corresponding to Budburst, a portion of the available carbon simulated by MAIDEN comes from stored non-structural carbohydrates from the current and previous years (parameter Cbud; see Table 1). In our case, Cbud was quantified as about 1.69 g C•m⁻² day⁻¹ (Fig. S8f) and this remobilization improves the correlations between Dstem and RWhighF (Fig. S20). However, the Cbud selection was also sensitive to the period and the site used in the optimization (Figs. S9 and S10).”

Comment 9

9. Page2 line 5: “compartments” mean “component”?

Response

We replaced “compartments” by “component”.

Comment 10

11. Figure 5: Please enlarge the scatter plot for both the Daily GPP and the Annual GPP

Response

We did the modification.

Comment 11

13. Figure 7: Please enlarge the scatter plot for both the detrended and raw Dstem.

Response

We did the modification.

Comment 12

14. Figure 9: The information about the colour scale is needed in the caption.

Response

We added in the caption (Fig. 7) the requested information: “unitless multiplier”

Comment 13

15. Table 1: It would be good to add the prior range in this table

Response

We added the prior range

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Interactive comment #1:

Comment 1

Title: Maybe it would make sense to remove “the climate imprint” and “North America” from the title: Ecophysiological modeling of photosynthesis and carbon allocation to the tree stem in the boreal forest. With this the title still informs about the content of the article: modeling of photosynthesis and carbon allocation and the link to tree stem growth, and as hinted in the article, the model can also be applied to other boreal forests outside of North America ! attract more readers with the article?

Response

We agree with this suggestion and modified the title.

Comment 2

Material and Methods: Overall well explained but tricky to get it straight. There are many factors and parts of the model explained but it would be helpful to have some kind of flowchart that explains in which order the model runs (see e.g. fig. 1 in Gea- Izquierdo et al., 2015 or Misson, 2004).

Figure 1: This figure is not optimal, although in its core it explains the MAIDEN model, text and visualization do not support each other and partly the text is not even clearly readable:

Response

We referred to the already published flowcharts and increased readability of Figure 1 reducing box transparency.

P 3 L 11 “(Fig. 1; see also flowcharts in Misson, 2004 and Gea-Izquierdo et al., 2015)”

Comment 3

Table 1: This table displays a significant amount of the authors work but has no real description.

Response

We added a more complete description.

Comment 4

One could argue that some parts in this chapter could be moved into the supplements: For extended reasoning to why something was done in whichever way: e.g. page 4, line 23 to 31 or page 5 lines 15 and 16, or page 7 sections 2.2.1 and 2.2.2.

This chapter is too long (especially compared to the discussion which is only half the size), having read this part, a reader must make a break or will lose attention during the next sections.

Response

We reduced several sections of our Materials and Methods and moved the information in the Supplement S2.

Comment 5

Figure 2 is not really adding something to the paper. Why no move into supplement?

Response

We moved Figs. 2 and 3 in the supplements (Figs. S2 and S3)

Comment 6

Chapter 2.2.3 Climate Data: Even though a considerable amount of work was put into acquiring climate data one might consider putting some part of this chapter into the supplements. This refers to the sentence ranging from line 9 to 13. It is an exhaustive sentence and could profit from a more detailed explanation within the supplements.

Response

We reduced the chapter and moved some information in the Supplement S2.

Comment 7

Results and Discussion: This part is – although to a lesser extent – still massive. It is quite difficult to find key aspects and concepts within the text. It would be nice to have a table (similar to Table 1), or bullet points or another form of highlighting of the key findings.

Response

Key findings are already highlighted by the figures:

Figs. 2 to 5 = Performance of MAIDEN in reproducing observed data

Figs. 6 to 8 = Impact of key model adaptations on the simulations and on the correspondence with observed data.

Comment 8

Figure 6: Is the indication “-1” really necessary when the title already states “previous year”?

Response

We deleted “-1” (Fig. 4).

Comment 9

Conclusion: Well written but also a bit too much text, one could remove lines 26 to 29 (page 12), (an interested researcher can always contact the authors for advice/guidance).

Response

We removed these lines.

Ecophysiological modeling of photosynthesis and carbon allocation to the tree stem in the boreal forest

Fabio Gennaretti¹, Guillermo Gea-Izquierdo², Etienne Boucher³, Frank Berninger⁴, Dominique Arseneault⁵, Joel Guiot¹

5 ¹CEREGE, Aix-Marseille University, CNRS, IRD, Aix en Provence, 13545, France

²Departamento de Sistemas y Recursos Forestales, CIFOR-INIA, Madrid, 28040, Spain

³Département de géographie, Université du Québec à Montréal, Montréal, H3C3P8, Canada

⁴Department of Forest Sciences, University of Helsinki, Helsinki, 00014, Finland

⁵Département de biologie, chimie et géographie, Université du Québec à Rimouski, Rimouski, G5L3A1, Canada

10 *Correspondence to:* Fabio Gennaretti (gennaretti@cerege.fr)

Abstract. A better understanding of the coupling between photosynthesis and carbon allocation in the boreal forest, with implicated environmental factors and mechanistic rules, is crucial to accurately predict boreal forest carbon stocks and fluxes, which are significant components of the global carbon budget. Here we adapted the MAIDEN ecophysiological forest model to better consider important processes for boreal tree species, such as non-linear acclimation of photosynthesis to temperature changes, canopy development as a function of previous year climate variables influencing bud formation, and temperature dependence of carbon partition in summer. We tested these modifications in the eastern Canadian taiga using black spruce (*Picea mariana* (Mill.) B.S.P.) gross primary production and ring-width data. MAIDEN explains 90% of the observed daily gross primary production variability, 73% of the annual ring width variability and 20-30% of its high frequency component (i.e. when decadal trends are removed). The positive effect on stem growth due to climate warming in the last decades is well captured by the model. In addition, we illustrate the improvement achieved with each introduced model adaptation and compare the model results with those of linear response functions. This shows that MAIDEN simulates robust relationships with the most important climate variables (those detected by classical response-function analysis), and is a powerful tool for understanding how environmental factors interact with black spruce ecophysiology to influence present-day and future boreal forest carbon fluxes.

25 1 Introduction

Photosynthetic production is the primary motor of growth of trees and other vegetation. However, empirical studies have shown that correlation between photosynthetic production and diameter growth of trees is far from being perfect (Gea-Izquierdo et al., 2014; Rocha et al., 2006; Berninger et al., 2004). This is due to the fact that plant hydraulics (e.g. turgor pressure) and thermal limitations during very short periods of time can be more important than carbon (C) availability for tree secondary growth (Kirdyanov et al., 2003; Rossi et al., 2016; Zweifel et al., 2016; Fatichi et al., 2014; secondary growth is the increase of the girth of the plant roots and stems). These factors influence the proportion of net primary productivity

allocated to stem growth each year, dampening the correlation between gross primary production (GPP) and growth. A better understanding of these factors and of carbon allocation mechanisms is needed when studying forest dynamics, forest carbon balance and the impact of climate change on forests. Indeed, carbon allocated in different tree **components** (e.g. canopy, stem **or roots**) has a specific function and is stored for a different length of time (Moorcroft, 2006).

- 5 The varying roles of allocation and photosynthetic production are integrated in ecophysiological models (Li et al., 2014). Such models are important tools to analyze the direct influence of climate and other environmental factors (e.g. CO₂ concentration) on tree growth and biogeochemical processes in forest ecosystems (Li et al., 2016). Climate-growth relationships have traditionally been assessed using empirical response functions based on linear relationships, thus considering the underlying processes as a black box. In contrast, ecophysiological models are built on mechanistic rules and
10 allow considering non-stationarity and non-linearity in tree responses to environmental variables as well as their interactions (Vaganov et al., 2006). Ecophysiological models may be refined using model-data fusion approaches and optimization techniques (Guiot et al., 2014).

Different models with a different degree of ecophysiological complexity and/or spatio-temporal resolution have already been used to investigate the influence of climate and weather on tree growth in the boreal forest. Some studies focused on the
15 drivers of photosynthetic capacity. For example, Mäkelä et al. (2004) proposed a model to study the influence of temperature on the seasonal variation in photosynthetic production of Scots pine through a delayed dynamic response. Other studies focused on the drivers of carbon allocation. For example, in Manitoba, Canada, a model related GPP and carbon allocation to absorbed photosynthetically active radiation as a function of environmental constraints (Girardin et al., 2008). Another model, called CASSIA (Schiestl-Aalto et al., 2015), was developed to investigate how environmental factors and the
20 ontogenetic stage of tree development influence the annual course of carbon sink–source dynamics in Scots pine stands. However, in spite of recent progress few models have been able to simultaneously simulate the meteorological control on daily photosynthetic production and the meteorological and phenological controls on daily carbon allocation for temperature-limited boreal forest ecosystems. **Such models should be able to simulate the following observed phenomena:** (i) delayed response of photosynthesis to temperature (Gea-Izquierdo et al., 2010; Mäkelä et al., 2004); (ii) influence of preceding
25 season conditions on current year canopy development (Salminen and Jalkanen, 2005); (iii) strong positive relationship between wood biomass production and temperature (Cuny et al., 2015).

Here we try to fill this gap by adapting the MAIDEN forest ecophysiological model, developed for temperate and Mediterranean environments (Misson, 2004; Gea-Izquierdo et al., 2015), to mimic how weather and climate influence photosynthesis, phenology and carbon allocation in the North American boreal forest on a daily basis. MAIDEN offers an
30 ideal framework to analyze the impact of introducing in the model relevant processes for carbon assimilation and allocation in temperature sensitive boreal trees. **Indeed, the model simultaneously simulates the course of photosynthesis and sets different phenological phases to determine the allocation of carbon to different plant compartments in a dynamical manner.** **In this study,** we **firstly** test and optimize new model features on GPP and growth data from black spruce (*Picea mariana* (Mill.) B.S.P.), the dominant tree species across the North American boreal biome. Secondly, we show the impact of single

processes in the model runs and the improvements achieved with the new model adaptations. Lastly, we compare the simulated GPP and stem growth results with those obtained with conventional empirical linear response functions. This comparison allows to verify that the process-based ecophysiological model satisfactorily reproduces the variability of the observed data and that its simulations keep robust relationships with the most significant climate variables.

5 2 Materials and Methods

2.1 The MAIDEN model

MAIDEN (Misson, 2004; Gea-Izquierdo et al., 2015) is able to consider the influence of several environmental factors on the forest water and carbon cycles. Starting from daily minimum-maximum air temperature, precipitation and CO₂ atmospheric concentration (these are the minimum required input variables which are completed by radiation, relative humidity and wind speed when additional meteorological data are available; Misson, 2004), MAIDEN models the phenological and meteorological controls on GPP and carbon allocation (Fig. 1; see also flowcharts in Misson, 2004 and Gea-Izquierdo et al., 2015). It explicitly allocates carbon to different pools (storage, canopy, roots and stem) on a daily basis using phenology-dependent mechanistic rules. The model has already been successfully optimized for *Quercus petraea* (Matt.) Liebl. and 12 Mediterranean species, including several *Pinus* spp. and *Quercus* spp. (Gaucherel et al., 2008a; Danis et al., 2012; Misson, 2004; Misson et al., 2004; Boucher et al., 2014; Gea-Izquierdo et al., 2015; Gaucherel et al., 2008b; Gea-Izquierdo et al., 2017). Up to now, the model has never been used to simulate forest growth in boreal conditions. MAIDEN requires the definition of species and site dependent parameters (Misson, 2004; Gea-Izquierdo et al., 2015), such as soil texture and depth and the root to leaf mass fraction in the studied trees. The parameters that could not be set for the studied black spruce sites were analyzed with a sensitivity analysis and the most influential of them were estimated with Bayesian optimization algorithms (Robert, 1996) using observed time series (daily GPP and annual ring width) as a reference. In total, six parameters influencing the GPP for black spruce and 12 parameters controlling the carbon allocation to the stem (Dstem) were optimized (they are described in the following paragraphs and in Table 1). The optimization was based on Markov Chain Monte Carlo (MCMC) sampling which, through its iterations, only retains combinations of parameters satisfying some conditions (Supplement S1; Fig. S1). Among the retained blocks of parameters, one block of six parameters controlling GPP (“Plausible Block GPP”) and one block of 12 parameters controlling Dstem (“Plausible Block Stem”) were selected to illustrate the results with likely parameter values (Supplement S1). The robustness of the parameters’ posterior distributions was tested on a cross-validation exercise (Supplement S1).

2.1.1 Modeling GPP of boreal forests

In MAIDEN, daily stand GPP (g C m⁻² day⁻¹) is derived from the modeling of the coupled photosynthesis-stomatal conductance system. Leaf photosynthesis is calculated following De Pury and Farquhar (De Pury and Farquhar, 1997), while stomatal conductance is estimated using a modified version of the Leuning equation (Leuning, 1995; Gea-Izquierdo et al.,

2015). The photosynthesis-stomatal conductance system is estimated separately for sun and shade leaves based on the photosynthetic photon flux density they receive. The partition of leaf area index (LAI) in its shaded and sunlit fractions and the transmission and absorption of photosynthetically active radiation (PAR) are computed as explained by Misson (Misson, 2004), following De Pury and Farquhar (De Pury and Farquhar, 1997). After a sensitivity analysis, and as stated in the literature for boreal forests (Gea-Izquierdo et al., 2010; Mäkelä et al., 2004; Mäkelä et al., 1996), we found that the modeling of assimilation/photosynthesis for black spruce is very sensitive to the parameters controlling the temperature dependence of maximum carboxylation rate (V_{cmax} ; $\mu\text{mol C m}^{-2}$ of leaves s^{-1}) and the water stress level (θg) influencing the stomatal conductance and consequently the intercellular CO_2 concentration. **The computations of V_{cmax} and θg used here are identical to those of the prior formulation of MAIDEN (Gea-Izquierdo et al., 2015). The V_{cmax} is modeled as:**

$$10 \quad V_{cmax_i} = \frac{V_{max}}{1 + \exp(Vb \cdot (Tday_i - Vip))} \quad (1)$$

V_{cmax} is a logistic function determining how daytime temperature ($Tday$; $^{\circ}\text{C}$) controls the maximum carboxylation rate at the day i if Rubisco is saturated. The parameters V_{max} , Vb and Vip are the asymptote, the slope and the inflection point of V_{cmax_i} , respectively. In the model, the temperature dependence when the photosynthesis is instead limited by electron transport (J_{max}) is considered as linearly related to V_{cmax} .

15 **The θg influencing stomatal conductance is modeled as:**

$$\theta g_i = \frac{1}{1 + \exp(soilb \cdot (SWC_i - soilip))} \quad (2)$$

θg is a logistic function, which varies from 0 (maximum stress) to 1 (no stress) at the day i depending on the soil water content (SWC ; mm). $soilb$ and $soilip$ are the slope and the inflection point of θg_i , respectively.

With its already published MAIDEN configuration (Gea-Izquierdo et al., 2015), the model overestimated black spruce GPP in spring. This is due to the fact that the model has been developed for temperate-Mediterranean trees where it can be assumed no time delay between **the recovery of photosynthesis and temperature increase in spring** (i.e. no temperature acclimation). However, such a delay is common in boreal trees (Gea-Izquierdo et al., 2010; Mäkelä et al., 2004). For this reason, we modified MAIDEN by including an extra function and an extra parameter (τ) to take into account acclimation of photosynthesis to temperature. Basically, we replaced $Tday$ in Eq. (1) by a temperature transformation (S), which responds smoothly with a determined time lag to temperature variations. S of the day i was computed from the following differential equation (Mäkelä et al., 2004), which was solved with the Euler's method:

$$25 \quad \frac{dS_i}{dt} = \frac{Tday_i - S_i}{\tau} \quad (3)$$

The new parameter τ is a time constant interpretable as the number of days needed by the photosynthetic apparatus to acclimate to changing temperature.

2.1.2 Modeling carbon allocation to the stem (Dstem) in boreal forests

MAIDEN allocates the daily available carbon from photosynthesis and stored non-structural carbohydrates to all plant compartments (stem, roots, canopy and storage) using functional rules specific to each of the five phenological phases characterizing a year (see Fig. 1). Although we maintained the original MAIDEN structure, we modified some previously used functional rules from Gea-Izquierdo et al. (2015) to consider significant processes for the boreal forest. We describe below the functional rules controlling Dstem, according to phenological phases.

During the “winter period 1” (phase 1) few processes are active. However, at the beginning of each year, the model defines the maximum amount of carbon that the canopy can potentially contain that year ($AlloCcanopy_j$; g C m⁻² of stand) as a function of previous year climate variables. Based on previous studies on black spruce forests (Girardin et al., 2016; Ols et al., 2016; Mamet and Kershaw, 2011), we modified the model to consider the effect of the previous year April precipitation and July-August temperature likely influencing the length and the thermal-hydraulic stress of the previous growing season, respectively. Previous year climate conditions of specific months are known to influence shoot extension of boreal trees likely because they control accumulation of resources in the buds (Salminen and Jalkanen, 2005). Here, we calculated the carbon potentially allocated each year to the canopy with the following equations:

$$CanopyMult = \frac{1}{1 + \exp(CanopyT \cdot Temp_{j-1})} \cdot \frac{1}{1 + \exp(CanopyP \cdot Precip_{j-1})} \quad (4)$$

$$AlloCcanopy_j = 0.7 \cdot MaxCcanopy + 0.3 \cdot MaxCcanopy \cdot CanopyMult$$

Where $Temp_{j-1}$ is the previous year mean July-August temperature (detrended and transformed to z-scores), $Precip_{j-1}$ is the previous year April precipitation (detrended and transformed to z-scores), and $MaxCcanopy$ is the absolute maximum canopy carbon reservoir according to forest traits, diameter distributions and previously published allometric equations (Chen, 1996; Bond-Lamberty et al., 2002a; Bond-Lamberty et al., 2002b). $CanopyT$ and $CanopyP$ are two parameters that were optimized and representing the slopes of the relationships between $CanopyMult$ (i.e. the overall climate dependence) and $Temp_{j-1}$ or $Precip_{j-1}$, respectively. In this way, $AlloCcanopy_j$ may vary between the 70% and the 100% of $MaxCcanopy$ as in the previous version of the model (Gea-Izquierdo et al., 2015).

During the “winter period 2” (phase 2), growing degree days (GDD) start to accumulate. We computed accumulation of GDD by summing the mean daily temperature values over 3°C (Nitschke and Innes, 2008; Man and Lu, 2010). MAIDEN simulates budburst (i.e. the transition from the phenological phase 2 to 3) either when the GDD sum threshold is reached (parameter $GDDI$) or when a selected day of the year related to photoperiod is passed (parameter $vegphase23$). With this model configuration, the start of the growing season overreacted to GDD yearly variations. To correct this simulated bias, we modified MAIDEN by adding a mechanism reducing the inter-annual variability of budburst dates. This mechanism simulates the acclimation of the plants to varying GDD sums from year to year. Basically, the yearly time series of days of the year corresponding to budburst (determined by GDD and photoperiod) is smoothed at the beginning of each simulation with a n -year cubic smoothing spline. The integer number n was called $day23_flex$ and optimized like the other parameters.

The “budburst phase” (phase 3) starts with budburst and ends when $AlloCcanopy_j$ is reached or when the carbon in the storage reservoir (i.e. stored non-structural carbohydrates) is lower than a minimum value (Misson, 2004). Here, this phase was set to be shorter than 51 days, based on available spruce budburst and shoot elongation data (Lemieux, 2010). During this phase, the daily available carbon (CT_i) comes from photosynthesis and mobilization of storage carbon. The parameter $Cbud$, which was optimized, is the amount of storage carbon that is used each day by the plant. The total CT_i amount is then allocated to the canopy, the roots or the stem following some functional rules. In the previous version of MAIDEN (Gea-Izquierdo et al., 2015), these rules were functions of daily soil moisture and air temperature. Here these rules did not improve the simulated results and we retained a simpler version independent from climate:

$$Cstem_i = CT_i \cdot (1 - h3) \quad (5)$$

where $Cstem_i$ is the portion of CT_i allocated to stem and $h3$ is a parameter to be defined in the range between 0 and 1. The rest of CT_i is allocated to the canopy or the roots, respecting a prescribed 1.65 root to canopy mass ratio for black spruce (Czapowskyj et al., 1985; Jenkins et al., 2003).

During the “growth and accumulation phase in summer” (phase 4), CT_i comes only from the photosynthesis and is allocated either to stem growth or storage as a function of climate forcing. In the previous version of MAIDEN for water limited sites (Gea-Izquierdo et al., 2015), the allocation rule used a combination of daily soil moisture and air temperature as predictors. Here for temperature limited sites, we only used temperature and set the soil moisture part to be with a null effect (i.e. always equal to 1, note that for more water limited boreal sites this water stress dependence can be used):

$$Cstem_i = CT_i \cdot \left(1 - 0.8 \cdot \exp \left(-0.5 \left(\frac{Tmax_i}{st4temp} \right)^2 \right) \right) \quad (6)$$

where $Tmax_i$ is the daily maximum temperature and $st4temp$ is a parameter that corresponds to the inflection point of the function. The value 0.8 was chosen to force a minimum threshold of C allocation to the stem in this phase (at least 20%) and to guarantee the correspondence between the inflection point and the temperature where roughly 50% of CT_i is allocated to the stem.

The transition from phase 4 to the “fall phase” (phase 5) is determined by either the parameter *photoper* (threshold of duration of daylight in hours) or by the occurrence of negative minimum daily temperature values after the 1st of September. During the “fall phase”, all photosynthetic products are allocated to the storage reservoir and mortality of fine roots occurs. No specific functional rule influences $Dstem$ during this phase.

The equation controlling partial carbon losses from the canopy (i.e. litterfall) and thus influencing the photosynthetic capacity through modifications of the total leaf area in the studied evergreen species, runs all year round. This equation is inspired from Maseyk et al. (2008):

$$outCcanopy_i = (PercentFall \cdot AlloCcanopy_j) \cdot \exp \left(-0.5 \left(\frac{DOY_i - 1}{OutMax} \right)^{OutLength} \right) - (PercentFall \cdot AlloCcanopy_j) \cdot \exp \left(-0.5 \left(\frac{DOY_i}{OutMax} \right)^{OutLength6} \right) \quad (7)$$

where $outCcanopy_i$ is the carbon loss from the canopy at day i and is influenced by parameters *PercentFall*, *OutMax*, and *OutLength* (to be optimized), which determine the yearly canopy turnover rate, the day of the year with maximum losses and the length of the period with losses, respectively.

2.1.3 Model evaluation

- 5 The proportion of the observed variability explained by MAIDEN was evaluated with the coefficient of determination (R^2), which compares the performance of simulated time series relative to that of straight horizontal lines centered on the data:

$$R^2 = 1 - \frac{\sum_i (Obs_i - Sim_i)^2}{\sum_i (Obs_i - \bar{Obs})^2} \quad (8)$$

2.2 Study sites and data

2.2.1 Eddy covariance observations

- 10 We used daily GPP data from one eddy covariance station located in a mature black spruce forest in the northern Quebec taiga (“Quebec Eastern Old Black Spruce” station - EOBS; 49.69N and 74.34W; data from 2003 to 2010; Bergeron et al., 2007; <http://fluxnet.ornl.gov/site/269>; additional information on Supplement S2 and Fig. S2) to optimize the six parameters influencing the stand GPP simulated by MAIDEN for the studied species.

2.2.2 Ring width data from the northern Quebec taiga

- 15 We assumed that the yearly D_{stem} is proportional to tree-ring growth in order to use ring width data to optimize MAIDEN (12 influential parameters). A regional chronology (hereafter RW) and a detrended regional chronology (hereafter RWhighF) were obtained from 46 black spruce trees sampled in the riparian forests of five lakes in the eastern Canadian taiga (Gennaretti et al., 2014; the coordinates of the central point are 54.26N and 71.34W; see Fig. S3, Dataset S1 and Supplement S2). RWhighF was then used as a reference for the optimization of the MAIDEN parameters, while observed and simulated
- 20 low frequencies were only compared after the optimization of the model parameters. MAIDEN outputs were simulated for the central point of the source area of ring width data over the 1950-2010 period.

2.2.3 Climate data

- MAIDEN needs daily climate data as inputs. These data were obtained from the gridded interpolated Canadian database of daily minimum–maximum temperature and precipitation for 1950-2015 (Hutchinson et al., 2009; <http://cfs.nrcan.gc.ca/projects/3/4>). CO₂ atmospheric concentration values for the same period were obtained extrapolating
- 25 the data from the CarbonTracker measurement and modeling system (2000-2015 period; Peters et al., 2007; <http://www.esrl.noaa.gov/gmd/ccgg/carbontracker/>) and the Mauna Loa observatory (1958-2015; Keeling et al., 1976; <http://www.esrl.noaa.gov/gmd/ccgg/trends/>). Additional information can be found in Supplement S2.

2.3 Response function analysis

Linear response functions are regression models used to quantify the proportion of the variability of the observed data (stem growth or GPP in our case) that can be explained by climate variables. These functions do not directly explore the mechanistic rules such as process-based models and are only optimized to achieve the best fit. Thus, comparing the results of linear functions and process-based models can help verify if model performance is satisfactory and if some important climatic factor related to some process is missing in the model. We used linear response functions to analyze the relationships between observed daily GPP at EOBS and daily mean, maximum and minimum temperatures or weekly precipitation (explored time lag from 0 to 30 days before; in the case of precipitation, lag n indicated the sum of the daily precipitation of the week ending in day n). In this analysis we excluded the winter days (days of the year between November 15th and April 1st) where GPP is zero. The 10 predictors most strongly correlated with GPP (and not highly correlated with each other; pairwise $r \in [-0.8, 0.8]$) were retained for the analysis. All linear response functions, resulting from a combination of these 10 predictors, were tested and classed according to their Bayesian information criterion (BIC).

We also used linear response functions to analyze the relationships between RWhighF and climate variables (same methodology than for GPP). We tested as predictors all monthly temperature and precipitation values of the previous and current years. Time windows of 31 days were used to obtain the time series of monthly data (over the 1950-2010 period) for each day (central day), averaging the values of each window and each year. These climate time series were also detrended such as RWhighF.

3. Results and Discussion

3.1 GPP and tree-ring growth variability explained by MAIDEN

The model explained a large proportion of the observed GPP daily variability (90%; $r=0.95$, $df=2918$, $p<0.001$; Fig. 2a). The posterior distributions of the parameters were quite sharp (Fig. S4; Table 1; by sharpness we mean the shrinking of the distribution relative to the prior acceptable range toward a posterior distribution with a well-defined, narrow peak). Sharp distributions with small posterior ranges relative to the prior ones indicate sensitive parameters. This means that the model posterior probability (i.e. model plausibility) increased significantly with the specific values of the selected parameters retained by the MCMC sampling. The slightly bimodal structures of the posterior distributions of V_{max} , V_b and V_{ip} were likely a consequence of their significant cross-correlations (Table S1). However, the posterior distributions of these three parameters were robust and consistent even when the Bayesian optimization was executed on independent periods (Fig. S5). Although the model was optimized with daily data, the GPP time series also reproduced the annual variability of the observed data quite well (Fig. 3). However, the ensembles of daily and annual time series retained by the MCMC sampling were not always centered on the observed time series (Fig. 3), in particular the simulated annual GPP values often underestimated the actual GPP especially at low observed GPP. This reflects the fact that the MCMC sampling maximized

the model plausibility according to the model structure and, by doing so retained similar blocks of parameters. Thus, the range of simulated values in Fig. 3 obtained with all retained iterations should be interpreted as the uncertainty due only to parameter selection while the uncertainty due to the non-perfect fit between observations and simulations was not taken into account.

5 As expected, the ring growth variability at our sites was more linked to temperature than to precipitation variables (see Fig. 4a and Gennaretti et al., 2014; Mamet and Kershaw, 2011; Nicault et al., 2014). The model was able to reproduce this correlation pattern (Fig. 4b) and explained about 20-30% of the observed yearly RWhighF variability corresponding to correlations of 0.58-0.66 (df=59, $p<0.001$; Figs. 2b and S6). This is a good result because simulated detrended annual GPP values (i.e. photosynthetic assimilation before any carbon allocation) had only negative R^2 with RWhighF (Fig. 2c; meaning performance worse than a straight line centered on RWhighF) and much lower correlations (Figs. S6 and S7). This suggests that the modified MAIDEN daily partition of carbon in the plant compartments significantly improved the concordance with tree-ring observations. Most posterior distributions of parameters were quite sharp (Fig. S8; Table 1), meaning that the MCMC sampling selected similar blocks of parameters resulting in high model posterior probabilities. However, the optimization of some parameters (the three related to the start of the growing season and *Cbud*) was sensitive to the choice of the period and the site in the cross-validation exercise (Figs. S9 and S10) likely as a result of the short length of the available observed data (61 yearly RWhighF values). The variance explained by the model increased importantly when the time series of stem growth were analyzed with their trends ($R^2=0.73$ and $r=0.86$, df=59, $p<0.001$; Fig. 5b). Indeed, the positive trend in response to the warming of the last few decades was well captured by the model simulations of stem increments, which included some CO_2 fertilization contribution (Fig. S11). This explained variance was higher than that explained by MAIDEN for Mediterranean sites (R^2 slightly above 0.5; Gea-Izquierdo et al., 2015).

3.2 Mechanistic diagnostics

The modeled impact of temperature on the maximum rate of Rubisco-catalyzed carboxylation (V_{cmax}) is shown in Fig. S12. This figure was obtained using Eq. (1) and (3) with the parameters of Plausible Block GPP and using actual temperature data. The obtained V_{cmax} values were comparable to those obtained for another mature black spruce forest in Saskatchewan, Canada (Rayment et al., 2002). Furthermore, the impact of soil water content on the water stress level (θg) influencing the stomatal conductance is shown in Fig. S13. Simulated GPP values were sensitive to all single parameters controlling V_{cmax} or θg , except *soilb* (Fig. S14-S18). The temperature transformation (S) introduced here in MAIDEN also influenced the simulation results (Fig. 6). With no time delay between photosynthesis and temperature increases (i.e. $\tau = 1$ and $S = Tday$) MAIDEN overreacted to temperature variations in spring and the GPP annual cycle was antedated (start in spring and highest summer values were too early). In contrast, the use of S with τ values between 10 and 15 days synchronized the GPP annual cycle with observations. This means that black spruce photosynthetic capacity needs about 10-15 days to acclimate to higher daily temperature (e.g. τ equal to 12.43 days was selected for Plausible Block GPP). This time

delay is a little longer than that previously found for black spruce but comparable to values found for Scots pine (Mäkelä et al., 2004; Gea-Izquierdo et al., 2010; Gea-Izquierdo et al., 2014).

We modified important processes for carbon allocation in order to adapt MAIDEN to black spruce. For example, previous year precipitation and temperature values influenced the potential maximum amount of carbon that the canopy can contain during the growing season as illustrated in Fig. 7a (see Eq. (4)). Basically, if both previous April precipitation and July-August temperature indexes are negative, the potential amount of carbon simulated by the model would be maximum, otherwise it would be minimum. This was coherent with the correlations shown in Fig. 4 and we can propose the following reasons to explain this behavior: warm previous Aprils with infrequent late snowfalls may accelerate snowmelt and the start of the previous growing season, allowing optimal reserve accumulation during the previous year which would influence tree performance the following growing year. This mechanism may be significant especially if we do not observe high temperatures limiting soil water availability and reserve accumulation during the previous summer (Girardin et al., 2016). It has already been shown that shoot elongation of boreal conifers is determined by climate conditions during bud formation (Salminen and Jalkanen, 2005). However, for Scots pine, previous summer temperatures are positively correlated with shoot elongation, while in our case, the opposite process was simulated and the simulations were even more sensitive to the values of the temperature dependent parameter *CanopyT* than to those of the precipitation dependent parameter *CanopyP* (Fig. 7b-e). Clearly, we need more data on canopy development and shoot elongation to verify the model results.

Another important process is the start of the growing season. According to our simulations, the start could not happen later than June 17th (Figs. S8d and S19; Table 1) and was influenced by the GDD sum and the photoperiod, which are known to be relevant for black spruce budburst along with the tree provenance (Rossi and Bousquet, 2014). However, because we added a mechanism to smooth yearly variations (see the *day23_flex* parameter), more years were needed by the plants to acclimate to more or less fast GDD accumulations in winter-spring. With the selected parameters to simulate stem growth, the median onset of the growing season was June 10th (similar to observations for black spruce in northern Manitoba, Canada; Bronson et al., 2009) with a standard deviation of 7.8 days. If the smoothing term was excluded, the standard deviation increased to 9.4 days (see Fig. S19a). The inclusion of the smoothed mechanism also decreased the correlation between the simulated detrended annual *Dstem* and May average temperature from 0.70 to 0.59 ($df=58$, $p<0.001$). Although this is still a high correlation, it was closer to the correlation between *RWhighF* and May temperature ($r=0.27$, $df=58$, $p<0.05$; Fig. 4). These results show how the new model configuration decreased the yearly variability of the growth onset and helped achieving more plausible correlations with climate variables. According to the simulations, the onset of the growing season shifted by 7 days from June 14th to June 7th between the 1950-1970 and 1990-2010 periods (Fig. S19b-c). This result is consistent with the study of Bronson et al. (2009) on the effect of warming on black spruce budburst but should be taken with caution because the parameters *GDD1*, *vegphase23* and *day23_flex* were sensitive to the data used in the optimization (Figs. S9 and S10) and were also significantly inter-correlated (Table S2).

In phase 3, corresponding to Budburst, a portion of the available carbon simulated by MAIDEN comes from stored non-structural carbohydrates from the current and previous years (parameter *Cbud*; see Table 1). In our case, *Cbud* was

quantified as about $1.69 \text{ g C} \cdot \text{m}^{-2} \text{ day}^{-1}$ (Fig. S8f) and this remobilization improves the correlations between *Dstem* and *RWhighF* (Fig. S20). However, the *Cbud* selection was also sensitive to the period and the site used in the optimization (Figs. S9 and S10). During phase 3 in our simulations, almost all available carbon was allocated to the canopy and roots ($h3 \approx 0.9905$; Eq. (5); Fig. S8g; Table 1). For this reason, the previously used soil moisture and temperature dependences, determining the portion of carbon allocated to the stem in Mediterranean evergreen woodlands (Gea-Izquierdo et al., 2015), did not improve the results and could be excluded here. The partition of carbon during the growth and accumulation phase in summer (phase 4) was instead modeled as a function of temperature (Eq. (6)). Warmer temperature corresponded to a greater portion of carbon allocated to the stem and less to non-structural carbohydrates (Fig. 8a-b), being the simulations highly sensitive to the *st4temp* parameter (Fig. 8c-d). These results are in part in line with those of Cuny et al. (2015), who showed that woody biomass production is low in the first part of the growing season for most coniferous tree species because it follows the seasonal course of temperature (highest peak in summer). The simulated accumulation of carbon to the stem ended each year when the photoperiod became shorter than about 13.41 hours (Fig. S8i; Table 1), corresponding to September 2nd. The model performance was very sensitive to this parameter which is known to impact black spruce dormancy induction (D'aoust and Cameron, 1982).

Another important process for carbon allocation is the definition of the carbon losses from the canopy, a process that influences the seasonal course of the photosynthetic capacity. According to the simulations, the canopy mean annual turnover rate was about 13-14% (Fig. S8j; Table 1), which corresponds well to previously published values for boreal spruce species (Tůpek et al., 2015). The simulated annual cycle of canopy losses (Fig. S21) culminated on July 2nd and 80% of litterfall occurred between May 27th and July 19th. This cycle is also similar to published results showing that the majority of litterfall ($\approx 80\%$) occurs in summer during needle growth for conifer species (Maseyk et al., 2008).

3.3 Comparison between MAIDEN and response functions

The comparison between MAIDEN simulations and classic linear response functions confirmed the quality of the simulated results with the process-based model and justified our modeling choices.

In the case of daily GPP, we were able to draw the following conclusions by the response function analysis (Table 2). First, MAIDEN performed better than response functions in explaining the variability of daily GPP ($R^2=0.90$ vs 0.69), suggesting that it properly simulates climate-driven processes governing photosynthetic assimilation, which are well known to be a result of several non-linear processes. Second, most of the variance explained by the response functions was due to temperature variables, reflecting the greater sensitivity of northern black spruce forests to temperature as compared to drought stress (Gennaretti et al., 2014) and justifying the modeling in MAIDEN of the maximum carboxylation rate as a function of temperature. Third, only temperature variables of preceding days were retained, justifying the inclusion of our acclimation function of photosynthesis to temperature in order to increase the influence of previous days. Fourth, the coefficient estimate for precipitation of lag 0 (i.e. week ending in day 0) was negative, while the one of lag -2 was positive,

even though these variables share 5 out of 7 days of data. The reduction of absorbed photosynthetically active radiation associated to cloudiness during raining days could explain this result.

In the case of annual **radial growth**, the selected response function (Table 3) captured 50% of the observed R_{HighF} variability using only three temperature variables. This, once again, confirms that black spruce forests in the study area are especially sensitive to temperature (Gennaretti et al., 2014). The MAIDEN simulated time series were able to respect the relationship with the significant monthly climate variables detected with the response function analysis. Indeed, correlation coefficients of -0.39, 0.46 and 0.57 ($df=58$, $p<0.01$) were obtained between MAIDEN D_{stem} ($g\ C\cdot m^{-2}\ year^{-1}$) and previous July-August, growing year July and growing year May-June temperature values, respectively (Fig. 4b; these coefficients are to compare with those in Table 3). This concordance supports the plausibility of the simulated series. However, the explained variability with the best response function (50%) was greater than with MAIDEN (20-30%; $r \approx 0.65$, $df=59$, $p<0.001$; Fig. 2b), suggesting that the process-based modeling can potentially be improved with additional data and including stronger legacy effects of the year preceding ring formation (Girardin et al., 2016). Indeed, most of the variance explained by the response function was due to a negative correlation with the temperature of the previous summer. Contrasting correlations with summer temperature values of the previous and **the current** growing year are also visible in Fig. 4a and have already been observed for black spruce (Mamet and Kershaw, 2011; Ols et al., 2016).

3.4 Limits and error sources of the study

Although the simulated results with MAIDEN were satisfactory, we have to consider two important limits and error sources of the study. First, for the optimization of carbon allocation, we assumed that stem biomass (or carbon) increments were proportional to ring growth. This was necessary because data from field plots were not available from all study sites. A recent study showed that the maximum rate of ring width increase during the growing season precedes the maximum rate of increase in wood biomass and that these processes could exhibit differential sensitivities to local environmental conditions (Cuny et al., 2015). However, Cuny et al. (2015) also highlighted that wood biomass production follows the seasonal course of temperature in coniferous forests and this is exactly what we got once MAIDEN was optimized. Indeed, almost all available carbon in spring was allocated to the canopy and roots (Fig. S8g; Table 1), whereas C allocation to the stem (D_{stem}) in summer increased with temperature (Fig. 8). Furthermore, the used ring width series were highly correlated with July-August temperature as expected for wood biomass production and for climate-growth analysis for the studied species. Second, we modeled GPP and carbon stem increments of a boreal tree species using mechanistic rules which increased the capability of MAIDEN to reproduce observed variations. However, our choice of mechanistic rules was subjective in part and depended on previous physiological knowledge and on model-data comparisons. Such model refining is an important step of all model-data fusion approaches (Guiot et al., 2014) and increases our understanding of ecosystem functioning and responses. Nevertheless, the proposed mechanistic rules should be verified in the future with additional data from a wider boreal area.

4. Conclusion

In this study, we adapted a process-based forest ecophysiological model, developed for temperate and Mediterranean forests, to simulate gross primary production and stem biomass increment for black spruce, the dominant species across the North American boreal forest. The model used, MAIDEN (Misson, 2004; Gea-Izquierdo et al., 2015), has the specificity to simultaneously simulate the course of photosynthesis and phenological phases characterized by specific allocation rules dependent on climatic conditions. The model was able to represent the tree-ring inter-annual variability even though detrended radial growth was poorly explained by the simulated annual GPP (Fig. 2b-c), which suggests that the relationship between GPP and wood production is complex and non-linear (Rocha et al., 2006). Significant simulation improvements were obtained introducing in the model important processes for temperature sensitive boreal forests, such as: (i) the acclimation of photosynthesis to temperature over several days (see Gea-Izquierdo et al., 2010; Mäkelä et al., 2004); (ii) the influence of previous year climatic conditions affecting bud formation on the potential amount of carbon allocated to the canopy each year (see Salminen and Jalkanen, 2005); (iii) the positive relationship between temperature and the carbon allocated to the stem in summer (see Cuny et al., 2015). Although we used black spruce data from the northern Quebec taiga to test and optimize the model, the new model modifications have the potential to work within other boreal regions and tree species. Indeed, the effect of the introduced functions can be amplified, reduced or canceled out in the Bayesian optimization procedure according to the relevance of specific processes in the studied forest.

Boreal ecosystems are crucial carbon stores that must be urgently quantified and preserved (Bradshaw et al., 2009). Their future evolution is extremely important for the global carbon budget. Development of process-based models, such as the one used and improved here, combined with continuous field data acquisition, will help disentangle the role of the different environmental factors and underneath mechanisms on present and future boreal forest carbon fluxes. In this context, we believe that our study helps to understand how boreal forests assimilate and allocate carbon depending on weather/climate conditions.

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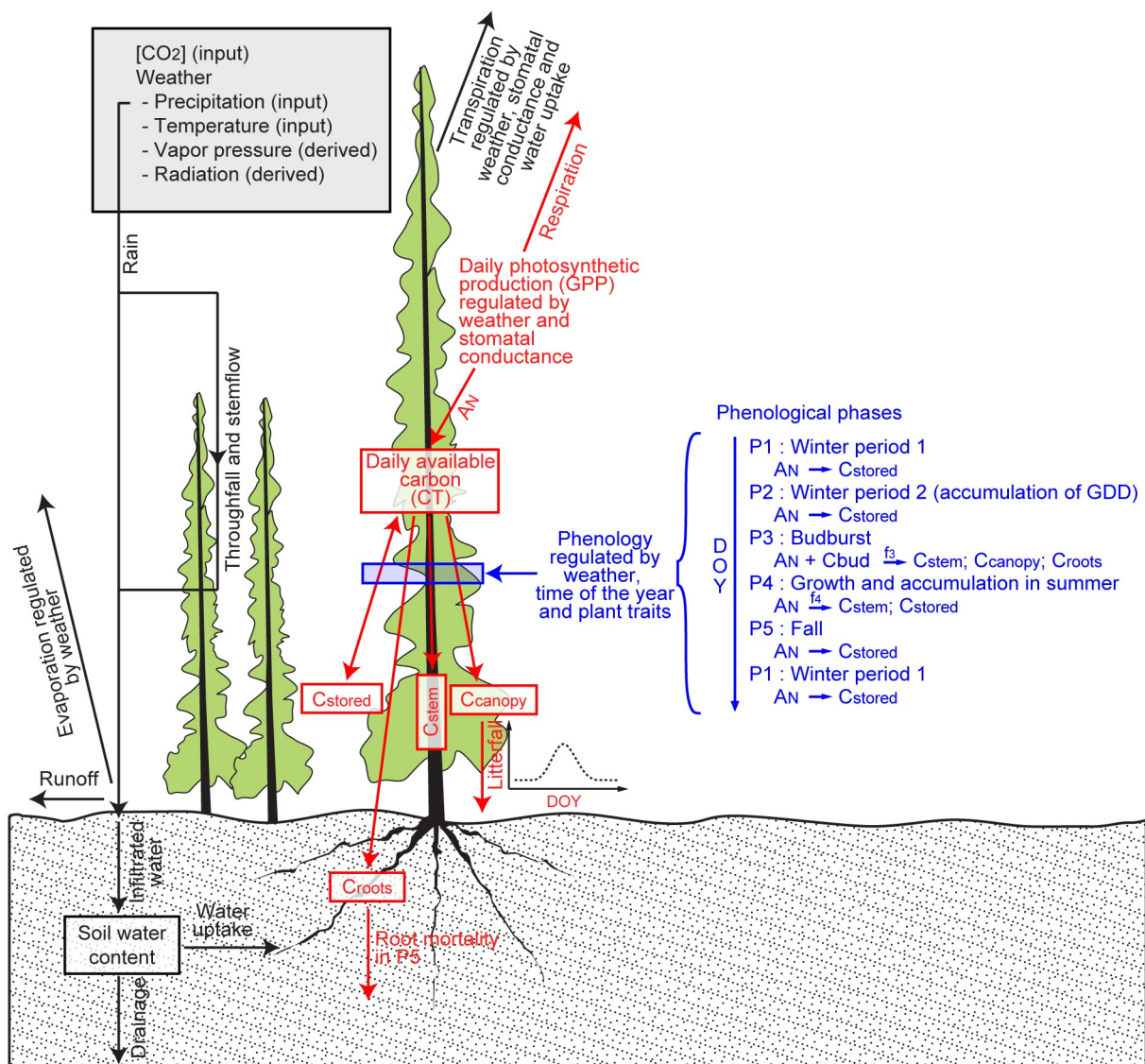


Figure 1: MAIDEN simulated phenology (blue), water (black) and carbon (red) fluxes. AN: net photosynthesis corresponding to net primary production. C_{stored}, C_{stem}, C_{canopy}, C_{roots}: carbon allocated daily to stored non-structural carbohydrates, stem, canopy or roots. DOY: day of the year (1-365). GDD: growing degree days. f₃ and f₄: functions determining carbon allocation in phase 3 and 4. C_{bud}: amount of storage carbon that is used each day by the plant in phase 3.

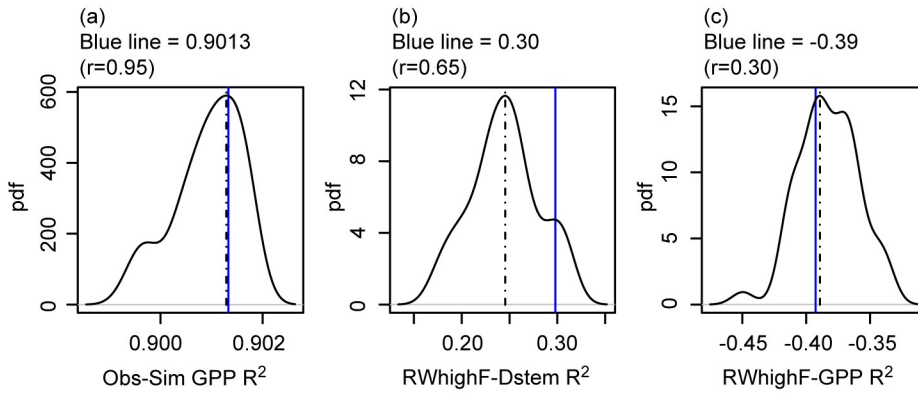


Figure 2: Variance explained by the model. (a) R^2 between observed and simulated GPP daily values. R^2 (computed on data transformed to z-scores) between the mean of the detrended series of black spruce ring growth (RWhighF) and simulated yearly detrended C allocation to the stem (b) or GPP (c). Vertical dashed line is the mode and blue line is the value with Plausible Block GPP (in (a)) or with Plausible Block Stem (in (b) and (c)). All pdfs are based on 50 simulations.

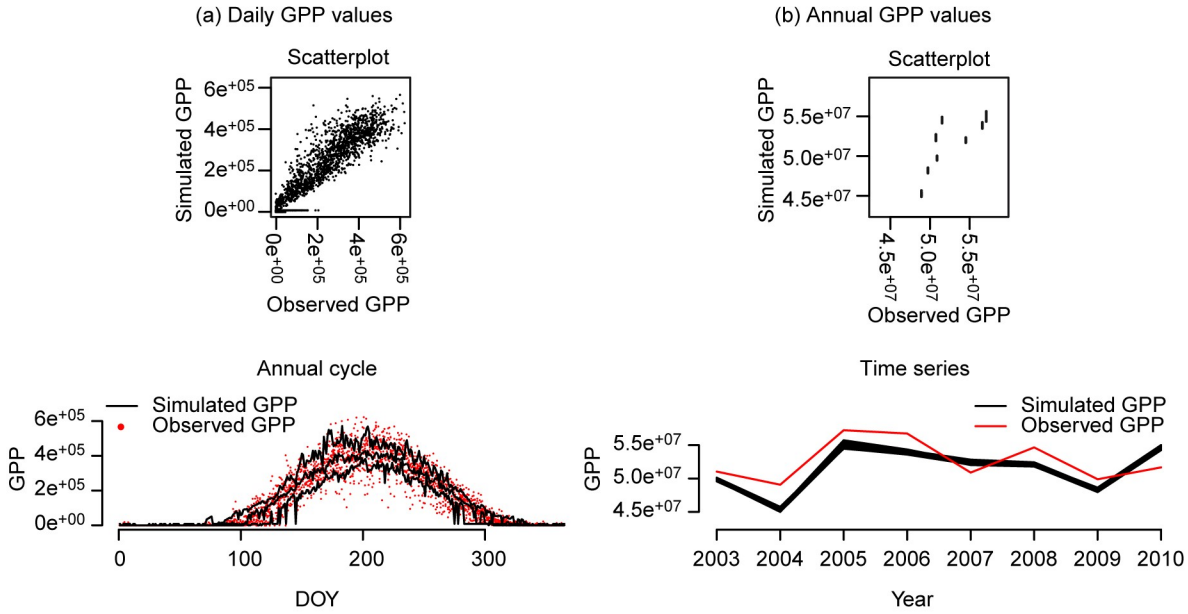


Figure 3: Comparison between observed GPP values and MAIDEN simulated values at the Quebec Eastern Old Black Spruce site. (a) Daily values (units are $\mu\text{mol C m}^{-2} \text{ day}^{-1}$). In the scatterplot ($R^2=0.90$; $r=0.95$, $df=2918$, $p<0.001$), observations are compared with the values obtained with Plausible Block GPP. In the annual cycle plot, black lines are the medians, the 5th and the 95th percentiles of the simulated values from all iterations retained by the MCMC sampling. (b) Annual values (units are $\mu\text{mol C m}^{-2} \text{ year}^{-1}$). In both plots, observations are compared with the values from all iterations retained by the MCMC sampling. In the scatterplot, the R^2 of the data is 0.31 ($r=0.76$, $df=6$, $p<0.05$).

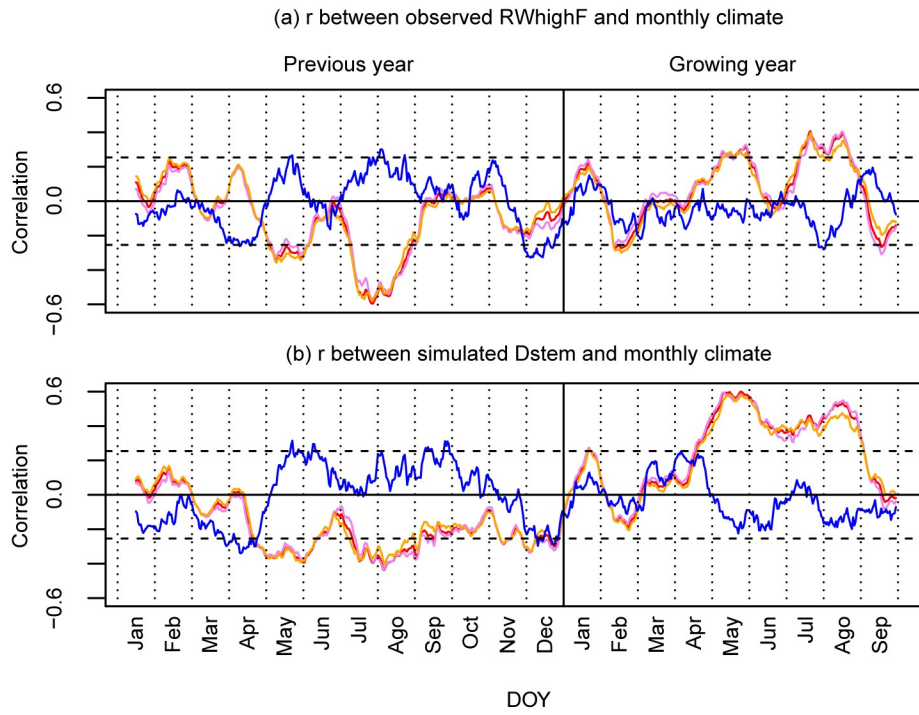


Figure 4: Correlation between monthly climate variables of the study area (precipitation in blue and mean, maximum and minimum temperature in red, violet and orange respectively) and the mean of the detrended series of black spruce ring growth (RWhighF; a) or the simulated detrended annual carbon allocation to the stem (Dstem; b). For the climate variables, time windows of 31 days are used to obtain time series of monthly data (over the 1950-2010 period) for each day (central day), averaging the values of each window and each year. These climate time series are then also detrended. **Thresholds of significance ($p < 0.05$) are shown by horizontal dashed lines.**

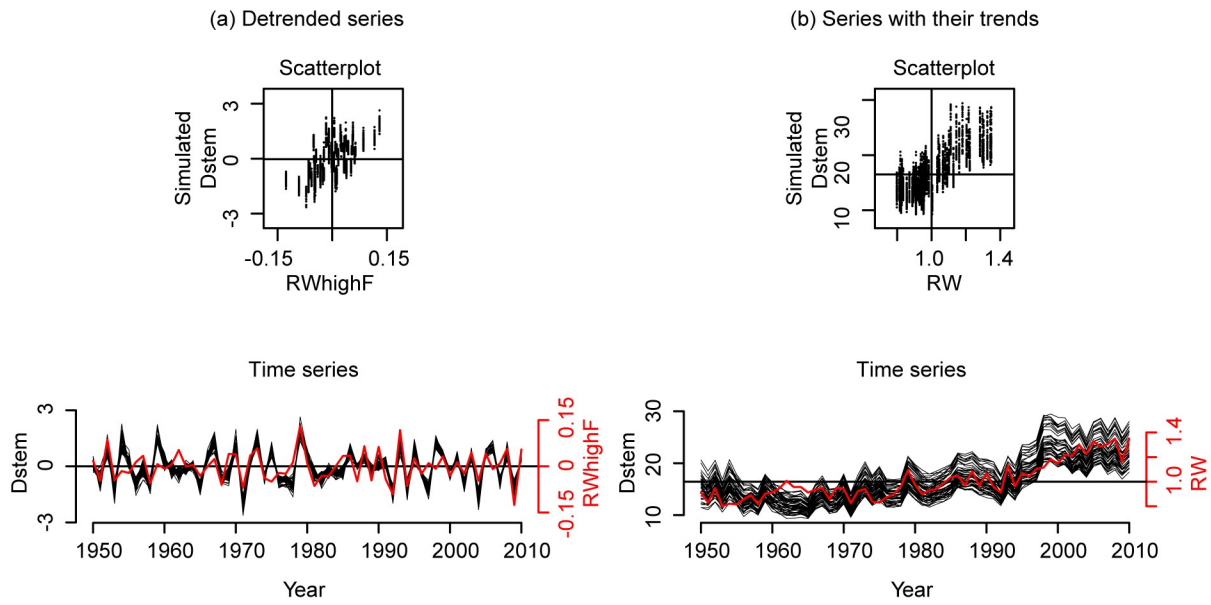


Figure 5: Comparison between the observed mean series of black spruce ring growth (**unitless** growth indexes) and MAIDEN simulated carbon allocation to stem (**Dstem**; $\text{g C m}^{-2} \text{ year}^{-1}$). (a) Detrended series (in the scatterplot the R^2 computed on data transformed to z-scores is 0.24; $r=0.62$, $df=59$, $p<0.001$). (b) Series with their trends (in the scatterplot the R^2 is 0.73; $r=0.86$, $df=59$, $p<0.001$). In all plots, observations are compared with the values from all iterations retained by the MCMC sampling.

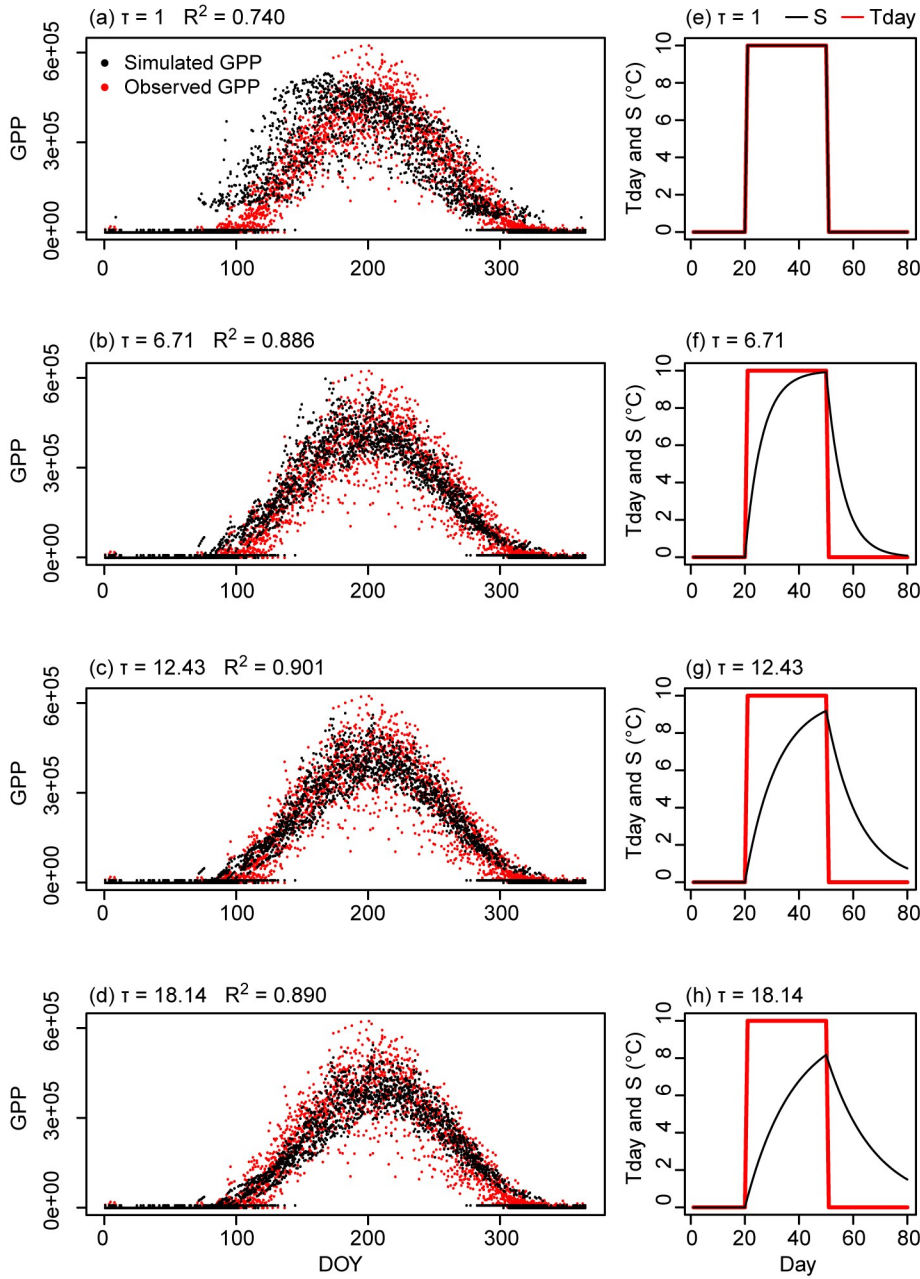


Figure 6: Influence of the temperature transformation (S) on the modeled annual cycle of GPP daily values ($\text{umol C m}^{-2} \text{ day}^{-1}$) at the Quebec Eastern Old Black Spruce site. Only the τ parameter determining the S values was allowed to vary, while the other parameters were fixed to the values of Plausible Block GPP. (a) τ is 1 **day** (S same as T_{day}). (b) τ is 6.71 **days** (a middle value between 1 and 12.43). (c) τ is 12.43 **days** (same τ than in Plausible Block GPP). (d) τ is 18.14 **days** (a higher value than in Plausible Block GPP). The R^2 between observations and simulations is reported in each plot. Plots e-h show the impact of the respective τ values on S if the daily T_{day} time series corresponds to a single step of 10°C lasting 30 days.

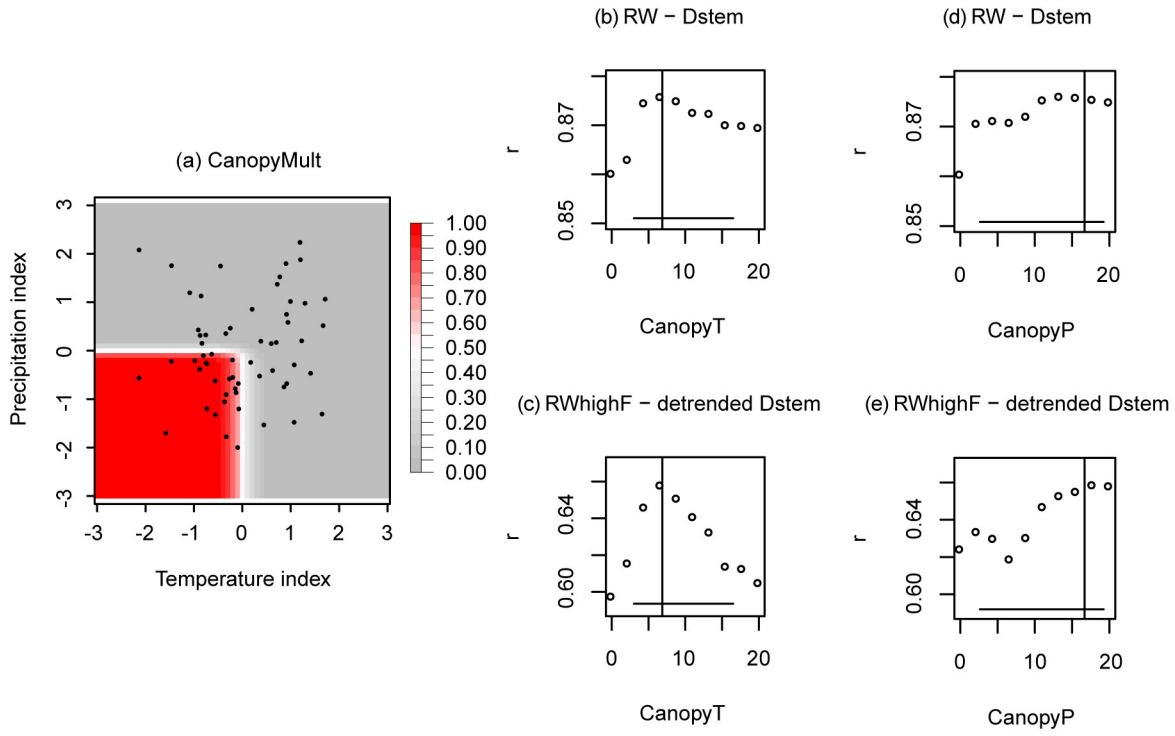


Figure 7: Temperature and precipitation dependence of *CanopyMult* (plot a; unitless multiplier; Eq. (4); *CanopyT* and *CanopyP* are those of Plausible Block Stem), which determines the yearly canopy potential amount of carbon. Previous year mean July-August temperature indexes are on the x-axis and previous year April precipitation indexes are on the y-axis. Black dots are observed values in the central point of the region with ring width data. Plots b-e show how *CanopyT* and *CanopyP* (varying over their prior acceptable ranges) impact the correlations between simulated Dstem ($\text{g C m}^{-2} \text{ year}^{-1}$) and observed ring width data (RW or RWHighF; unitless indexes), when all other parameters are fixed to the values of Plausible Block Stem. The vertical lines are the selected values for Plausible Block Dstem and the horizontal lines are the 90% confidence intervals based on the parameters' posterior densities (Fig. S8).

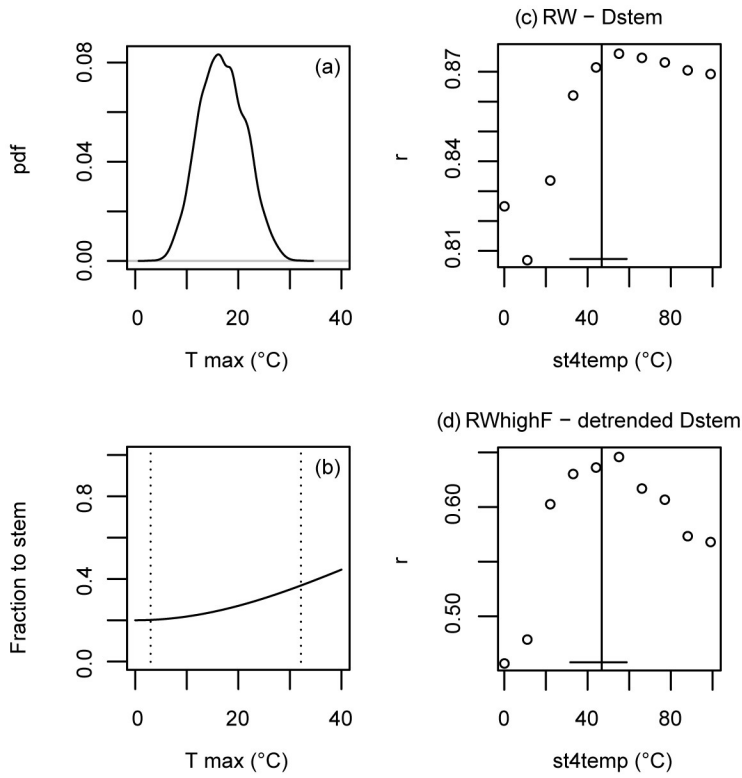


Figure 8: Temperature dependence of the daily partition of carbon in phase 4 (growth and accumulation phase in summer) when MAIDEN is run with the parameters of Plausible Block Stem at the center of the region with ring width data in the northern Quebec taiga. (a) Probability density of daily maximum temperature values in summer. (b) Relationship between maximum temperature values and portion of carbon allocated to the stem (Eq. (6)). The vertical dashed lines show the range of maximum temperature values. **Plots c-d show how the parameter $st4temp$ influencing this process impacts the correlations between simulated Dstem and observed ring width data (RW or RWhighF), when all other parameters are fixed to the values of Plausible Block Stem and $st4temp$ varies over its prior acceptable range. The vertical line is the selected value for Plausible Block Dstem and the horizontal line is the 90% confidence interval based on the parameter's posterior density (Fig. S8).**

Table 1: Definitions, symbols, prior and posterior ranges of calibrated parameters. Small posterior ranges relative to the prior ones indicate sensitive parameters.

Overall process	Specific Process	Eq.	Parameter	Meaning	Units	Prior Range	Posterior range (value in Plausible Block)
GPP	Temperature dependence of V_{cmax}	1	V_{max}	Asymptote / maximum value	$\mu\text{mol C m}^{-2}$ of leaves s^{-1}	5 / 150	39 / 67 (45)
	Temperature dependence of V_{cmax}	1	V_b	Slope	NA	-0.30 / -0.10	-0.21 / -0.17 (-0.20)
	Temperature dependence of V_{cmax}	1	V_{ip}	Inflection point	$^{\circ}\text{C}$	10 / 30	17.5 / 22.3 (18.8)
	Water stress level influencing the stomatal conductance	2	$soilb$	Slope	NA	-0.025 / -0.005	-0.023 / -0.008 (-0.012)
	Water stress level influencing the stomatal conductance	2	$soilip$	Inflection point	mm	100 / 400	102 / 193 (129)
	Acclimation to temperature of photosynthesis	3	τ	Needed days	days	1 / 20	11.6 / 13.7 (12.4)
C allocation to stem	Definition of canopy maximum amount of C	4	$CanopyT$	Slope of the temperature dependence	NA	0 / 20	0.54 / 19.24 (6.87)
	Definition of canopy maximum amount of C	4	$CanopyP$	Slope of the precipitation dependence	NA	0 / 20	1.70 / 19.85 (16.68)
	Start of growing season (budburst)	NA	$GDD1$	GDD sum threshold	$^{\circ}\text{C}$	10 / 120	56.75 / 87.05 (70.22)
	Start of growing season (budburst)	NA	$vegphase23$	Day before the later start	day of the year	152 / 181	161.5 / 171.0 (167.0)
	Start of growing season (budburst)	NA	$day23_flex$	Acclimation to changing GDD sums	years	1 / 10	1.53 / 3.29 (2.24)
	Daily available C in phase 3	NA	$Cbud$	Storage C used by the plant	g C m^{-2} of stand $\cdot \text{day}^{-1}$	1 / 3	1.59 / 1.86 (1.69)
	Partition of C in phase 3	5	$h3$	Portion allocated to canopy and roots	fraction (0-1)	0 / 1	0.983 / 1.000 (0.991)
	Partition of C in phase 4 (stem versus storage)	6	$st4temp$	Inflection point of the temperature dependence	$^{\circ}\text{C}$	1 / 100	27.53 / 59.11 (46.78)
	Transition from phase 4 to 5	NA	$photoper$	Photoperiod threshold	hours	12 / 14	12.96 / 13.72 (13.41)
	C losses from the canopy	7	$PercentFall$	Yearly canopy turnover rate	fraction (0-1)	0.09 / 0.15	0.093 / 0.149 (0.143)
	C losses from the canopy	7	$OutMax$	Approximate day of the year with maximum losses	day of the year	150 / 200	154.2 / 195.0 (171.7)
	C losses from the canopy	7	$OutLength$	Index proportional to the length of the period with losses	NA	4 / 12	4.80 / 10.80 (9.91)

Table 2: ANOVA table for the best response function (here a combination of 4 out of the 10 tested predictors minimized the BIC) with daily GPP at EOBS as dependent variable (excluding days between November 15th and April 1st). All F values are highly significant ($p < 0.001$). For precipitation, lag n indicates the sum of the daily precipitation of the week ending in day n.

Predictor	Pairwise correlation with GPP	ANOVA table				BIC
		Regression coefficient	d.f.	Variance explained	F value	
Maximum temperature – lag -2 days	0.79	0.149	1	0.630	3716.16	5288.3
Maximum temperature – lag -19 days	0.69	0.057	1	0.049	291.29	
Precipitation – lag -2	0.21	0.019	1	0.005	31.99	
Precipitation – lag -0	0.16	-0.013	1	0.005	29.90	
Total variance explained				0.690		
Residuals	NA	NA	1827	0.310	NA	5315.4
Function with all 10 tested predictors				0.694		

Table 3: ANOVA table for the best response function (here a combination of 3 out of the 10 tested predictors minimized the BIC) with the observed mean detrended ring width series (RWhighF) as dependent variable.

Predictor (monthly data around the indicated day of the year)	Pairwise correlation with RWhighF	ANOVA table				BIC
		Regression coefficient	d.f.	Variance explained	F value	
Mean temperature – Previous July 28 th	-0.60	-0.477	1	0.355	39.88***	
Mean temperature – July 22 th	0.41	0.247	1	0.055	6.14*	
Maximum temperature – May 30 th	0.33	0.146	1	0.093	10.48**	
Total variance explained				0.502		148.7
Residuals	NA	NA	56	0.498	NA	
Function with all 10 tested predictors				0.568		169.0

***($p < 0.001$); **($p < 0.01$); *($p < 0.05$)