report for the COST STSM

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Title: A drought induced mortality model based on physiological mechanisms. Model structure development, Bayesian calibration, global sensitivity analysis and validation of the model.

1. Purpose of the STSM

During the last decades forests are experiencing increases in the frequency, length and intensity of extreme climatic events. The increase in tree mortality caused by climatic changes is altering the structure and the functionality of forest ecosystems (Allen et al., 2010; McDowell et al., 2008). Driest ecosystems are becoming more vulnerable to drought, therefore there is a growing interest in understanding mechanisms of plant mortality induced by water stress. The processes underpinning tree mortality are still poorly understood. McDowell et al. 2008 proposed a general framework to explain mortality; the framework consisted of three hypothetical mechanisms: biotic agent demographics, hydraulic failure and carbon starvation. The biotic agent demographics hypothesis states that mortality agents (i.e., pathogens and insects) effects can be enlarged by drought. The hydraulic failure hypothesis suggests that high evaporative demand in combination with reduced soil water availability can encourages cavitation of xylem conduits and rhyzosphere, causing plant death. The carbon starvation hypothesis suggests that stomatal closure to minimize hydraulic failure provokes a reduction of C uptakes and plants can succumb as the metabolic demand for carbohydrates continues.

The aim of the short term scientific mission is to calibrate a process-based model, developed by Mencuccini et al. (in prep.), that reproduces the mechanisms determining plant mortality. To better understand model behaviour and to identify the key parameters and variables a global sensitivity analysis of the model was carried out by means of canonical correlation analysis (CCA) (Minunno et al., submitted).

2. Description of the work carried out during the STSM.

Model

First of all a study of the model was carried out. Mencuccini et al. (in prep.) developed a steady-state physiological model that simulates the major processes involved in drought-induced mortality. The model reproduces the water and carbon fluxes in plants; it describes the gas exchange at leaf level (i.e., photosynthesis, stomatal conductance and transpiration), the transport of water and carbohydrates through the phloem and xylem systems and the water and carbohydrates uptake from the sink tissues. In total 13 processes are represented in the model and 17 parameters describe the relationships between driving and state variables; for the calculation of phloem and xylem transport, the plant was divided vertically into N elements (N=40). Eleven of the 17 parameters of the model were identified as the most important for the mode of plant failure (Mencuccini, personal communication). In the model, the possible modes of plant failure are: carbon starvation, hydraulic failure and phloem transport failure. A drought sequence was imposed on the model, starting from a soil water potential of -0.005 MPa and decreasing water potential in steps of 0.005 MPa each. At each step the steady-state values for all the model variables were calculated and it was checked whether one of the modes of plant failure was encountered. The water potential was further decreased if any of the modes of plant failure occurred.

Data

Subsequently we searched for a dataset that was suitable for the calibration of the mortality model and we identified a database assembled by Choat et al. (submitted). This database provided information about the xylem pressure at which 50% loss of conductivity occurs (PLC50) for 480 woody species. PLC50 is the most commonly used index of plant cavitation and it is a parameter in the model. Choat et al. (submitted) provided also few data of soil water potential, leaf water potential, photosynthesis rate and stomatal conductance for each species, however the data were scarce.

From the database we selected the species that had the highest number of data. At this stage we calibrated the model just for Ponderosa Pine.

Sensitivity Analysis

To analyse the influence of the different parameters on model outputs we used the Canonical correlation analysis (CCA), a multivariate technique. CCA is particularly suitable for global sensitivity analyses of process-based models (Minunno et al., submitted) because it allows to find the relations between the parameters and multiple outputs. Canonical correlation analysis was introduced by Hotelling in 1936 (Hotelling, 1936). As many multivariate techniques, CCA application has recently increased with the availability of computer programs that facilitate its implementation. Minunno et al. (submitted) for the first time used CCA to study the sensitivity of a process-based model outputs to its parameters. Hair et al. (1998) provided a detailed description of CCA and its implementation as sensitivity analysis technique.

Model calibration

For the calibration of the model we used the Bayesian statistics that is based on probability theory and provides invaluable methods for model calibration and evaluation (Van Oijen et al., 2011). Bayesian calibration (BC) allows to reduce uncertainty in both parameters and model outputs when new data are available. Furthermore the BC, in combination with other analyses (i.e., sensitivity analysis and analysis of model data mismatch) gives a better understanding of model behaviour (Van Oijen et al., 2011; Minunno et al., submit.).

By means of Bayesian calibration, it is possible to revise the state of knowledge about parameters values, expressed as a joint probability distribution, using new data.

Bayes' Theorem is given by the formula:

$$P(\theta|O) = c\ P(O|\theta)\ P(\theta) \qquad (1)$$

where θ is the parameter vector, O are the observed data and c is a constant.

The prior probability distribution ($P(\theta)$) represents the modeler's beliefs about parameter values before using the data. The data, by means of the likelihood function ($L(\theta) = P(O|\theta)$), are used to modify the prior uncertainty. The updated joint probability distribution for the parameters is called the posterior distribution ($P(\theta|O)$).

Model simplification

Because BC is computationally demanding, it was searched if the model can be simplified without altering model performances. The method proposed by Minunno et al. (submitted) was used to test model simplifications. The method consists in comparing the likelihood distribution from a Bayesian calibration of a model with the likelihood distribution of a simplified version of the same model. If the distributions are similar it means that the simplifications made to the model do not affect its performance. In this study we used this method to find the lowest N that can be used in the model, in order to speed up the Bayesian calibration.

3. Description of the main results obtained

Sensitivity analysis and model simplification

The sensitivity analysis carried out by means of *canonical correlation analysis* allowed to identify the parameters that are more influential on model outputs. In this way was possible to better understand model behaviour. In general the most important parameters of the models are the Xylem conductance, the respiration rate, the photosynthesis rate and the leaf osmotic concentration.

Using the procedure of Minunno et al. (submitted) it was possible to simplify the model without altering its performances. After the model has been simplified the computational cost of the calibration process was significantly reduced and the calibration became less time consuming.

Bayesian calibration.

The Bayesian calibration of the model allowed updating the joint probability density function of the parameters. Even though the data for Ponderosa pine were scarce, parameter uncertainty was significantly reduced. The most informed parameters were the most influential parameters on model outputs. The BC of the model provided the joint posterior distribution of the 11 parameters more influential on the mechanism of plant mortality. The joint posterior distribution provides information about parameters uncertainty and also takes into account of the interactions between parameters. This exercise showed that even few data points, by means of Bayesian calibration, are useful to improve our knowledge about model parameters and model structure. Surprisingly the data contained more information than modelers expected.

Once calibrated, the model was run for Ponderosa pine to understand the response of this species to extreme drought events. When extreme events occur, xylem failure is the most probable mechanism determining Ponderosa pine mortality, while it is slightly less probable that this species dies of carbon starvation; phloem failure is unlikely to occur.

4. Future collaboration with the host institutions.

The STSM gave the opportunity to strengthen and consolidate the existing network between the Instituto Superior de Agronomia (Lisbon, Portugal), the School of Geosciences (Edinburgh, UK) and the Center of Hydrology and Ecology (Penicuik, Scotland). Possible future works and collaborations were also discussed during the STSM. In the future it would be interesting to calibrate a dynamic version of the drought induced mortality model used for this exercise. Furthermore we outlined simple drought-induced mortality models that could be built-in stand level process-based models such as BASFOR (Van Oijen et al., 2005) and 3-PG (Landsberg & Waring, 1997). These developments in forest modeling would provide useful tools for sustainable forest management.

5. Foreseen publications/articles resulting or to result from the STSM.

The calibration process carried out for Ponderosa pine will be repeated for different species for which data are available in the database of Choat et al. (submitted), with the aim of developing a scientific article.

6. Bibliography

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