PROCESS BASED FOREST MODELLING: A THOROUGH VALIDATION AND FUTURE PROSPECTS FOR MEDITERRANEAN FORESTS IN A CHANGING WORLD

La modelización basada en procesos de los ecosistemas forestales: validación y posible evolución futura de los ecosistemas mediterráneos bajo escenarios de cambio climático

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Abstract

Predicting the effects of climate change on the future performance of current forest stands can benefit from highly mechanistic process based models which can accurately describe the responses of forest stands under a variety of conditions. The lack of understanding of the effect of water stress on ecosystem function leads to big discrepancies when modelling in these conditions but recent advances allow us to successfully reproduce water and carbon balances during periods of stress. This will be of particular importance for modelling future scenarios, where water stress is expected to increase in Mediterranean ecosystems. The availability of new high precision field data, and highly developed models allows for large scale validation. A forest ecosystem model, GOTILWA+, is developed and validated against FLUXNET data in a water stressed Mediterranean site. The recently released level 4 Euroflux data uses detailed gap filling techniques to provide high quality half hourly measurements of the carbon and water fluxes at many sites throughout Europe.This work presents the validation process and results from the model application at a site in Puechabon, France, and an in depth investigation into forest ecosystem function under stressed conditions. Particular attention was paid to the modelling of water and carbon fluxes, and in assessing different approaches to modelling the effect of water stress on the photosynthetic apparatus, autotrophic and heterotrophic respiration. We focus on the techniques used to confront problems which arose in the validation process. In particular the interaction of the photosynthetic apparatus with soil water availability, through stomatal conductance, mesophyll conductance and the hydrological stress induced changes in physiological capacities of photosynthesis. The inversion of latent heat fluxes allowed for the reconstruction of the annual evolution of soil water, and the decoupling of the hydrological cycle from the photosynthetic model. Further techniques such as the inversion of the McNaughton-Black equation for evapotranspiration to back-calculate canopy conductance allowed for a high quality validation of all aspects of the model concerning carbon and water fluxes. Statistical methods were

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applied to gauge the accuracy of the model.The results give a detailed look at process based modelling of forest ecosystems, and shed some light on the functioning of Mediterranean ecosystems under stressed conditions and their possible future evolution under climate change scenarios.

Keywords: *Gotilwa+, Ecosystem models, Fluxnet, Drynen, Forest growth*

Resumen:

Los modelos basados en procesos son una herramienta esencial para predecir los efectos del cambio climático en la evolución que tendrán nuestros bosques, lo cual nos permitirá describir en detalle y con exactitud sus respuestas bajo una gran variedad de condiciones. El escaso conocimiento del efecto del estrés hídrico en el ecosistema, lleva a grandes discrepancias cuando modelizamos bajo estas condiciones, pero avances recientes nos permiten con éxito reproducir los balances del agua y el carbono durante periodos de sequía. Esto resulta de gran importancia para la modelización de futuros escenarios, en especial para ecosistemas Mediterráneos, donde se espera que el estrés hídrico aumente considerablemente. La disponibilidad de medidas de campo de gran precisión y resolución, y el gran desarrollo de modelos basados en procesos permiten la validación a diferentes escalas temporales y espaciales. Un modelo basado en procesos para el estudio de ecosistemas terrestres, GOTILWA+, se desarrolló y validó usando medidas FLUXNET en un emplazamiento Mediterráneo, que presenta estrés hídrico periódicamente cada año. Los datos Euroflux proporcionan medidas con resolución temporal cada media-hora de los flujos de agua y carbono de gran calidad, así como medidas meteorológicas en muchos emplazamientos en toda Europa. Este trabajo presenta la validación de los procesos y resultados a partir de la aplicación del modelo en Puéchabon, Francia, y una detallada investigación del comportamiento del bosque bajo condiciones de estrés. Se puso especial atención en modelizar los flujos del agua y del carbono, y en evaluar diferentes enfoques para modelizar el efecto del estrés hídrico en el aparato fotosintético, y en la respiración autotrófica y heterotrófica. Nos centramos en las técnicas usadas para resolver problemas que aparecen en el proceso de validación. En particular la interacción del aparato fotosintético con la disponibilidad de agua en el suelo, a través de la conductancia estomática, conductancia del mesófilo y el estrés hídrico, que inducen cambios en la capacidad fisiológica de la fotosíntesis. La inversión de los flujos de calor latente permitieron la reconstrucción de la evolución anual del agua en el suelo, y desacoplar el ciclo hidrológico del modelo fotosintético. Otras técnicas como la inversión de la ecuación de McNaughton-Black a partir de la evapotranspiración, permite calcular la conductancia estomática y efectuar una validación en detalle de todos los aspectos del modelo que conciernen los flujos de carbono y agua. Se aplicaron métodos estadísticos para estimar la precisión del modelo. Los resultados proporcionan en detalle una visión de la modelización basada en procesos de los ecosistemas forestales, y del funcionamiento de los ecosistemas mediterráneos bajo condiciones de estrés hídrico, así como su posible evolución futura bajo escenarios de cambio climático.

Palabras clave: *Gotilwa+, Modelos de ecosistema, Fluxnet, Sequía, Crecimiento del bosque*

INTRODUCTION

Classical forest modelling has focused on the use of empirical relations drawn from field data to calculate expected stand performance in the future, assuming different site quality classifications. This has proved relatively successful, and until recent developments in our knowledge of the processes driving forest ecosystem responses to climatic and site characteristic drivers such an approach was the only available reliable tool for calculating the expected stand performance.

It is now widely accepted that climate change will alter weather patterns throughout the world, and changes have already been observed and documented. For Mediterranean ecosystems, an increase in air temperatures coupled with changes in the distribution of precipitation is expected to lead to a higher rate of evapotranspiration, and increased levels of summer drought (IPCC, 2007). In Mediterranean ecosystems, water is already the limiting factor for growth, and an increase in the occurrence of drought could have a large impact on the growth rates of new and current forest stands. The potential application of empirical models, based on statistics gathered under current or past climatic conditions, for the prediction of the future performance of forest stands is therefore questionable.

Some process based models attempt to mathematically describe the processes which govern carbon and water fluxes in forest ecosystems, and thus forest growth or decline. They are complex dynamic simulators, with each process interacting in real time with other key variables. Thus they can be used as excellent tools for the exploration of future forest ecosystem performance under different assumptions of climate change (HAUS, 1990, MOHREN & BURKHART, 1994). Used in conjunction with management orientated growth and yield models, they can also prove very useful in verifying and backing up the predictions of such models in a changing climate, and suggesting modifications in methodology where necessary.

Recent advances in data gathering techniques now allow for a thorough validation of such process based models. In particular here, we focus on the validation of fluxes of carbon and water in ecosystems which regularly suffer drought. Carbon assimilation and water use are tightly coupled. Once these fluxes are well validated we can have strong confidence in the predictions of other variables such as growth and wood production, as we can say with confidence the amount of carbon retained by the system. If the quantity of carbon retained by the system can be calculated, then we can accurately predict the amount of organic matter retained, as all carbon retained in the system is converted to organic matter in a ratio of 2.1:1.

Here we present techniques for the validation of a process based model, and results from the validation of the process based model GOTILWA+ at Puechabon, a drought prone Mediterranean *Quercus ilex* forest in the south of France. Once validated, we then present simulation results for the future performance of the forest, and suggest a methodology for the expansion of the technique throughout Europe.

MATERIAL AND METHODS

GOTILWA+

GOTILWA+ (Growth of Trees Is Limited by Water), (GRACIA et *al.*, 1999, www.creaf.uab.es/gotilwa+/), is a process based forest growth model that has been developed to simulate the processes underlying growth and to explore how these processes are influenced by climate, tree stand structure, management techniques, soil properties and climate change. The GOTILWA+ model simulates carbon and water fluxes through forests in different environments, for different tree species, under changing environmental conditions, either due to climate or to management regimes.

The Leaf – The most difficult, and the most important for water stress responses: Leaf energy balance and processes related to carbon fixation

Only a small fraction of solar radiation that reaches the leaf is used in photosynthesis. The incident solar radiation in the leaves determines its temperature, along with the amount of transpired water. The leaf temperature itself controls the physiological processes in the leaf. The ecophysiological model GOTILWA+ uses the approximation of GATES (1962) which defines the energy balance on the leaf level. For a determined leaf temperature, the energy gains of the leaf must equal the energy losses. The energy balance of the leaf is thus coupled to the photosynthetic process, transpiration, and stomatal conductance, as governed by leaf temperature.

To enter the leaf, CO_2 must diffuse across the laminar layer and the stomata. The resistance of the stomata to the diffusion of water vapour and CO_2 plays an important role in the control of internal carbon concentrations available for assimilation. This is of particular importance in conditions of water stress, where the stomata react by closing. GOTILWA+ uses the LUENING (1995) version of the semi-empirical model proposed by BALL et *al*. (1989).

Carbon fixation is controlled by temperature and radiation, and limited by the availability of water and nutrients. In GOTWILA+, the rates of assimilation are estimated using the biochemical model of FARQUHAR & VON CAEMMERER (1982). This model calculates two distinct rates of assimilation: the assimilation rate Ac, which is limited by the activity of Rubrisco (from the carboxylation efficiency), and the assimilation rate Aj, which is limited by the transport of electrons. The model then uses the most limiting rate. The total amount of carbon assimilated during photosynthesis is Gross Primary Production (GPP, m^{-2} $leaf.day^{-1}$), and is calculated as the sum of the assimilation rates, less dark respiration, over the total leaf area. Dark respiration is the process which continues in the mitochondria during daylight hours, and represents an important loss of carbon for plants.

In conditions of water stress, the capability of the system to assimilate carbon is reduced significantly. This is due to three factors: the availability of internal carbon when the stomata close; the conductance of this carbon through the mesophyll, and the effect of stress on the photosynthetic apparatus. How each affect's the leaf during drought, and to what extent, is largely unknown. The availability of new high quality data from the Euroflux network allows us to look closely at the key processes involved.

Euroflux data

Euroflux is the European part of a global network of micrometeorological tower sites that use eddy covariance methods to measure the exchanges of carbon dioxide (CO_2), water vapour, and energy between the terrestrial ecosystem and the atmosphere. The project aims to understand the mechanisms controlling the exchanges of CO_2, water vapour and energy across a spectrum of temporal and spatial scales. Such high quality data is essential in the validation of terrestrial ecosystem models. In this context it allows us to analyze the variables that determine energy partitioning by forests in different climatic conditions, including extreme events and stress limitations, on very short timescales (half hour measurements for many years) over a wide range of environmental conditions and ecosystems.

The study of the interactions between forests and atmosphere has recently been made more routine by new developments in the eddy covariance technique (LEUNING AND MONCRIEFF, 1990), and now provides an excellent tool for high quality validation exercises. This technique has primarily been used in intensive short-term land surface experiments and has provided new opportunities for estimating fluxes at larger spatial and temporal scales (KANEMASU et *al*., 1992). Within FLUXNET, eddy covariance is used for long term continuous measurements of mass and energy fluxes, to capture seasonal dynamics and allow for a meaningful scaling with respect to time. Indeed, many of the processes driving water and carbon fluxes at ecosystem level are strongly dependent on seasonal changes in climate. Seasonal changes of phenology and biomass production significantly affect the rates and properties of water and carbon exchanges in the atmosphere. The technology is available for continuous measurement of carbon dioxide and water fluxes on a seasonal basis with half hourly discrimination (WOFSY et *al*., 1993). Within EUROFLUX the equipment and methodology is standardized using a common software and instrumentation design in order to have a solid basis for site inter-comparisons (MONCRIEFF et *al*., 1995). Thus, the Euroflux site at Puechabon, our case study site, provides us with 5 years of half hourly measurements or calculations of climate variables, carbon and water fluxes.

Although the methodology is highly refined, and eddy covariance techniques have developed to apply very sophisticated algorithms and techniques for the back calculation of variables as diverse as Gross Primary Production and Growth Respiration, and indeed Net Ecosystem Exchange itself, which is a result of calculations involving many variables, it should be kept in mind that the resulting measurements of ecosystem variables are results of modelling techniques, not to mention gap filling techniques employed. Thus, any comparison between models such as GOTILWA+ or Orchidee and FLUXNET data is, in reality, an inter-model comparison. That said, the data generated by the

FLUXNET eddy covariance techniques is probably as close as we will ever get to the truth, and certainly is as close as we can get right now.

Site Details: Puechabon

Puechabon is a coppiced forest, situated in the south of France, 60 km north-west of Montpelier. It was last clear cut in 1945. The site suffers from drought each year, and a particularly strong drought occurred in 2003. Euroflux measurements of sufficient quality to be used for the validation are available from 2001 to 2005. Site particulars are given in table 1.

RESULTS

Data manipulation: The back calculation of Soil Water

EUROFLUX measurements provide half hour values for Latent Heat Flux, which is a measure of the amount of water leaving the forest system, equivalent to evapotranspiration. They also provide half hourly data for precipitation. Using these two values, and a simple one bucket soil water model which accounts for interception, stemflow, runoff and drainage, it is possible to recreate the evolution of soil water throughout the year, as is shown in figure 1. Here the typical Mediterranean climate pattern can be seen, with rains in spring maintaining a high soil water level, but high temperatures and the lack of summer precipitation leading to drought conditions in summer. Autumnal and winter precipitation refills the soil water level, and the pattern is repeated in each year. Europe suffered from a very strong drought in 2003, and this can be seen in the reconstruction of soil water in Puechabon, with 2003 soil water levels falling quicker and remaining lower for a longer period of time than any other year.

Such data is very useful as it allows us to relate other observed changes in ecosystem fluxes to changes in soil water levels, without actually making direct measurements of water in the soil.

Data Manipulation: The Back Calculation of Canopy Conductance

The conductance of the canopy can also be calculated from the Latent Heat flux measurements, using an inversion of the McNaughton and Black (1973) approach to calculating Evapotranspiration. As latent heat flux is a mea-

Variable	Units	Puechabon
Region		France
Longitude	Degree	1º 06´ E
Latitude	Degree	43º 74´ N
Altitude	Meters	270
Mean Global Radiation	$MJ.m^{-2}$	5345
Mean Minimum Temperature	ºC	9.4
Mean Maximum Temperature	ºC	17.85
Mean Precipitation	mm	966
Species	Dimensionless	*Quercus ilex*
Tree Density	$stems.ha^{-1}$	8500
DBH	cm	7
VcMax	$\mu mol\ m^{-2}.s^{-1}$	35
JMax	$\mu mol\ m^{-2}.s^{-1}$	70
Respiration	$\mu mol\ m^{-2}.s^{-1}$	0.63
Q10	Dimensionless	2
Soil Rooting Depth	m	4
Soil Water Holding Capacity	mm	175

Table 1. *Details of the site at Puechabon*

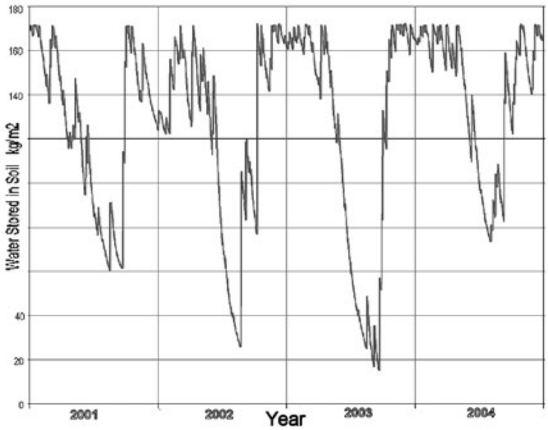

Figure 1*. Calculated soil water content at Puechabon for the period 2001 to 2004, using a soil hydrology model and measured Latent heat fluxes*

surement of the amount of water leaving the system, it can be taken as the equivalent of evapotranspiration. Thus, the following equation can be used to back calculate canopy conductance, assuming that evaporation from bare soil is minimal in a forest with a closed canopy.

$$Gc = LH.\varepsilon.\lambda.\gamma /(\rho.Cp.vpd) \quad (1)$$

Figure 2 shows the calculated Canopy Conductance for Puechabon, plotted against proportional soil water availability. The effect of drought becomes significant at 70% of the relative soil water holding capacity. Below this level, the stomata begin to close, cutting off conductance and thus the diffusion of carbon dioxide into the leaf.

Data Manipulation: Extracting the slope of the Ball, Berry & Leuning function for stomatal conductance at different soil water stresses

The BALL, BERRY & LEUNING (1995) approach for calculating stomatal conductance applies a

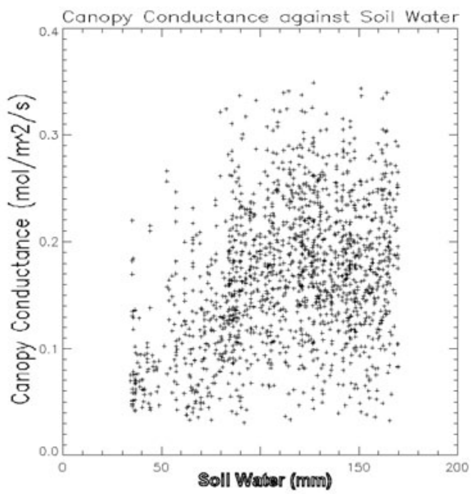

Figure 2*. Canopy conductance at different levels of drought, as calculated from the EUROFLUX measurements*

slope factor which varies depending on soil nutrient contents. It also varies depending on soil moisture, but little work has been done to quantify the effect of soil water stress on the slope. Fluxnet data gathered at the sites gives a perfect opportunity to calculate how the required slope is required to change with water stress. By using the approach outlined earlier, the hourly canopy conductance can be calculated for the entire modelled period. By inverting the BALL, BERRY & LEUNING model of stomatal conductance, and applying it to these values for canopy conductance, the slope and intercept can be reconstructed, and values can be extracted for different soil water contents. Thus the effect of soil water stress on leaf conductance (and therefore on leaf internal carbon and subsequently photosynthesis) can be incorporated by applying a function which changes the slope of the stomatal conductance calculation depending on modelled soil water content.

Data Manipulation: Calculating non-stomatal limitations

Under water stressed conditions, the rate of optimum photosynthesis is affected by both stomatal and non stomatal limitation. Once we know the stomatal conductance of the canopy and the rate of carbon assimilation, we can calculate the concentration of CO_2 inside the leaf, assuming infinite mesophyll conductance. This can then be used to look at the correspondence between the rate of assimilation and the internal carbon concentration. It is known that stomatal conductance exerts a control over the rate of assimilation by controlling the concentration of leaf internal carbon dioxide. Thus, in periods of drought, the stomata close, the internal carbon is used up, and assimilation rates become limited by the carbon supply limitations. Recently, it has been hypothesised that drought also effects assimilation rates through non stomatal related limitations, with the two main actors proposed being a change in the capacity of mesophyll conductance, and a reduction in the carboxylation capacity. Here we separate stomatal limitations from non stomatal limitations by considering the reaction of the assimilation rates to drought under otherwise non-limiting conditions. i.e. changes in the assimilation rates under optimum levels of temperature, internal carbon and radiation, which can therefore be associated with changes in available soil water. This allows us to separate the effects of stomatal and non stomatal limitations on assimilation, and thus model the timing and extent of the effects correctly.

Modelling the Observed Fluxes

Once the abovementioned values have been calculated, we can use them to validate the different parts of the model, and it's responses to drought.

Soil water:

Modelling soil water is not an easy task, as small changes in the level of transpiration accumulate to big changes in the amount of water held in the soil. We modelled soil water with the soil hydrology sub-model of GOTILWA+,

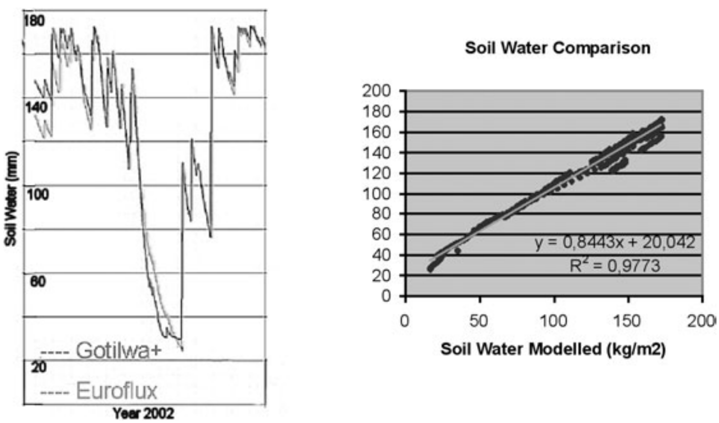

***Figure 3**. Soil water as modelled by GOTILWA+, and that of EUROFLUX, for 2002*

which takes into account water filled porosity and various soil site characteristics, interception, stemflow, runoff and drainage. Figure 3 shows the modelled soil water over 2002, compared with that of EUROFLUX. There is remarkably good agreement between the two data sets. This means that not only is the soil model sufficient in describing the main characteristics of the soil hydrology, but if the assimilated carbon is also accurate, then the transpiration and water use efficiency are also well described by the model.

GPP:

On site measurements were used to describe the structure of the forest, in particular the Leaf Area Index and photosynthetic potential. Climatic data gathered on a half hour time resolution was used to drive the photosynthetic model over the 5 year period. The data analysis described in an earlier section highlighted the need to change the structure of the photosynthetic module of the model, as the previously held theory of stomatal conductance being the main driver for responses in assimilation rates to drought proved to be incorrect. Once the model was developed to incorporate a more accurate description of the effect of drought on assimilation through stomatal and non stomatal limitations, the model proved very accurate in describing the response of the canopy to environmental drivers and site conditions. Figure 4 shows the model output compared with the data gathered by EUROFLUX for a two year period. Of particular interest here is the ability of the model to effectively reproduce the summer decline of assimilated carbon, both in the timing of the decline and the extent. This is arguably the most difficult part of modelling in arid environments.

Respiration:

Respiration in the model is divided into many different parts. There are individual descriptions for both autotrophic and heterotrophic respiration, with autotrophic respiration divided into compartments for growth and maintenance, with each described separately for the roots, wood and leaves. Measurements from EUROFLUX give only an estimate of total ecosystem respiration, but individual investigations through other projects can give us an idea of the contribution of each respiration compartment to the total ecosystem respiration. The timing and magnitude of observed peaks in the EUROFLUX respiration can also give us an idea of the extent of contributions from particular respiration compartments. Figure 5 shows a comparison between modelled and EUROFLUX ecosystem respiration rates. The model effectively captures both the magnitude and the seasonal changes in ecosystem respiration. A sharp decline in respiration rates is again observed in summer, under drought conditions. This is due to the effect of drought, not only on heterotrophic respiration, but also on autotrophic respiration, and both growth and maintenance respiration in all compartments falls. It was assumed that sapwood respiration would not be affected by drought, but leaf and root respiration would be affected in parallel with the decline in photosynthesis.

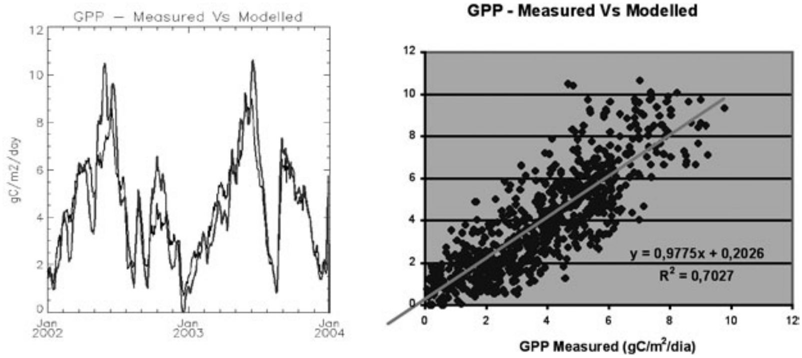

***Figure 4**. Modelled and Euroflux Gross Primary Production at Puechabon*

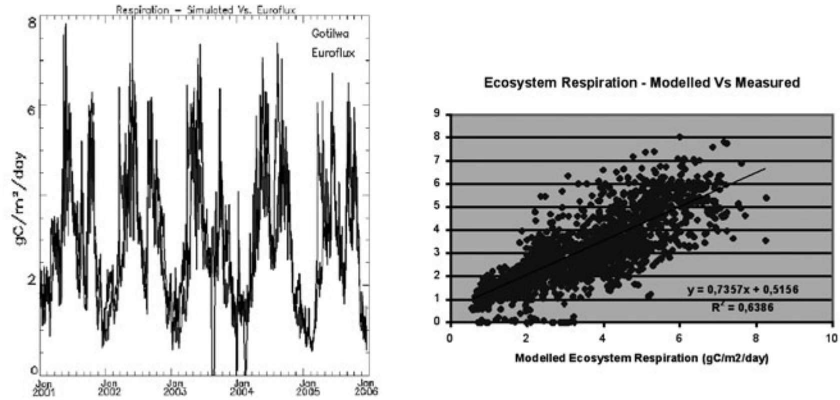

Figure 5. *Modelled and EUROFLUX total Ecosystem Respiration at Puechabon.*

An accurate description of net assimilation and ecosystem respiration equates to an accurate description of the quantity of carbon being retained by the ecosystem, as shown in figure 6. This carbon is equivalent to biomass, with a general mass ratio of 2.1:1.

So, for every gram of carbon retained by the system, 2 grams of organic biomass are produced. This can be above or belowground biomass, or organic matter in the soil. Assuming proportional relations between above and belowground biomass, and assuming the soil organic matter pool is in stable equilibrium, we can then calculate how much of this retained carbon is invested in above ground biomass. I.e. we can predict, under different climate conditions, the growth of the forest at Puechabon.

Predicting the Future at Puechabon

Climatic Data used

Projecting forest growth into the future is highly dependent on the climate data used to run the model. The best tools available for predicting future climate evolution are Global Climate Models or General Circulation Models (GCMs). GCMs aim to describe climate behaviour by integrating a variety of fluid-dynamical, chemical, or even biological equations that are either derived directly from physical laws (e.g. Newton's Law) or constructed by more empirical means. A large number of GCMs exist for predicting future climate evolution. Each applies the laws of physics and mathematical descriptions of atmospheric interactions to varying intensity to give a prediction for the evolution of future climate.

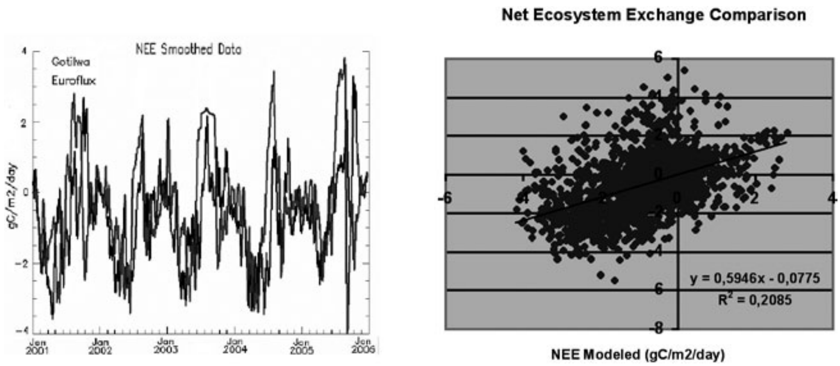

Figure 6. *Modelled and EUROFLUX net ecosystem exchange at Puechabon. Negative values correspond to periods in which the system retains more carbon than is releases into the atmosphe*

A range of socio-economic scenarios have been created to explore future paths of carbon emissions related to the burning of fossil fuels. These can be used to force GCMs. This approach, currently used by the IPCC (Inter-governmental Panel on Climate Change), is used as a driver for the GCMs, with various potential future greenhouse gas emissions, depending on the economic model applied and the resulting changes in population, land use change and energy consumption. Future emissions scenarios are derived from the IPCC's SRES1 (The global Intergovernmental Panel on Climate Change Special Report on Emissions Scenarios): A1 Fossil-Intensive, A2, B1, and B2, ranging from pessimistic to optimistic regarding future anthropogenic impact on the climate system.

The Future in Puechabon: Higher Potential, Fewer resources

It is predicted that under climate change scenarios, the Mediterranean region will suffer increased periods of drought due to higher temperatures. It is also predicted that the growing period will lengthen; giving forest stands more productive potential. What is unclear is how these two factors will interact, as more productive potential requires a higher consumption of available soil water, which is already limiting and expected to become more so. Simulation results show that in Puechabon, the extra demand on a diminishing soil water supply will not be enough to diminish production. On the contrary, results predict that the stand at Puechabon will benefit from the assumed future climate change, with a steady increase in production despite increased drought. Figure 7a shows the increase in the length of the growing period predicted by the model assuming moderate climate change, and the reduction in available soil water (due to a higher atmospheric demand and higher transpiration). Figure 7b shows the net effect of these changes on the stand production.

Expanding the methodology throughout the Mediterranean

The results presented for the future production in Puechabon can not be generalised to the whole of the Mediterranean climate region. It is a site with very deep soil, and although it suffers droughts annually, it has large soil water reserves which allow high production in spring which compensates for the loss of production in summer. Most Mediterranean sites have very low soil water reserves and lower production than that observed in Puechabon. It is expected that most Mediterranean sites will not benefit from climate change to the extent observed in Puechabon, and indeed many studies predict high mortality in some regions. To investigate the response of forests in the Mediterranean, we have developed a methodology for simulating on a regional basis.

Once the model has been validated with different species, using the methodology described above, it is possible, using extensive databases with the necessary information, to model forest stand performance anywhere in Europe, or indeed over all of Europe, or the Mediterranean, on a pixel basis. Figure 8 outli-

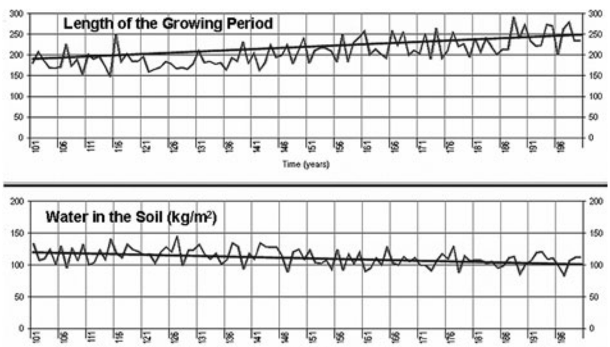

***Figure 7a**. Future modelled predictions of the length of the growing period and water in the soil at Puechabon over the period 2000 to 2100*

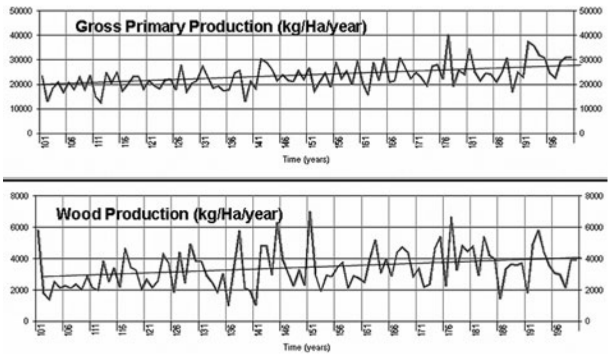

Figure 7b*. Modelled predictions of future gross primary production and the corresponding wood production in Puechabon over the period 2000 to 2100*

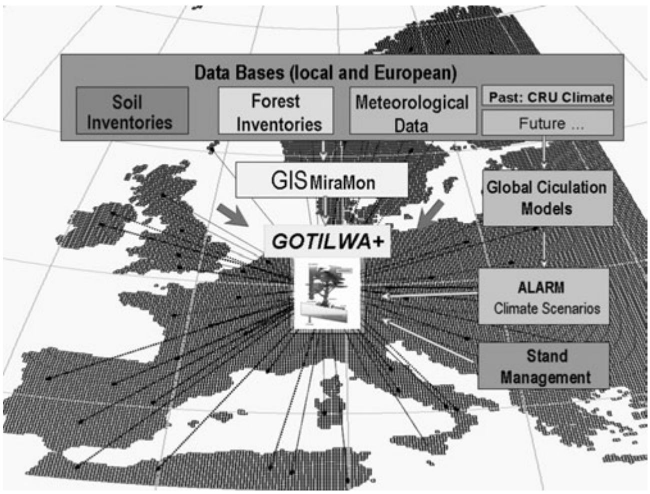

Figure 8*. A schematic representation of the methodology used for the application of Gotilwa+ on a regional scale, and the databases required*

nes the methodology applied and the databases used.

CONCLUSIONS

In the light of climate change, it is expected that Mediterranean forests will respond based on the complex interaction of the availability of water and their ability to use it efficiently. Statistical modelling can be a powerful tool, but the application for future predictions could lead to large errors if the effect of climate change is not considered. Process based models can accurately reproduce ecosystem fluxes and growth, and are designed to take into account the effect of changing climatic conditions. It is suggested that they be used in parallel with statistical modelling, as a two pronged approach to asses the performance of both methods under assumptions of climate change.

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