Forest Eco-physiological Models and Carbon Sequestration

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1 Introduction

Modeling and monitoring the processes involved in terrestrial carbon sequestration are often thought to be independent events. In fact, rigorously validated modern modeling techniques are very useful tools in the monitoring of the carbon sequestration potential of an ecosystem through simulation, by highlighting key areas for study of what is a complex dynamical system. This is ever more important in the light of climate change, where it becomes essential to have an understanding of the future role of terrestrial ecosystems as potential sinks or sources in the global carbon cycle.

The study of the effects of climate change on terrestrial ecosystems is one field of interest which requires the use of predictive tools such as functional simulation models. There are many possible applications of such models, from studying the responses of individual processes, the interactions of various processes, up to the responses of whole forest stands and ecosystems. This can be performed focusing on the response of forests to climate change (and in turn identifying feedbacks from forest ecosystem responses that may affect the rate of climate change), the effect of climate change on ecosystem service supplies which are necessary for societies well being (such as water supply, soil fertility and productivity), the effect of management on forest productivity, or in assessing the suitability of a certain site for plantation.

Models can be taken as quantitative predictors of ecosystem responses by translating a particular "stress" of interest to a key ecosystem parameter, taking into account a margin of error, but perhaps more importantly, they give us a way to scale up our understanding of individual process reactions to drivers on the individual tree level to the ecosystem scale. The quantitative predictions have a large range of uncertainty, and are actually by no means predictions, but estimates. However, the

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qualitative descriptions of ecosystem responses give a very valuable insight into the functioning and potential response of the ecosystem as a whole.

In this chapter, we first outline the different approaches to forest eco-physiological modeling, with their associated pros and cons, and applications. We then give an example of the application of one such forest growth model, Gotilwa+, to sites along a latitudinal transect in Europe, as an example of how the method can be applied throughout Europe. The methodology is then extended to the application of the model to the whole of Europe for the coming 100 years, with an exploration of the forest eco-physiological responses to climate change, in particular the effects on carbon and water balances.

1.1 Forest Services

Modelling can prove a useful tool in assessing the expected future state of forest ecosystem services (e.g. water availability, soil fertility, wood production, fire hazard reduction etc.) that are vital for human well being. This is of particular interest in the light of climate change. Global change is continually altering such services, and is expected to do so to an even greater extent in the future. Previous Europe wide studies have applied terrestrial ecosystem models such as those described in this chapter to asses the expected future status of services such as soil fertility, water availability and the risk of forest fires (Schröter et al., 2005). Both positive and negative trends were reported, with increases of forest area and productivity on one hand, but an increase in the risk of fire, and a decrease in soil fertility and water availability on the other.

By applying the assumed changes in land use and climate, the models can be used to gauge the effect of such changes on ecosystem services. The Gotilwa+ model presented in this chapter has been involved in such studies and uses the same approach to assessing the future of European forests and ecosystem service supply. This is often coupled with an assessment of possible management strategies to assess the capability of forest management to offset or counteract any potentially negative or undesired effects.

1.2 Applications in Forest Management

Modelling can also be used to assess the potential of forest management strategies. Forest management practices aim to optimise the productivity of the forest and minimise the risk posed by environmental stresses. The suitability of a management strategy is highly dependant on site characteristics and the general state of the forest stand. It is a difficult balance to achieve, where over-harvesting can lead to serious damage to a forest ecosystem, whilst under-harvesting can fail to make full use of the ecosystems potential, or indeed lead to a significant loss of aboveground biomass (e.g. in the case of fire). Models allow for the evaluation of many alternative

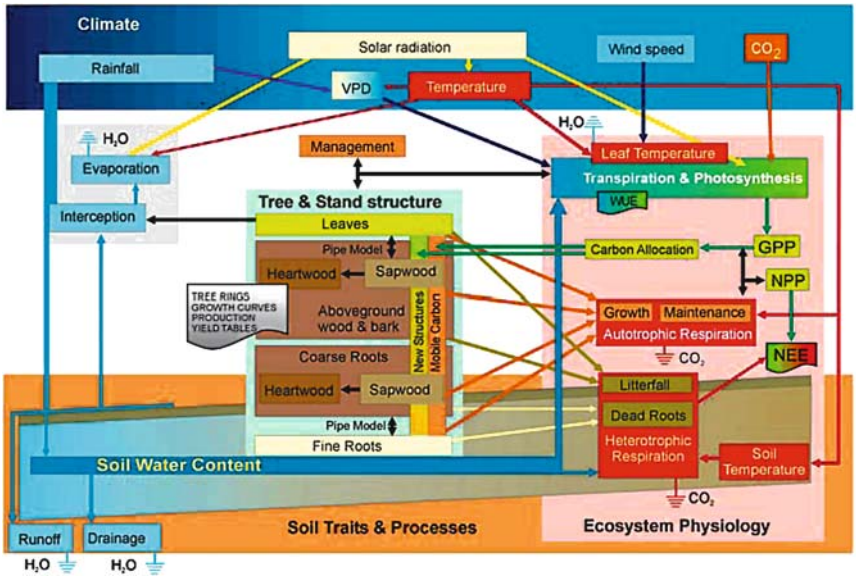

Fig. 1 A schematic graph of processes and interactions accounted for in the GOTILWA+ model (Kramer et al., 2002)

strategies, and the effectiveness of each can thus be tested based on the requirements of the manager. This is relevant both in the maximising of the potential for the ecosystem to sequester carbon, and in protecting ecosystems which are threatened by changing environmental conditions (with the aim to be to give the system more time to adapt naturally, and avoid threshold limits) (Kellomaki and Valmari, 2005).

This 'virtual management' allows the forest manager to enter the forest and invoke management strategies, with the potential to remove selected trees based on different removal criteria, either at prescribed intervals based on a certain value such as average diameter at breast height, or at regular time steps. The value of this virtual management is that it immediately gives the forest planner the results of his strategy for the future. The effect of the strategy can be focused on maximising whatever variable the planner is interested in, or indeed finding the optimal maximum considering a variety of requirements. It is important to note that today's management strategy for a particular site might not be suitable in a changing world, and a modelling approach testing a range of plausible strategies can warn a planner of the need of a strategy change before damage is done to the ecosystem.

1.3 Process Based Models Versus Empirical Models

There are two main approaches available to modellers: The empirical approach and the process based approach. The choice of approach taken is highly dependent on the problem being addressed. As always, both approaches have valid applications,

each with their own strengths and weaknesses. In reality, the two options are not quite independent, with many models containing a synergy of the two approaches.

Empirical models attempt to simplify the system description, by relying purely on known system wide responses to external drivers. They are statistically based, are easy to feed (require less parameters) and generally have faster execution times.

This is very useful, making it easy to build a simple and accurate description of a system with very few parameters. As their name suggests, they are based on empirical functions, which attempt to describe direct ecosystem responses. This simplicity and speed also helps in the analysis of model results, and is useful in giving insight into the general functioning of a system, highlighting the key processes and possible reactions. However the applicability of empirical models is restricted and their application as true exploratory tools is questionable. Limited by their simplicity and their basis of empirical responses, they lack the ability to explore new scenarios and conditions outside of those on which they were built and tested.

Process based models, in contrast, are complex simulators that attempt to mimic the real world. The aim is to include mathematical descriptions of both the processes that govern a system, and their interactions, thus recreating the system in a virtual environment. Each process in the system is described separately, and dynamically interacts with other processes. Given an accurate description of each processes separately, it is argued that a better description of the ecosystem in general, through the interaction of these processes, can be achieved. Due to their detail, a large number of parameters are necessary. The parameters determine the response of each function describing an individual process, and are based on detailed field work or lab experiments. This allows an accurate description of all factors affecting a process, but such parameters are not always available. This can be a problem, and a lack of data often leads to assumptions and approximations, but the approach leads to a model with a wide applicability. The detail and dynamic characteristic of process based models allows them, theoretically, to function as effective exploratory tools and they should be fully applicable under new conditions and scenarios.

The scientific community is often somewhat sceptical about the effectiveness of complex process based simulation models, and the role they should play in ecological studies. Many ecologists will laugh if you explain that you are trying to mimic the real world. And indeed they might! The environment is highly variable, and could be said to be the most complex system in existence. However, complex process based models can have a much wider applicability than that of simpler empirical models that are simply designed to fit data. Although far more complicated than empirical models, and much more expensive to build, they give an insight into the internal functioning of the system itself, which could never be achieved with empirical models. For studies involving climate change, this is essential, as complex process are involved in ecosystem wide responses to global change. Unfortunately, our current understanding of many processes is still too limited to allow fully process based modelling, and most so called processed based models use a range of semi to fully empirical equations. This is perfectly valid, but one must keep in mind that most process based models, including the Gotilwa+ model, are actually hybrids of the two approaches.

2 GOTILWA+: A Process-Based Model

2.1 The Model

GOTILWA+ (Growth of Trees Is Limited by WAter) (Gracia et al., 1999), is a process based forest growth model that has been implemented 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.

Results of GOTILWA+ are computed separately for 50 DBH (diameter at breast height) classes and they are integrated at the stand level. The processes are described with different sub-models that interact and integrate the results of simulated growth and the evolution of the whole tree stand through time (hourly calculations integrated at a daily time step). Horizontal space is assumed homogeneous and the vertical profile distinguishes two canopy layers (sun and shade conditions).

2.1.1 Input and Output Variables

The input data includes: climate (max. and min. temperatures, rainfall, VPD, wind speed, global radiation and atmospheric CO_2 concentration); stand characteristics (tree structure including the structure of the canopy; DBH class distribution); tree physiology (photosynthetic and stomatal conductance parameters, specific growth and maintenance respiration rates), site conditions including soil characteristics and hydrological parameters and also forest management criteria.

Many output variables can be extracted from the model. These can be separated into three main categories: canopy variables, tree and stand structural variables, and root and soil variables.

Canopy variables include: Gross Primary Production, Net Primary Production, Net Ecosystem Exchange, Leaf Area Index, Transpiration, Water Use Efficiency, Leaf Production, Leaf Respiration, Leaf Biomass, Growth Activity, The Length of the Growing Period and Volatile Organic Compound emissions.

Tree and Stand structural variables include: Tree Density, Sapling Density, Basal Area, Sapwood Area, Mean Quadratic Tree Diameter, Vigour Index, Tree Height, Wood Production, Wood Respiration, Mobile Carbohydrates, Tree Ring Width, Aboveground Biomass, the Weight of the Sapwood Column, Wood Volume, Dead Wood Volume and Yield (when considering management).

Root and Soil variables include: Soil Temperature, Water Stored in Soil, Fine and Gross Litter Fall, Soil Organic Carbon, Fine Root Biomass, Fine Root Production, Fine Root Respiration, Heterotrophic Respiration, Maintenance Respiration and Growth Respiration.

2.1.2 How GOTILWA+ Copes with Processes

Process based models start at the very basic physiological leaf level, combining and describing the different processes involved. Figure 2 shows a schematic of the most fundamental compartment, the leaf. Here, photosynthesis is calculated dynamically, based on internal and external conditions.

Gotilwa+ comprises of a two layer canopy photosynthetic model, coupled with a carbon allocation and growth model and a soil respiration and hydrology model. It describes monospecific stands, which can be even or uneven aged. The key environmental forcing factors taken into account are precipitation, air temperature, vapour pressure, global radiation, wind speed, and atmospheric carbon dioxide concentration. Using this data, the response of ecosystem processes is calculated to estimate the carbon and water fluxes in a forest ecosystem. It is an individual based model, where individual trees in the forest are grouped into 50 DBH (Diameter at Breast Height) classes, with calculations being performed separately for each class. Stand characteristics are taken into account and species specific parameters, to give highly accurate predictions of forest growth and carbon or water fluxes in the system.

The two layer canopy photosynthesis submodel splits the available leaf area index into sun and shade leaves, depending on the time of the day, leaf area angle

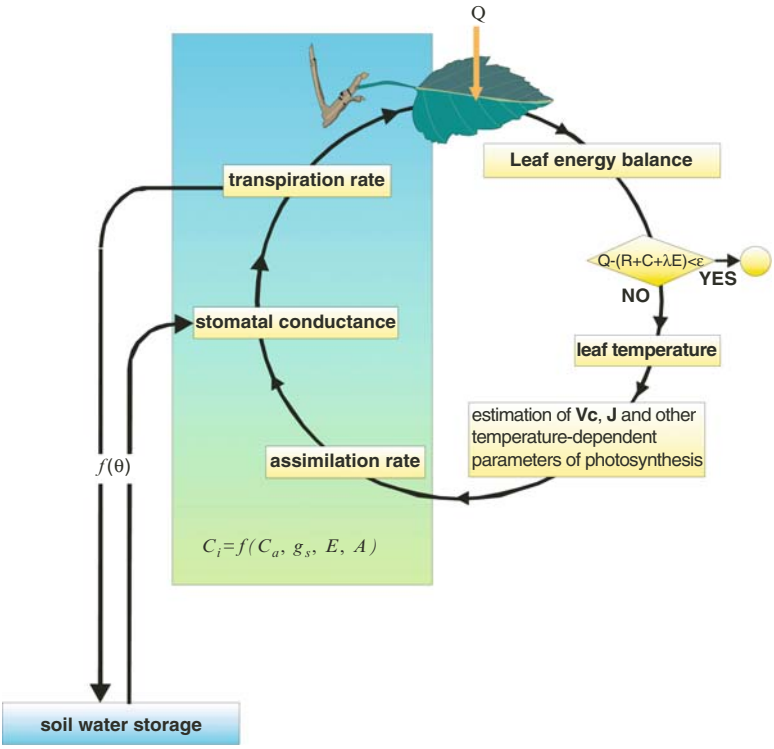

Fig. 2 A schematic diagram of the representation in GOTILWA+ of the photosynthetic assimilation rate

and the canopy's ellipsoidal distribution. Assimilation rates depend on the direct and diffuse radiation intercepted, the species specific photosynthetic capacities, leaf temperature, available carbon, the extent of stomatal opening, and the availability of soil water.

Growth and the allocation of mobile carbon for tree maintenance are considered through three compartments: Leaf respiration, Sapwood respiration, and Fine roots respiration.

Fine litter fall (e.g. leaves), gross litter fall (e.g. bark, branches) and the mortality of fine roots add to the soil organic carbon content. The soil in Gotilwa+ is divided into two layers, an organic layer and a mineral layer, with a rate of transfer between them. Soil organic carbon is decomposed depending on to which layer it belongs, with both decomposition rates depending on a Q_{10} function taking into account soil water content and soil temperature. Soil temperature is calculated from air temperature using a moving average of 11 days. The amount of soil water available for organic layers is calculated taking into account the cumulated rainfall of the previous 30 days and soil water availability for mineral layers depends on the soils water filled porosity which in turn is a function of the organic matter present in soil.

Soil water content is described as one layer, taking inputs though precipitation less leaf interception, which is evaporated, (stem interception, or stemflow, is not evaporated, but directed to the soil), and outputs though drainage, runoff, and transpiration. Surface evaporation only occurs when the canopy is not closed.

Flux calculations are performed hourly, whereas slower processes such as growth and other state variables are calculated daily.

2.1.3 Model Validation

Gotilwa+ model validation has been carried out at various sites across Europe and the United States (Kramer et al., 2002; Morales et al., 2005; Keenan et al., 2008), using canopy level measurements gathered by the FLUXNET network. Figure 3 shows the results at one such site, a *Quercus ilex* forest in the south of France, giving 2 years of field data (2002, 2003) for daily Gross Primary Production, against modelled values. It can be seen that the model successfully captures both the high productivity in spring and autumn and the decline in summer due the effect of drought on the photosynthetic apparatus.

2.1.4 Unknowns in Forest Modelling

A correct description of each process is crucial. This requires intense and extensive field work, data collection and experimentation. Thus, by using field work to better our understanding of the processes involved and the factors that affect them, we can build more accurate models. There is yet a lot to be understood, and many interactions between species, soil and atmospheric processes are still poorly understood. Such factors include the role of belowground biomass (the "hidden half" of the forest), the effect of nutrient availability, factors affecting soil organic matter decomposition,

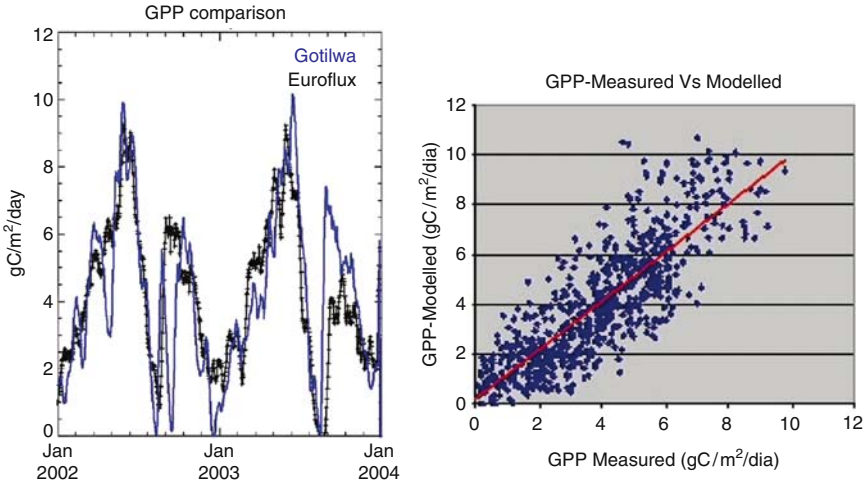

Fig. 3 Daily primary production (10 day smoothed) modelled by Gotilwa+, compared against field data gathered by the FLUXNET network at the Puechabon site, a *Quercus ilex* forest in southern France

and species specific responses to climate change factors such as elevated CO_2, drought and the role of acclimation.

This lack of information is exacerbated by the problem of scale. Many questions remain as to how processes scale up from the chloroplast or mitochondrial level, to the leaf, the stand, and the ecosystem as a whole. The problem of physiological scale is coupled by a problem of temporal scale. An ecosystem incorporates many processes, each with their own temporal scale. Fast processes (such as the leaf energy balance, photosynthesis, stomatal conductance, transpiration, autotrophic and heterotrophic respiration, water and light canopy interception) interact with slow processes (tree ring formation, sapwood to heartwood changes, tree mortality, wood increment, management, soil decomposition, climate change). These questions are all approached with as much accuracy as possible in the model, but many factors could be improved. Such problems go hand in hand with any modelling attempt but each year we are improving our knowledge, and our ability to use it.

3 Model Applications

3.1 The Future of European Forests – A Case Study on a Latitudinal Gradient

Before presenting the results from Europe-wide simulations, we give, as an example, results from simulations at select sites along a latitudinal gradient. Theoretically, any tree species can be simulated by the Gotilwa+ model, given the availability of species

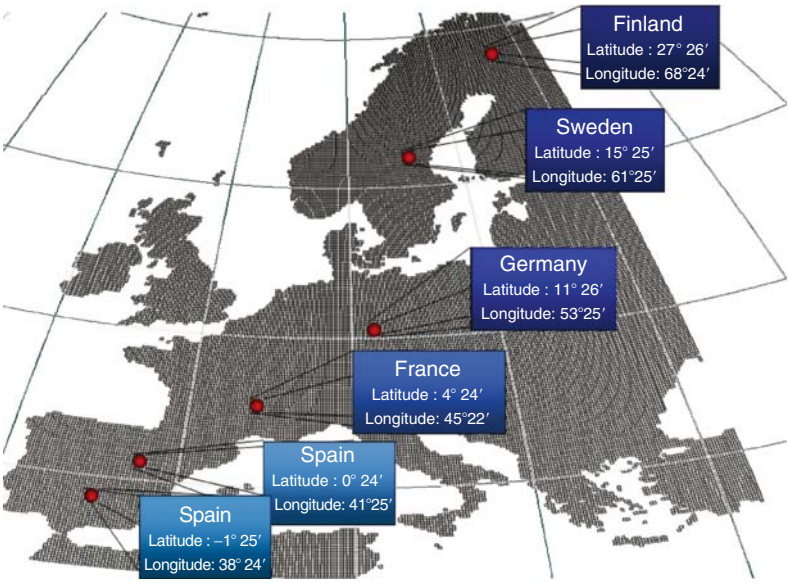

Fig. 4 A map of selected pixels with Pinus sylvestris stands in Europe

Table 1 Pixel climate details – current yearly averages

Country	Lon	Lat	Q	P	dP	PET	Min T	Max T	VP
1 Finland	27°26′	68°24′	1,991	448	194	513	–6.41	2.10	0.51
2 Sweden	15°25′	61°25′	2,671	600	180	730	–2.36	7.12	0.61
3 Germany	11°26′	53°25′	3,226	607	225	805	5.19	12.11	0.98
4 France	4°24′	45°22′	4,270	847	191	944	4.09	13.07	0.89
5 Spain	0°24′41°25′		5,354	366	62	1,340	9.39	20.55	1.27
6 Spain	–1°25′38°24′		5,375	386	61	1,380	8.86	20.83	1.22

Column headings are: Lon – longitude, Lat – latitude, Q – global radiation (MJ/m^2/year), P – annual precipitation (mm/year), PET – potential evapotranspiration (mm/year), Min T/Max T – minimum/maximum temperature (^{0}C), VP – vapour pressure (kPa) dP – number of days with precipitation

specific parameters. Here, we report on the modelling of *Pinus sylvestris*, as the predominant species along the gradient. Each site in Fig. 4 is the site of a current *Pinus sylvestris* stand. Site locations and climatic conditions are given in Table 1.

3.1.1 Future Climate Data – A Multi GCM Ensemble

Past climate data is often locally available, and the Climate Research Unit at Norwich has developed an extensive database of reconstructed climate (CRU) for the past 100 years (Mitchell et al., 2004). This is used to ‘spin up’ the model, and validate the key processes.

Projecting forest growth into the future is highly dependant 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 behavior 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 degrees to give a prediction for the evolution of future climate.

A range of socio-economic scenarios has been developed to explore future paths of carbon emissions related to the burning of fossil fuels. These can be used to force GCMs. This approach is currently used by the IPCC (Inter-governmental Panel on Climate Change) is used as a driver for the GCMs, giving various possible future greenhouse gas emissions, depending on the economic model applied and the resulting changes in population, land use change and energy consumption. Four 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.

A large difference exists between the predictions of each of the GCMs, and each of the scenarios. They differ in: (a) their climate sensitivity and (b) the spatial pattern of change, making multi model assessments essential for a good understanding of potential changes.

Here a multi model ensemble was used to provide a probability distribution function for per pixel climate evolution. Thus, inter-model and inter scenario uncertainty can be assessed, and the effect of this uncertainty on terrestrial eco-physiological models can be gauged. Data from four GCMs were used, with each one qualified through its use by the IPCC Data Distribution Centre. The specific data used was compiled through the ATEAM (Advanced Terrestrial Ecosystem.

Analysis and Modelling, www.pik-potsdam.de/ateam) project, and ALARM project (Assessing Large-scale Risks for biodiversity with tested Methods, www.alarmproject.net/alarm).

Climate data from the following four GCMs were applied along the latitudinal gradient:

1. The HadCM3 model from the Hadley Centre in England (Mitchell et al., 1998)
2. The NCAR-PCM model from the National Centre of Atmospheric Research, USA, which has the smallest sensitivity of all models compared to forcing at the global scale (Washington et al., 2000)
3. The CSIRO2 model from the Commonwealth Scientific and Industrial Research Organisation, Australia, which has above-average climate sensitivity, a little higher than HadCM3 (Flato & Boer, 2001)
4. The CGCM2 model from the Canadian Centre for Climate Modelling and Analysis (Laprise et al., 2003)

Results from the multi model ensemble for the latitudinal gradient give the mean predicted values for the range of ecosystem indicators available, but also give a measure of the uncertainty associated from the choice of climate model and scenario, as can be seen in Fig. 5.

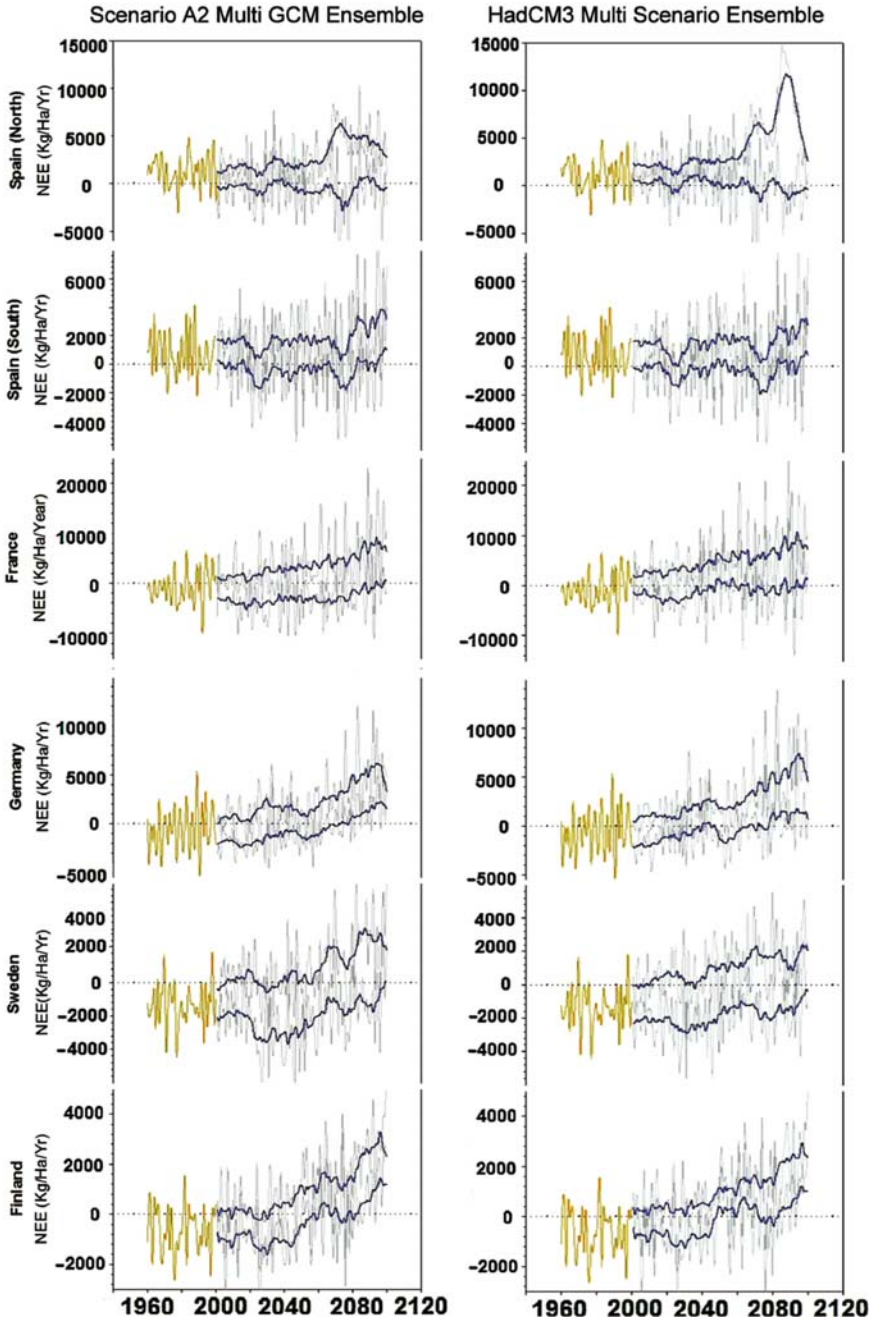

Fig. 5 **Left**: The evolution of GOTILWA+ outputs of NEE at each site, with CRU climatology until 2000 and an ensemble of GCMs using the A2 climate scenario, from 2000 to 2001. **Right**: The evolution of NEE at each site, with CRU climatology until 2000, and an ensemble of climate change scenarios with the HadCM3 GCM from 2000 to 2100. The grey lines represent the maximum and minimum range of NEE, and the blue line gives the 10 year running average of the maximum and minimum range

Although the climate models and scenarios vary in their predictions, they agree in qualitative terms and there is a general consensus that, although it would refine the results, increased accuracy would not change the conclusion with regards to many ecosystem variables. From Fig. 5, the effect of climate change predicted by the models and scenarios can be seen. Here, each ecosystem is predicted to become a net source of carbon, thus constituting a positive feedback on the climate system. The amount of uncertainty in this prediction is broken down into two categories: the uncertainty that derives from the choice of emissions scenario, and the uncertainty that derives from the choice of GCM to supply the climatic variables.

As can be seen from Fig. 5, the choice of which GCM to use accounts for almost as much variability as the choice of socio-economic scenario. That the variation due to the choice of emission scenario used is only slightly greater than that associated with the choice of GCM, highlights that important climate processes are imperfectly accounted for by these climate models.

3.1.2 Stand Performance at the Selected Sites

Given the computational cost of performing simulations with an entire multi model ensemble, most studies choose a particular model and scenario. Here, to ease the interpretation of the results, we present results from the HadCM3 model predictions with the A2 emission scenario as our description of future climate (this gives mid-range levels of future climate change). Figure 6 shows the Gross Primary Production and Net Primary Production predicted by the model for each pixel of the transect using the HadCM3 models climatic variables. Here an increase in GPP can be observed, resulting from higher temperatures and CO_2 fertilisation. This trend is followed by all sites, except the more northern Spanish site, which suffers high mortality. This increase in GPP leads to only a slight increase in NPP, as higher production is balanced by higher respiration rates.

A wide variety of variables are available as output from the model. Here we present those of a potentially greater interest, such as Wood Production and Aboveground Biomass as shown in Fig. 7 below.

Wood Production and Above Ground Biomass are strongly coupled variables, and show a strong response to the imposed climate change conditions. Both show a marked increase at sites where water stress is not a restricting factor.

3.2 The Effect of Management

Management can play a very important role in ecosystem function. In the model, various different management regimes and strategies can be defined, and their effect on the forest ecosystem can be gauged. Such strategies are often focussed on optimizing carbon sequestration, wood production, yield, or aboveground biomass. Particular interest in the Mediterranean region is focused on using management to

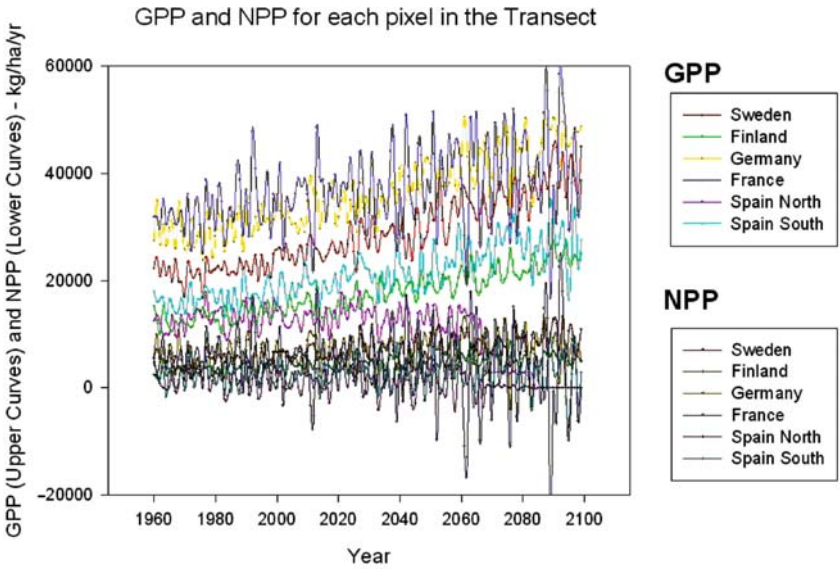

Fig. 6 The GOTILWA+ projection of gross primary production and net primary production at each site, between 1960 and 2100, using HadCM3 – A2

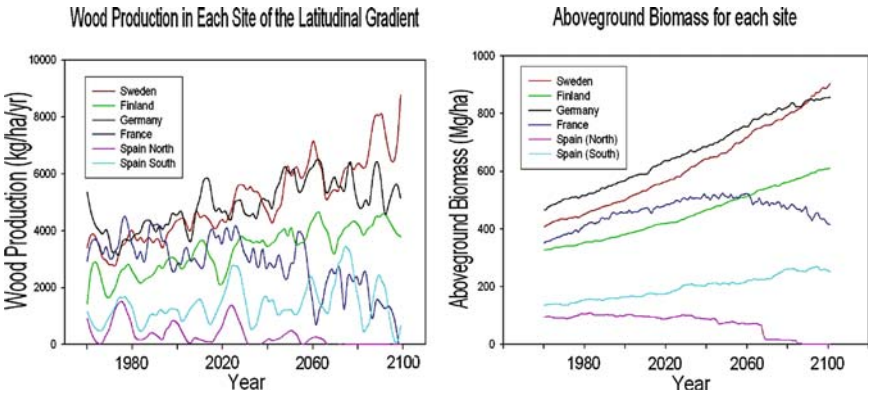

Fig. 7 The GOTILWA+ projection of wood production (**Left**) and aboveground biomass (**Right**) at each site, between 1960 and 2100

mitigate the effects of drought on forest stands. Here, an example is given of a management strategy applied to the forest stand at the French site. The management strategy in this simulation is to enter the forest when the basal area reaches 42 m^2/ha and remove the larger trees until a basal area is reached of 38 m^2/ha. This has the effect of increasing wood production, while giving a high yield from the system, thus increasing the capacity of the stand to act as a net sink for atmospheric

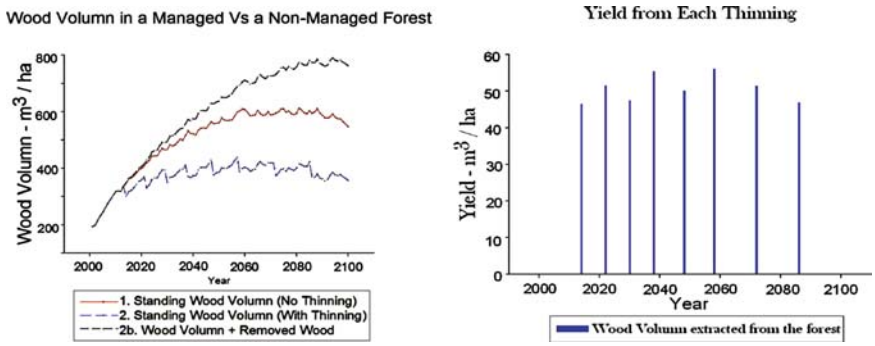

Fig. 8 **Left**: The GOTILWA+ projection of wood volume remaining in an unmanaged forest and in the same forest with management. **Right**: The wood volume extracted from the managed forest at each intervention in the simulation

CO_2. This strategy can be contrasted against alternatives, and an optimum strategy found, depending on the prerequisites of the user.

Figure 8 shows how management can increase the productivity of the forest, with the total wood volume (Yield + Standing Volume) at the end of 100 years being greater in the managed forest than in the unmanaged forest. This occurs due to the response of the forest to decreased competition for resources. It has been argued to increase the lifetime of a forests sequestration capacity. It can also increase the capacity of the forest to act as a sink of atmospheric CO_2. On the other hand this also depends on what use the extracted wood is put to. The mean life time of wood products is estimated to be about 30 years, though this is highly dependant on the product, thus any additional sink that results from the extraction of wood from the system can be presumed to be short lived.

3.3 The Future of European Forests – Europe-wide Simulations

Gotilwa+ has been validated extensively in Europe (Kramer et al., 2002; Morales et al., 2005). This has helped refine the model, and now the same modelling approach can be applied throughout Europe. This can be a very useful tool for those monitoring future carbon sequestration trends in European forests. To supply the input data required by the model, an extensive database has been built within the framework of the European ALARM project (Assessing Large-scale Risks for biodiversity with tested Methods, www.alarmproject.net/alarm), connecting diverse information sources at a European level and adapting them to fit the same spatial resolution.

The database contains data related to forest functional types, forest cover, forest structure (tree density and size distribution), forest function (photosynthesis, respiration rates), soil hydrology, organic matter decomposition rates and management strategies. This data base provides the model with all the necessary information to

run in each pixel and it also provides the climatic series at this level of detail for different climate change scenarios generated by several general circulation models (GCMs). Given the computational expense of running GOTILWA+ with the predictions of each GCM and each climate scenario, we chose the HadCM3 GCM with the IPCC scenario A2 to simulate future forest stands over Europe.

Here, in Fig. 9, we see a shift in the majority of European forest ecosystems from being net sinks of carbon to net sources of carbon. This reflects what we observed earlier for the latitudinal transect in Fig. 5. It represents a potential feedback on the climate system, where terrestrial ecosystems themselves do not help to solve the problem of climate change and may even serve to augment it. Currently, most are acting as sinks, effectively removing and storing carbon from the atmosphere.

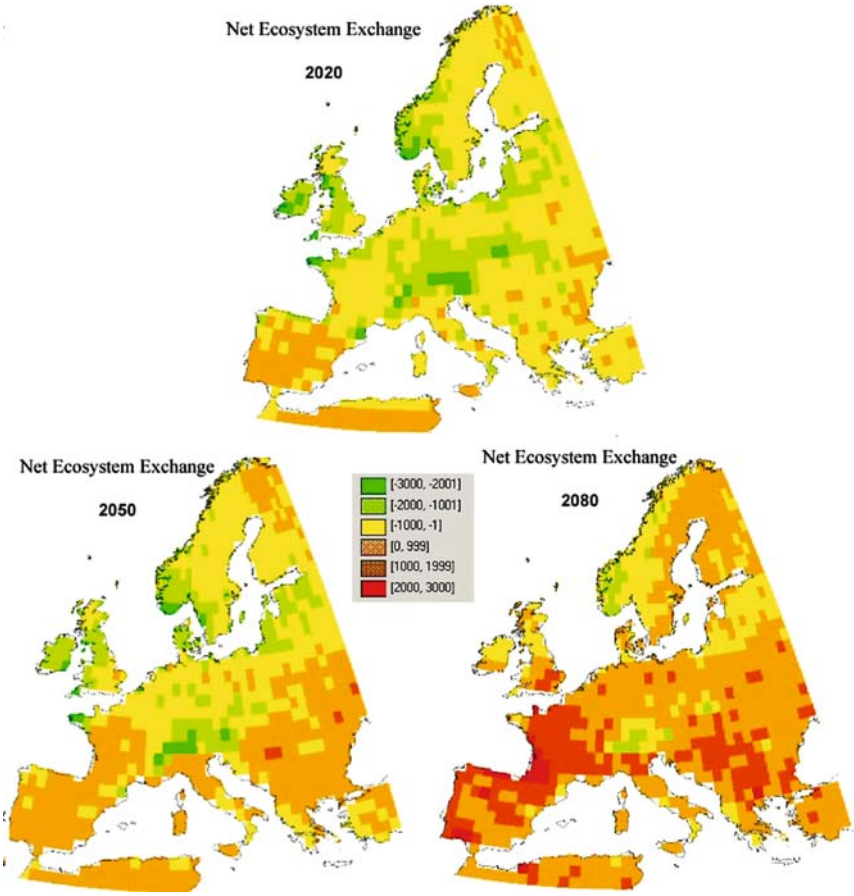

Fig. 9 GOTILWA+ projections of net ecosystem exchange (kg/ha/year) from Pinus sylvestris forests in Europe wide simulations (values represent the annual average for each time slice 2020: 2010 to 2030, 2050: 2040 to 2060, and 2080: 2070 to 2090)

The perspective of them becoming sources is not a pleasant thought, with vast amounts of carbon currently stored in soils, and ready for release.

Figure 10 allows us to further explore this response. As can be seen, productivity, in general (in areas not under stressed conditions) is expected to increase, thus constituting an increase in the ability of the ecosystem to remove carbon from the atmosphere. The conversion of the ecosystem to a net source of carbon results from the reaction of respiration rates and the large available pool of carbon in the soil. The description of soil respiration is as good as our current understanding of these processes allows (Fang et al., 2005; Jannsans et al., 2005), though undoubtedly further work is required to reduce our uncertainty. Figure 5 gives an estimate of the uncertainty which is attributable to the uncertainty in predictions of climatic data, but the same conclusion can be applied here, that the quantitative conclusion may be questionable, but the qualitative conclusion should not vary greatly with a better understanding of the processes involved.

In Fig. 11, a general tendency for a decrease in soil water content can be observed. This is due more to higher Evapotranspiration rates, from a combination of increased productivity and higher temperatures, than to changes in the distribution of precipitation. The effects are expected to be more extreme in the Mediterranean region, where soil water content is already extremely low. This can have repercussions outside of the ecosystems in question, effecting other ecosystems and society at large.

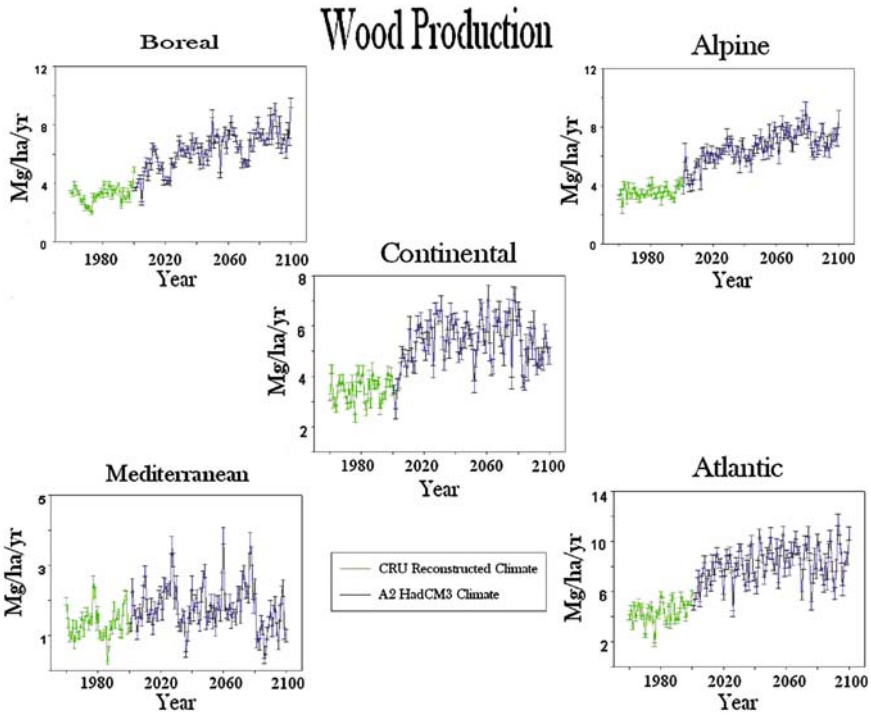

Fig. 10 GOTILWA+ projections of wood production (Mg/ha/year) for five main European climate regions from 1960 to 2100

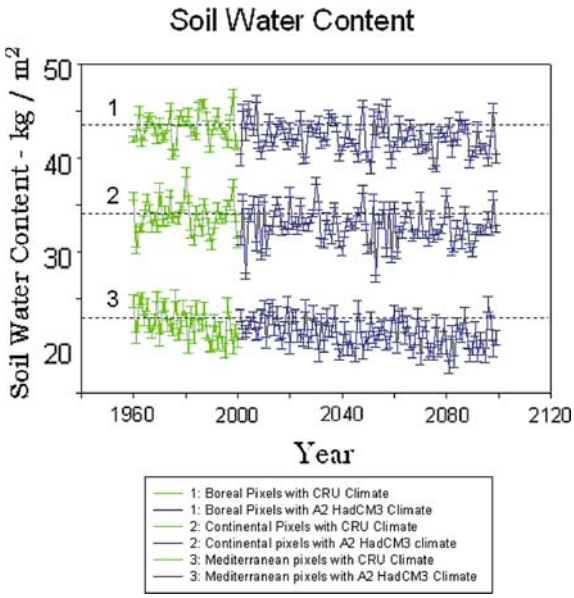

Fig. 11 GOTILWA+ projections of the quantity of water in the soil for three climate types, Boreal, Continental, and Mediterranean climates, with reconstructed climate from 1960 to 2000, and the Hadley Center HadCM3 model with scenario A2 until 2100

4 The Future of Eco-physiological Models

As our knowledge of processes and ecosystem responses develops, in parallel with computing science, so too does our ability to build eco-physiological models with higher accuracy and a broader applicability. Future efforts will be focused both on the development of our scientific knowledge of the processes involved, and in using the models themselves to better our understanding of how these processes link together to form an ecosystem. This will be carried out through extensive field work and experimentation, from field trials to stand simulations, up to the coupling of vegetation ecosystem models with global climate models.

4.1 Climate Models and Eco-physiological Models

It has long been accepted that regional climate affects the local distribution of vegetation and soils, with natural undisturbed vegetation effectively mirroring the long term local climate (Koppen, 1936). In recent years, a broader understanding of the interaction between vegetation and climate has been developed. Not only does climate effect the distribution and functioning of vegetation, but vegetation also has an affect on climate, and the two are inextricably linked. This feedback mechanism is now recognised as being crucial to the evolution of the Earths climate (Bonan,

2002), and equally crucial in predicting the anticipated change in the earths climate in the future (Cox, 2000). Potentially one of the most interesting future prospects for eco-physiological models is their coupling with regional climate models, in an attempt to incorporate the dynamic relationship between vegetation and climate.

4.2 Development

Our current understanding of terrestrial processes is limited in many areas, with various key features only relatively weakly represented. The advancement of our understanding of these critical processes should better enable us to accurately model real world situations. This will be achieved by integrating the latest understanding in climatic, hydrologic and edaphic controls on forest ecosystem process, obtained from the analysis of intensive field and laboratory data, into novel model parameterisations.

The list is long, but key areas currently being developed include: the representation of soil organic matter decomposition, which is very variable and not always best described by a simple temperature-water relationship; the coupled Nitrogen cycle, which is being greatly altered throughout the world due to anthropogenic global change, and is at present very poorly understood; eco-physiological responses to elevated concentrations of atmospheric CO_2, and the problem of acclimatation; accurate descriptions of the functioning of belowground biomass, the hidden half of terrestrial ecosystems. Belowground biomass can account for half of the total biomass of a terrestrial ecosystem in the Mediterranean, but it is difficult to study; species interactions (competition/mutualism) provide one of the key problems in describing succession and dynamic vegetation problems; the role of Volatile Organic Compounds, which play a part in protection and the processing of assimilated carbon in many species, and Fire events.

5 Conclusion

Process based forest eco-physiological models are very useful tools and have a wide application through many streams of research. Their functions range from assessment tools for forest managers and policy makers, to predictive tools for studies on ecosystem functioning, to essential components of large scale global models of climate evolution. The concept of this chapter has been to give a general overview of the structure and applications of such models, using the process based model GOTILWA+ as an example. We have discussed both empirical models, and process based models, and their relative pros and cons, and used GOTILWA+ as an example of how their application can give useful insights into current and future ecosystem functioning, both on a local, regional, and indeed global scale.

Although our knowledge is far from complete, and qualitative results are associated with a large amount of uncertainty, it is a rapidly developing area of research, and state of the art techniques are constantly being applied to improve our understanding, and the ability to produce accurate results. Current efforts are focusing on using highly accurate field data (such as that produced by the EUROFLUX network, using eddy covariance techniques (www-eosdis.ornl.gov/FLUXNET)) to further validate the models over a wide range of site conditions and ecosystem structures. This newly available high quality data also allows us to highlight important processes that are not sufficiently described.

Little by little, as our understanding grows, so too does the capability of such models to accurately replicate real life processes. Here we have given an overview of the current state of the art of biogeochemical terrestrial modelling, although unfortunately, what has been presented is already out of date.

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