Recent advances in the mechanistic modelling of forest stands and catchments

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Introduction

Mechanistic approaches describing the complex processes that underpin forest system dynamics are increasingly required in order to manage forests from a multi-purpose perspective. When describing future forest dynamics the environmental implications of climate change on long-lived organisms such as trees also focus attention on the need to adopt a holistic perspective. In turn, any future perspective has to account for the interacting dynamics of the wider processes resulting from environmental, ecological and land-use change. Therefore considerable understanding of the biological, biophysical and physical processes influencing the life cycle of trees and the forest ecosystem is required to achieve full representation of the system and its dynamics.

¹See Acknowledgments, page 110.
Modelling is increasingly used to complement and integrate the hypothetico-deductive approach to experimentation, as a means of encapsulating the current, mechanistic knowledge base on process dynamics. The large knowledge base on biophysical processes, coupled with the increased availability of detailed data availability for both parameterisation and validation, allows such an approach to be used and provides the basis for extrapolating beyond the range of observation.

In forests, growth dynamics are determined by the interactions between species and ecosystems with the terrestrial water, carbon and nitrogen cycles. Such interactions are modified by management, which in recent years has become more complex following the UK’s adoption of multi-purpose forestry practice and the rural agenda (European Union, 1998, 1999; United Nations, 1992, 1997). For example, management strategies now include methods for dealing with issues such as biodiversity, carbon sequestration and pollution uptake. Increasingly a landscape perspective is being adopted that requires integration of our understanding on forest systems with other land uses.

Given the complexity of options now facing the forest industry and land-use planners, forecasting systems that support decision-making are required at the research and operational levels. Such systems must accurately:

- describe the interactions between the forestry land use component and the terrestrial water, carbon and nitrogen cycles, as a function of soils, climate, species and management practice
- account for the forecasted impacts of climate change on growth conditions as they affect the environment at a range of spatial and temporal scales.

Over the past 5 years Forest Research has undertaken a major research programme that has developed mechanistic models describing forest stand growth dynamics. This programme complements ongoing work to characterise stand dynamics using an empirical approach. The observational approach relies on Forest Research’s extensive and long-term tree growth monitoring network to propose the growth and yield curves widely adopted in British forestry. This article describes the initial outcomes of the mechanistic modelling programme, using a selection of results achieved to date.

The ForestETp model

ForestETp is a fully coupled, point scale and daily timestep soil–vegetation–atmosphere transfer (SVAT) model, which predicts vertical and lateral water movement through the soil–plant–atmosphere continuum and gross primary productivity (GPP). The model simulates relevant terrestrial hydrology processes (rainfall interception, vertical and lateral soil water movement, runoff, soil and canopy evaporation, and photosynthesis-coupled transpiration) for a forest stand of known structure, growing in locally determined soil and climate. Particular attention has been given to the parameterisation, kept as simple as possible and reliant on widely available relevant data. As an alternative to observational meteorological daily data, the model is coupled with a weather generator that generates daily time series from monthly summary data. The model structure is illustrated in Figure 1 and detailed in the following sections.
The climate module

ForestETp can accept either daily meteorological data or monthly mean climatic values. If daily values of air temperature, air pressure, wind speed, global solar radiation, air humidity and rainfall are available, the model uses these data as inputs. If total net radiation is not available, it is estimated using the weather generator, otherwise, the measured value is used. Solar radiation is also split into direct and diffuse radiation as explained later. Where only monthly input values are available, the model uses a stochastic-deterministic site-scale weather generator to downscale the monthly timestep input data to the daily scales and generates the other meteorological fields. Figure 2 shows the model structure.

The canopy radiative transfer module

This module considers the heterogeneity of radiation in the canopy, as the necessary precursor to approximating the non-linear response of photosynthesis to irradiance. The model employs a radiative transfer scheme that approximates the transmittance, reflectance and absorption of long wave, near infrared and direct and diffuse photosynthetically active radiation (PAR) by canopy layers, where canopy interactions are determined by the area and distribution of foliage. After Norman (1980) and De Pury and Farquhar (1997) the module separates penetration of direct and diffuse radiation (net of albedo) through a canopy in which two classes of leaves (sunlit and shaded) are distributed in a multi-layer canopy model. This approach allows the explicit description of within-canopy profiles (on a per layer basis) of both environmental (e.g. wind profile, vapour pressure deficit) and physiological (e.g. leaf temperature) variables in response to radiation attenuation. It does so through a canopy with uniform leaf distribution (spherical in the first instance; Russell et al., 1989) as prescribed by Beer’s law (Monseu and Saeki, 1953) for each leaf class. The model
does not allow for foliage clumping. By dynamically calculating the leaf areas of sunlit and shaded leaves, and their mean irradiance, mean layer assimilation, transpiration and conductance rates are obtained, adjusted for the photosynthetic capacity of each leaf class. Through integration, data are upscaled to approximate total canopy photosynthesis and gas exchange. In each layer, sunlit leaves are assumed to receive both direct and diffuse radiation from the macroclimate model; shaded leaves receive diffuse light only, assuming no radiative energy transmittance through leaves. The within-canopy profiles of leaf nitrogen follow the predicted distribution of absorbed irradiance through each canopy layer, separately for sunlit and shaded leaves and assuming a uniform leaf angle distribution (spherical). Seasonal variation of nitrogen content in foliage can also be represented with suitable input. Given the separate descriptions of sun and shade leaves and within-canopy variation of photosynthesis, the module allows non-uniform vertical profiles of photosynthetic capacity to be developed.

The gas exchange and carbon productivity module

Within each canopy layer, and to account for the changing light environment, the gas exchange and carbon productivity module operates at the leaf level. The well-tested theoretical representation of C₃ photosynthesis developed by Farquhar et al. (1980) and von Caemmerer and Farquhar (1981) has been widely used and tested across a range of species and that describes the regulation of ribulose 1,5-biphosphate carboxylase and electron transport in the leaf. This has been combined with additions from Long (1991), McMurtrie and Wang (1993) and Friend (1995), with further adaptation. In turn the modified C₃ photosynthesis model is tightly coupled with the C₃ version of the Ball et al. (1987) stomatal conductance model that provides a robust phenomenological description of stomatal behaviour. This coupling is required in order to predict leaf response to varying environmental conditions including atmospheric CO₂ concentrations. After Farquhar et al. (1980), leaf nitrogen content (linearly) influences two of the rate-limiting photosynthetic processes, namely...
the potential maximum velocity of fully activated Rubisco that is inhibitor free ($V_{c_{\text{max}}}$) and the maximum potential rate of electron transport ($J_{\text{max}}$). After Friend (1995), the module explicitly describes the role of nitrogen as a major influence on photosynthesis through influencing the Rubisco concentration in soluble leaf proteins involved in electron transport. Leaf nitrogen content also (linearly) influences mitochondrial (dark) respiration. After Ball et al. (1987), internal leaf CO$_2$ pressure ($C_i$) is determined within the leaf as a function of the interactions between CO$_2$ assimilation and stomatal conductance to CO$_2$, regulated by the leaf boundary layer and mesophyll cell surface resistances to CO$_2$ transfer. The same processes are assumed to apply for water vapour. As assimilation (demand) and conductance (supply) are inter-dependent, the values of $C_i$ and assimilation are resolved by iteration, and account for both leaf water potential and canopy temperature. Foliage respiration is accounted for within the assimilation model. The balance of whole plant respiration during the leafy and non-leafy periods is approximated using a $Q_{10}$ function, based on actual whole system respiration using eddy-covariance measurements of CO$_2$ flux which are data measured at each site.

The canopy rainfall interception module

The tree canopy partitions gross rainfall into three downward water fluxes (free throughfall precipitation, canopy drip and stemflow) and an upward gaseous flux, intercepted water vapour resulting from evaporation. Along with meteorological conditions that determine the conditions for evaporation and canopy properties (evaluated from stand structure and growth as well as by management practices), the precipitation process, i.e. amount, intensity and its varying distribution in time and space, regulates rainfall interception. The canopy water environment module describes rainfall interception and wet canopy evaporation according to the revised analytical model of Gash et al. (1995). In this model each rainfall event is decomposed into three phases, a wetting up phase before canopy saturation occurs, a phase of canopy saturation and a drying phase after rainfall has ceased. Each phase contributes differently to the interception loss process, which is determined by the canopy structure and meteorological conditions. The canopy structure is characterised by four parameters, namely the canopy and trunk water storage capacities, the canopy cover fraction and the trunk diversion coefficient. The meteorological conditions are described through the ratio of mean evaporation rate from the wet canopy over mean rainfall rate.

There are four main assumptions implicit in the model:

1. There should be enough time between storms to allow the canopy to completely dry.
2. There is no evaporation from the trunks during the storm.
3. No water drips from the canopy before saturation.
4. The ratio of average evaporation rate over average rainfall rate is equal for all storms.

Figure 3 shows a comparison of observational data for throughfall (rainfall minus interception) with simulated module outputs.

The evapotranspiration module

After Ritchie (1972), selected outputs from all modules are used to parameterise the Penman-Monteith equation (Thompson et al., 1981; Burman and Pochop, 1994). In turn this equation is disaggregated to approximate daily leaf and canopy level evapotranspiration, bare and shaded soil evaporation and wet canopy evaporation, separately for wet and dry days as determined by the climate module.
The soil hydrology module

This module outlines a daily timestep, multi-horizon capacity model of soil-water balance which requires climate data, together with soil survey and laboratory-measured physical data as input. The module simulates the generation of surface runoff, lateral and vertical drainage and the formation of transient perched water tables. It has been designed for application over a wide range of soil lower boundary conditions that commonly occur in most temperate high latitude countries such as the UK, that range from free-draining to impermeable. At each time step, after having computed the rainfall interception, wet canopy evaporation, tree transpiration, bare and shaded soil evaporation, light interception and photosynthesis, the water balance is updated for each soil layer as detailed in Evans et al. (1998).

A summary of the general features of ForestETp is provided in Table 1. A comparison of process components from a range of stand and ecosystem models operating at various temporal and spatial scales highlights significant commonality of approaches between the models; differences tend to refer to the scale of resolution in process description. The comparison indicates that ForestETp is comprehensive in the range of relevant processes simulated by the model. The principal innovations are the addition of a weather generator model, to downscale widely available gridded observational meteorological data and the use of generic parameters from available databases.
Table 1
General features of the ForestETp model.

<table>
<thead>
<tr>
<th>Process</th>
<th>Strategy</th>
<th>Key references</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weather generator</td>
<td>Stochastic-deterministic, site-scale model downscaling widely available monthly timestep input data to the daily scales</td>
<td>Richardson (1981), Ross (1983), Hutchinson (1991)</td>
</tr>
<tr>
<td>Radiative transfer</td>
<td>Direct and diffuse radiation are accounted for though a canopy in which two classes of leaves (sunlit and shaded) exist</td>
<td>Norman (1980), De Purry and Farquhar (1997)</td>
</tr>
<tr>
<td>Photosynthesis</td>
<td>Biochemical model where photosynthetic rate is limited either by RuBP regeneration or by Rubisco kinetics</td>
<td>Farquhar et al. (1980), von Caemmerer and Farquhar (1981)</td>
</tr>
<tr>
<td>Stomatal conductance</td>
<td>Ball and Berry stomatal conductance model</td>
<td>Ball et al. (1987)</td>
</tr>
<tr>
<td>Rainfall interception</td>
<td>Tree canopy partitions gross rainfall into three downward water fluxes (free throughfall precipitation, canopy drip and stemflow) and an upward gaseous flux, resulting from evaporation of the intercepted rainfall</td>
<td>Rutter et al. (1975), Gash et al. (1995), Valente et al. (1997)</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>Evapotranspiration is computed using the Penman-Monteith equation separately for the tree transpiration, bare soil evaporation, shaded soil evaporation and rainfall intercepted water</td>
<td>Thompson et al. (1981), Burman and Pochop (1994), Ritchie (1972)</td>
</tr>
<tr>
<td>Hydrology</td>
<td>Multi-horizon capacity model of soil–water balance simulating the formation of transient perched water tables and the generation of surface runoff and lateral drainage</td>
<td>Evans et al. (1998)</td>
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The integrated site model

Testing of the integrated model (excluding the weather generator) has been conducted against published data on whole-ecosystem exchanges of CO₂ and water vapour collected in UK and European forest stands using the eddy-covariance technique (CARBOEUROPE project). Simulation experiments were conducted for each site at the daily timestep using observational meteorological data as input. Model output was evaluated by comparison with experimentally derived approximations of Gross Primary Production (GPP) and evaporation data provided by Falge et al. (2001). As shown in Figure 4 which the comparison between observational data and model output at the daily timestep for a coniferous site in Finland (Hyytiälä), the model is well able to reproduce the whole system whole-ecosystem exchanges of CO₂ and water vapour. The overestimation by the model of evapo-transpiration can in part be explained by deviations in the observational record, as outlined below. Some temporal divergence between the simulated observed data is also evident, resulting from the use of fixed ecophysiological parameters used in the model, while some variability is known from field data. Across sites, the model showed good agreement for GPP (R² ranging from 0.51 to 0.79 with an average R² of 0.69), with no significant bias detected. The whole ecosystem evapotranspiration presents a slightly lower correlation (range 0.35–0.62, average 0.47). As shown in Figures 5 (a) and (b), annual timestep simulations were significantly better during dry days (without precipitation) than during rainy days. This difference between wet and dry estimates would suggest errors with the instrumental data, rather than with model outputs. A small bias has been detected with the model presenting higher values than a slight overestimation of the evaporation, possibly
resulting from the use of a daily rainfall interception model and on the quality of eddy-covariance measurement during rainfall event.

Given the good approximations of GPP ($R^2$ ranging from 0.51 to 0.79 with an average $R^2$ of 0.69) and whole system evaporation (range 0.35–0.62, average 0.47) obtained at the site scale, national scale approximations have been developed, as shown by Figures 6 and 7. These simulations use spatial datasets, such as the National Soils Database for England and Wales (National Soils Research Institute, Cranfield University) and gridded climatologies such as that developed by the Climate Research Unit, University of East Anglia, as input. Scotland has had to be excluded from the simulation experiments, as soils data are the copyright of the Macaulay Land Use Research Institute which makes data available on a licence fee basis only. Given the mechanistic approach of the model it is possible to disaggregate the signals into constituent components, as shown for example in Figure 6.

**Figure 4**

Comparison of modelled GPP and ETp with measurement over 5 years. For GPP two methods (I and G) have been used to estimate the value from NEE and are shown with the model predictions (solid line). For ETp the measured (●) and simulated (○) are shown.
The ForestETp 3-D model

ForestETp 3-D is an extension of the stand-scale model (ForestETp 1-D) that simulates the relevant processes involved in the water and carbon cycle of a forested catchment. Model extension was required to obtain better approximations of (a) water available for plant growth at any point in the catchment and (b) the impact of land cover and land change on catchment discharge. In particular, the 3-D model accounts for the effects of topography and the heterogeneity of surface properties on the water and carbon budget, while requiring a minimum of input parameters. Again, the model was specifically developed to make use of widely available spatial data as its input source.

Computation in the ForestETp 3-D model is divided into two main steps:

- In a preliminary step, the TOPOG Digital Elevation Analysis models (Dawes and Short, 1994; O’Loughlin, 1986) are used to separate the catchment into discrete elements as a function of topography using a flow net technique. These elements have an irregular shape defined by topographic contours and flow lines which has been shown to be more realistic for representing convergence and divergence of lateral flows than classical scared grids (Dawes and Short, 1994). For each topographic element local properties such as slope, aspect and drainage percentage to adjacent downslope neighbours are calculated. By overlaying a soils and/or vegetation map of the area to the topography, it is also possible to account for the heterogeneous distribution of soil types and/or tree properties in the catchment.

- In a second phase, the ForestETp 1-D model, modified to account for incoming lateral water flows, is run for each element at every timestep to compute the energy balance, photosynthesis, evapo-transpiration fluxes, surface runoff and drainage. Solar and long-wave radiation are corrected for slope and aspect and, if required, rainfall can also be corrected for elevation. At the end of each timestep runoff and drainage are distributed to the downslope elements, or to a stream/river if no connecting downslope element is found. All daily fluxes are then aggregated to compute mean values at the catchment scale.
Simulated annual forest system evaporation (mm m\(^{-2}\) year\(^{-1}\)) assuming total land coverage by ash, Scots pine, beech and Sitka spruce.

Outputs are available as (a) temporal series for a particular point or averaged over the catchment and (b) spatial maps for a particular day or as means for an entire period.

Evaluation of the ForestETp 3-D model has been conducted using long-term monitoring data on streamflow collected in the Coalburn catchment. Simulated streamflow is computed as the sum of lateral sub-surface drainage and surface runoff generated by those topographic elements bordering the river (confluence elements). Observed and simulated streamflow were then compared at the daily, monthly and annual time steps. Figure 8 shows the daily observed and simulated streamflow for a 7-year period (1993 to 1999); the model is efficient ($R^2=0.80$) over the entire period. On average the model underestimates peak discharge and slightly overestimates recessions after each rain event. This can be explained through a poor quantification of lateral soil hydraulic conductivity. At the annual time scale, streamflow volumes are, on average, well reproduced, with a small underestimation for the past two years (7% and 6% respectively), possibly due to underestimation of rainfall for some particularly strong events. Nevertheless, results indicate the model is well able to reproduce the volumes of water transferred to the river and, by derivation, the total catchment evapotranspiration and water balance, at the daily, monthly and annual timesteps.
Figure 7
Simulated annual gross primary productivity (kg C year\(^{-1}\)) assuming total coverage by ash, Scots pine, beech and Sitka spruce.

The ForestGrowth model
The ForestGrowth model represents a further extension of the ForestETp 1-D model, where carbon units simulated by this model (net of respiration) are allocated to tree compartments such as foliage, branches, stem and roots, to dynamically simulate trees and stand growth. Figure 9 shows a typical example of model output, interfaced with an existing graphical representation system (McGaughey, 1997). The output illustrates how the model can be used to generate stands of different structure and age, and, with appropriate model parameterisation, the growth dynamics of stands composed by different species.

Conclusions
Forest Research is developing a suite of mechanistic models simulating the dynamics of a range of biological, biophysical and physical processes that determine the growth of trees and forest stands. Extensive model testing is being undertaken to verify the predictive ability of models under a range of growth conditions representative of those observed in the UK and beyond. The structure of the model allows scenario testing to be undertaken to assess the impacts of, for instance, management and rapid environmental change on the growth dynamics of forest stands. Operating at the landscape scale, models appear well able to represent the impacts of, for example, land cover dynamics on the water cycle.
Further work is being undertaken to develop new model applications which meet the diverse requirements of evidence-based research in support of operational forestry. Further work is being undertaken to develop operational tools from the research applications outlined above. One such instance is ForestETp 3-D that will become a simulation system available to forest managers challenged with meeting the requirements of the European Water Framework Directive. It is foreseen that similar operational tools will increasingly be required to forecast and inform decision-making and policy to meet the challenges of multi-purpose forestry and rural land use.

**Figure 8**
Comparison between observational (pink line) and simulated (purple line) streamflow for the Coalburn catchment over the period 1993–1999 using the ForestETp 3-D model.

**Figure 9**
Outputs of the ForestGrowth model, interfaced with the Stand Visualisation System developed by USDA (McGaughey, 1997). The visualisation tool is unable to project model simulations of root biomass.
Acknowledgements

The programme of work has been undertaken with funding from the Forestry Commission, the Department for Environment, Food and Rural Affairs (DEFRA), the Scotland and Northern Ireland Forum for Environmental Research (SNIFER), the Natural and Environmental Research Council’s Centre of Excellence on Terrestrial Carbon Dynamics (NERC-CTCD) and the European Union (MEFYQUE project). Dr Sebastien Lafont is employed by the University of Sheffield as part of the Centre of Excellence on Terrestrial Carbon Dynamics, and at the time was based at Alice Holt. Jennifer Pellenq is a Forest Research post-doctoral Research Fellow based at the University of Sheffield. A number of organisations have made their copyright data and products available under licence and for use in this research including: inter alia, the National Soils Resource Centre, Cranfield University, the University of East Anglia’s Climate Research Unit, NERC’s British Atmospheric Data Centre, the Meteorological Office, the Forestry Commission’s Forest Enterprise and the Ordnance Survey. Collaborative research has been undertaken with a number of colleagues, most notably Dr Gaby Deckmyn (Antwerp University, Belgium) and Dr Mark Robinson (CEH-Wallingford). The authors are indebted to Richard Silberstein (CSIRO, Australia) for his help and support on the TOPOG model for providing extensive access to the model source code and to the USDA-Forest Service (www.forsys.cfr.washington.edu/svs.html) for use of the Stand Visualisation System software.

References and further reading


References


